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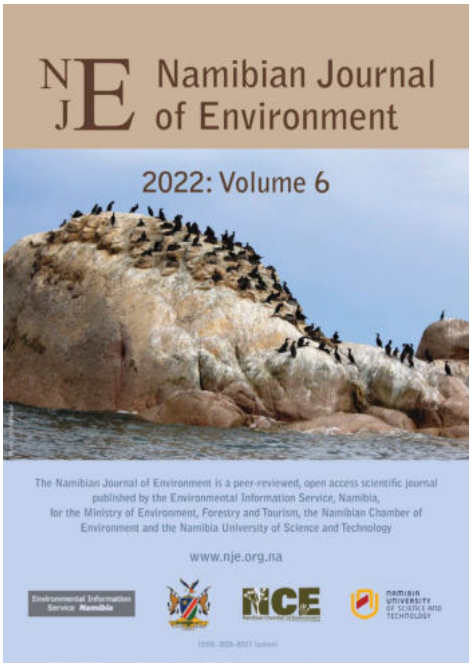

SECTION A: RESEARCH ARTICLES

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The historical effects of infrastructure development on the lion population of Etosha National Park, Namibia

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ABSTRACT
This article offers an historical overview of how colonial-era politics affected changing infrastructure in Etosha National Park, Namibia, and the subsequent effects on lions and prey species populations in the park. The article argues that infrastructure development, particularly the erection of perimeter fencing and construction of artificial waterholes, during the apartheid era, had lasting effects on lion and prey species' population numbers. The article also provides the first comprehensive historical account of lion numbers in Etosha, drawing from a variety of archival and published sources, and the first published account of historical recorded lion mortalities on farmlands bordering Etosha. By linking social and political factors to long-lasting environmental outcomes, the article provides historical evidence relevant to contemporary wildlife managers seeking to incorporate a variety of social, political, and ecological factors into management of large-bodied wildlife.

Keywords: Etosha National Park, fencing, infrastructure, lion, Namibia, *Panthera leo*, population trends

INTRODUCTION

Wildlife managers, researchers, and policy makers are no strangers to using historical data to assess population trends or to examine how ecological variables interact over time. Assembling available historical information can help contextualise contemporary data and provide lessons from the past. As Bennett and Van Sittert (2019) have shown, humanities and social science approaches can make meaningful contributions to environmental research and management, and can inform practical outcomes. This is particularly true in the Global South, or 'developing world,' where historical environmental data have not always been readily available. Such is the case in Namibia, which until independence in 1990 was largely closed to international researchers (Wallace 2011).

Namibia contains one of Africa's crown jewels of wildlife conservation: Etosha National Park (Etosha). When first gazetted in 1907 under the name 'Game Reserve No. 2', it was the largest game reserve in the world (88,000 km^2). Since that time Etosha's size has been dramatically reduced (currently 22,700 km^2), yet it remains an essential refuge for many of Namibia's threatened large mammals, such as black-faced impala (*Aepyceros melampus*), black rhino (*Diceros bicornis*), and elephant (*Loxodonta africana*). Etosha is also home to approximately half (+/- 400) of Namibia's free-ranging lions (*Panthera leo*) (Jacobson and Riggio 2018). Across Africa, lion numbers have declined by about 43% in less than twenty-five years, though geographically distinct populations in Namibia have increased or remained stable (Bauer *et al*. 2015). Since the mid-1990s, lion numbers in Etosha have more than doubled, and the population is thought to be secure (IUCN 2018). However, this recent period provides only a snapshot in the history of Etosha's lion population.

This article contributes to two, related, management challenges. First, we present all available data on Etosha's lion population numbers and provide historical context for interpreting trends and changes. The recent growth in Etosha's lion population requires historical context for management staff to make informed conservation decisions. In particular, we focus on the period from the mid-1970s to the late 1980s, as this includes the highest quality lion population data and covers a critical period for the Etosha lions.

The second management challenge concerns the effects of infrastructure on wildlife areas. Initially, perimeter fencing and the construction of artificial waterpoints appeared to maximise Etosha's lion population, which increased from approximately 200 to 500 individuals during the 1970s. Beginning in the 1960s, Etosha was enclosed by an 850-km game-proof fence that was completed in 1973. This fencing was erected primarily to satisfy the apartheid-era government's commitment to separating land-uses, including racial segregation of Namibia's people, rather than for environmental conservation concerns (Heydinger 2021a). The development of Etosha's

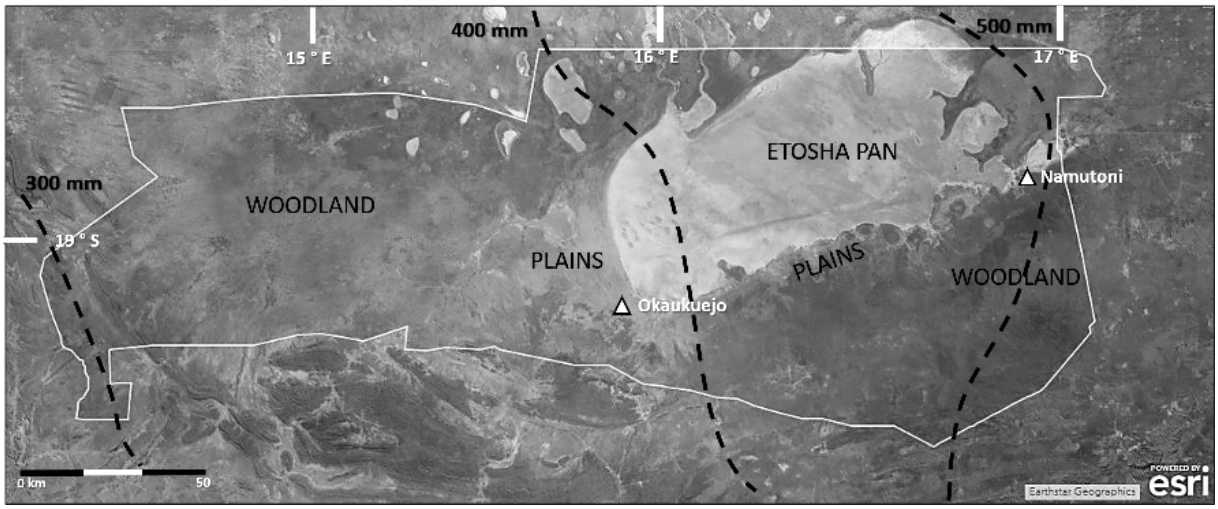

Figure 1: *Etosha National Park with major habitats and rainfall isohyets. Based on Berry & Siegfried (1991).*

infrastructure – fencing and waterpoints – during this period had long-lasting effects on the park's wildlife, leading to a redistribution of Etosha's herbivores and apparent subsequent increase in the lion population.

This history can contribute to the toolkit of managers and conservationists tasked with developing and implementing management policies for protected areas, particularly within dryland ecosystems such as Etosha (Durant *et al*. 2015). In recent years several statistical analyses have emphasised the importance of fenced protected areas to lion population management, as fenced populations are generally closer to their estimated carrying capacities, have largely held steady over the past few decades, and are more cost effective to conserve than unfenced populations (Packer *et al*. 2013; Bauer *et al*. 2015; Lindsey *et al*. 2017). Additionally, in high-conflict areas the cost of fencing may be less than the cost of remunerating neighbouring residents for property loss to wildlife (Di Minin *et al*. 2021). Lindsey *et al*. (2018) have shown African protected areas containing lions are often chronically under-resourced. Protected area managers must therefore maximise budget efficiency. This problem has been exacerbated by the recent decline in tourism receipts due to the COVID-19 pandemic: Namibia was estimated to have lost US$ 220 million in tourism receipts, or approximately 2% of its GDP due to a downturn in tourism stemming from the pandemic (World Bank 2021; Xinhua 2021). However, not all fencing is created equal. As we will show, the fencing around Etosha does not deter lions from moving on to, and being killed in, farmland bordering the park.

The more information available to managers and policy makers on the effects of past environmental management decisions, the better designed their practices and policies can be. Large protected areas are complex ecological systems. Human activities such as management practices and infrastructure construction not only affect lions, but other species upon which these apex predators depend. We show that transformations to the Etosha landscape had detrimental effects leading to an adjusted, lower, equilibrium for herbivore populations, most evidently for blue wildebeest (*Connochaetes taurinus*), plains zebra (*Equus burchelli*), and springbok (*Antidorcas marsupialis*). These detrimental effects on the park's herbivore populations yielded a mixed set of effects for the park's lions.

Study Area

Etosha National Park is located in north-central Namibia at the intersection of three major biotic zones: the southern savannah woodland, the southwest arid zone, and the northern Namib Desert. The 22,270 km^2 park itself can be subdivided into three distinct biomes: woodlands located in the far west and southeast portions of the park, open grassland plains, and a 4,590 km^2 hypersaline pan where only extremophiles can live permanently (le Roux *et al*. 1988) (Figure 1). Presently, the plains areas are dominated by perennial short-grasses and provide important grazing for springbok, plains zebra, blue wildebeest, and other ungulates. Numbers of large herbivores and large carnivores have been shown to be substantially lower in the woodlands (Stander 1991), which are dominated by *Acacia* species and mopane (*Colophospermum mopane*). From 1934 to 2009, mean annual rainfall within the park was 389 mm; though a distinct east-west rainfall gradient exists (Schalkwyk and Berry 2007) (Figure 2). The rainy season generally occurs from late November to April. About 80% of annual precipitation falls from December to March, with 48% in January and February (Gasaway *et al*. 1996).

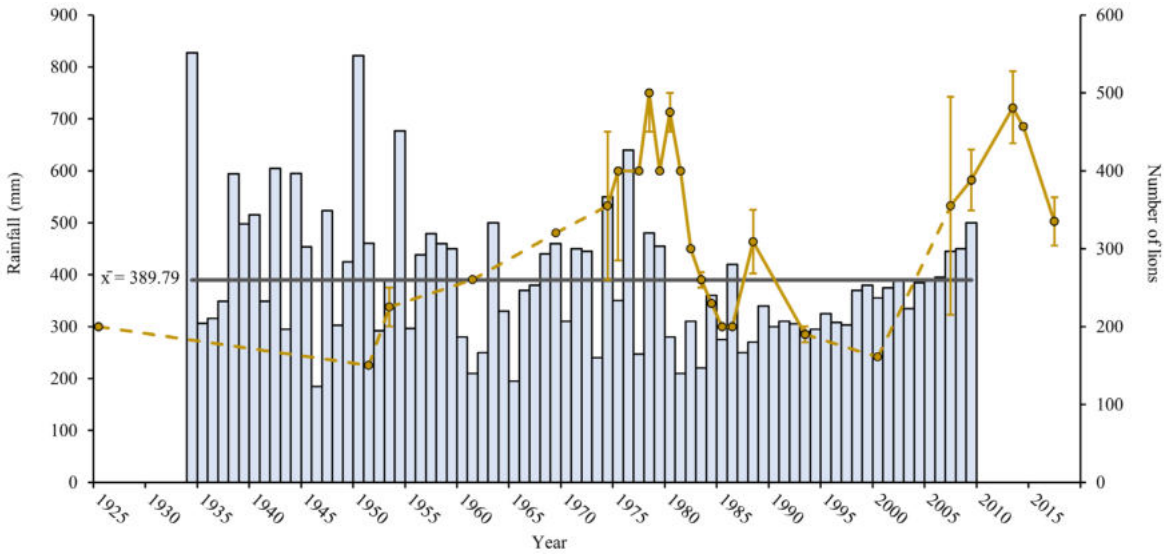

Figure 2: *Historical rainfall and lion numbers for Etosha National Park. All rainfall measurements were taken at Okaukuejo; data are from Bigalke (1961) [1934-1957], Berry and Siegfried (1991) [1958-1989], and Trinkel (2013) [1990-2009]. Dashed lines between lion population data points indicate where estimates may be inaccurate; vertical lines indicate minimum and maximum population estimates; data points either represent the midpoint of each estimated range or statements by quoted sources (see Table 1 for details).*

METHODS

We use methods from environmental history and historical geography to identify trends in Etosha's wildlife populations from the late nineteenth to the early twenty-first centuries. We have assembled qualitative and quantitative data from published, limited-circulation, and archival materials written by Etosha wildlife managers, researchers, and South West African/Namibian government staff. Limited-circulation documents were primarily retrieved from the Environmental Information Service Namibia, the Namibian Scientific Society, or the authors' personal files. Archival materials were collected from the National Archives of Namibia in Windhoek. Government reports were furnished by staff at the Namibia Ministry of Environment, Forestry and Tourism. Published documents were retrieved through Google Scholar searches and following reference lists in other works. Discrepancies and disagreements in materials were resolved after considering the preponderance of information and consistency with interpretations of population biology and ecosystem science.

RESULTS

Pre-1900s: colonial incursion and big game hunting

The first population estimate of lions in the Etosha area dates from 1926. Earlier evidence of lion presence is available in scattered accounts from European settlers, hunters, and traders moving through the region. These records indicate that Europeans killed high numbers of lions in the Etosha area. CJ Andersson and Francis Galton travelled through the area in the 1850s. Both recorded numerous lion hunts and detailed Africans' fear of lions, many of whom were known to be 'man-eaters' (Galton 1853; Andersson 1856, 1861). Dorsland trekkers journeying across Etosha in the 1870s were enthusiastic lion hunters (Möller 1899, p. 140; Stassen, 2016, pp. 140, 378, 386). Axel Eriksson, who was among the first permanent European settlers near Namutoni (1866-1901), was a fearsome and experienced lion hunter (Möller 1899, p. 62). When a German garrison was posted to Namutoni following the 1896/7 rinderpest outbreak, bored soldiers shot lions from their observation tower (Green 1952, p. 129; Schalkwyk and Berry 2007, p. 46). During this period lions in the area appear to have been relatively abundant, but their numbers may have declined dramatically. In 1912, Lieutenant Adolph Fisher heard lions roaring in the distance from Namutoni, noting this was the first evidence of lions in years (Berry 1997). In a letter to Etosha's game warden in 1952, Rudolph Böhme, a long-time resident of Onguma farm bordering eastern Etosha, noted there were no lions in the southern and eastern Etosha area until 1917 (SWAA 2331 1952). During this period unregulated commercial hunting took place throughout north and northwest Namibia. This coincided with increased militarisation by the German colonial regime, and greater availability of firearms for European settlers. At this time, trade routes running through Etosha (Bollig and Olwage 2016) would have brought well-armed, experienced hunters into greater contact with lions in the area.

Table 1: *Population estimates and source material for lions in Etosha National Park.*

Year	Lion pop.	Sources	Comments
1926	200	Berry (1997)	Minimum, biased to east Etosha (excludes woodlands)
1952	150	Schalkwyk and Berry (2007)	Etosha warden estimate
1954	225	Berry (1987)	B. de la Bat, pers. comm. 1979
1962	260	RSA (1964, p. 23)	Likely B. de la Bat, pers. comm. 1962
1970	320	Berry (1987)	Gaerdes, 1975
1975	355	Joubert and Mostert (1975); Stander (1990)	Range: 260-450
1976	400	Berry (1987, 1981b)	Excludes woodlands
1978	400	Berry (1987)	Excludes woodlands
1979	500	Berry (1987)	Berry, Bartlett and Bartlett, unpub. data; excludes woodlands
1980	500	Berry (1987)	Excludes woodlands
1981	475	Berry (1987); Orford *et al*. (1988)	Range: 450-500
1982	400	Berry (1987)	
1983	300	Berry (1987)	
1984	260	Berry (1987); Orford *et al*. (1988)	Range: 250-270
1985	230	Berry (1987)	
1986	200	Berry (1987)	
1987	200	Orford *et al*. (1988)	H. Berry unpub. data
1989	309	Stander (1991, 1990)	Range: 268-351
1994	190	Berry (1996)	Range: 180-200.
2001	161	Stander (2001)	Minimum
2008	355	MET (2008); Owen-Smith (2010, p. 556)	MET Etosha-Kunene estimate, revised using Owen-Smith
2010	388	Trinkel (2013)	Range: 349-428, O. Aschenborn, pers. comm.
2014	481	Kilian and Moeller (2015)	435-528 (95% CI)
2015	457	Bauer *et al*. (2015)	304-366 (95% CI)
2018	335	Goelst, Moeller and Kilian (2018)	304-366 (95% CI)

1907-1952: Game Reserve No. 2

In (German) South West Africa, veterinary concerns and efforts to protect a livestock-based White economy led to policies demarcating specific areas for European settlers, Africans, and wildlife; the last of which was conceptualised as an economic and social resource (Miescher 2012; Heydinger 2020a). The largest government-designated wildlife area was "Wildschutzgebiet Nr. 2". Originally encompassing the latter-day 'ethnic homeland' of Kaokoveld, as well as the Etosha area, Game Reserve No. 2, proclaimed in 1907, was approximately 88,000 km^2; making it the world's largest game reserve at the time (Figure 3). During the early twentieth century, humans and livestock were increasingly disallowed from the reserve. This coincided with the return of lions in numbers large enough that a nearby magistrate recommended hunting them at Okaukuejo (SWAA 2328 1922). In 1924, GC Shortridge stated lions were rare but could still be found in the "Kaokoveld and Etosha Pan areas, in the second of which districts, owing to trapping and poisoning in the Game Reserve, they have been very much thinned out during recent years" (NAN SWAA 1331 1924). The first wildlife census of Etosha in 1926 estimated a total of 200 lions. This census was limited to ground counts, and western Etosha was largely inaccessible (Berry 1997). Shortridge's (1934) overview of mammals in South West Africa showed lions occurred around Etosha but were more common further north.

During the 1920-30s, lions and other carnivores were nearly exterminated on White-owned farmlands, though they persisted in African areas (Heydinger 2020a). Until 1936, lions were classified as 'vermin' and the colonial government provided firearms, funding, and poisons to White farmers and 'vermin clubs' to destroy predators. Around Etosha, lions were killed in high numbers. In 1934 alone, farmers in the Grootfontein District east of Etosha reported 22 lions killed (SWAA 2230 1934). Later, one farmer noted "hundreds of lions" were shot on neighbouring farms during the 1920-40s. During this time the Etosha reserve was regarded as a safe haven for lions, and it was believed lion numbers increased dramatically within the reserve's boundaries (NAN SWAA 2329 1952), even though Whites passing through the reserve could kill lions without a permit until 1938 (SWAA 2328 1938a, 1938b). During World War II civilians' rifles were confiscated by the government, but many farmers still put out poison; in one instance killing nine lions with a poisoned zebra carcass (Green 1952, p. 130).

In the 1940s Etosha became a favoured tourist destination and lions were considered among the premier attractions (NAO 066 1948). Though no estimates of lion numbers are available, throughout

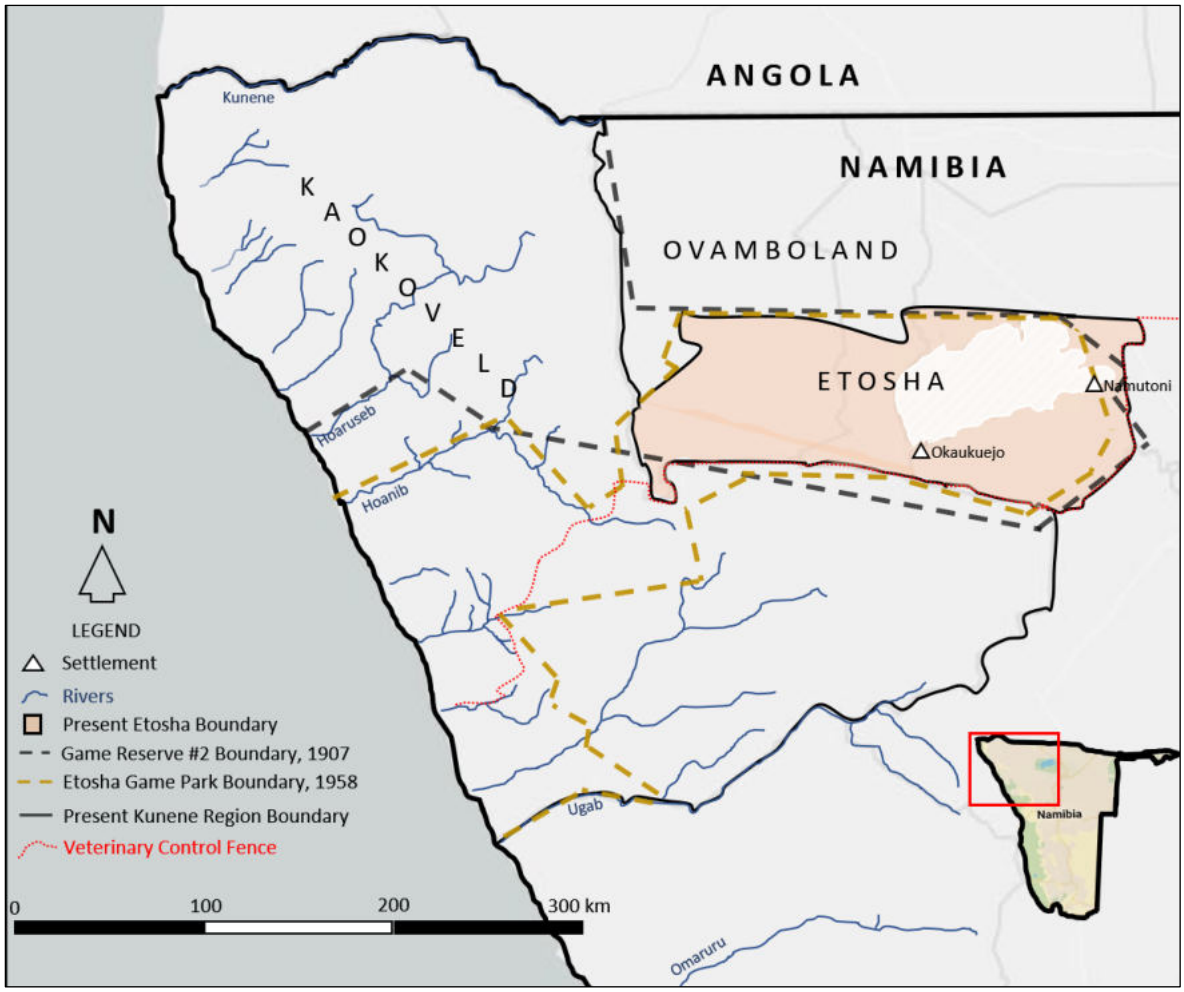

Figure 3: *Historical Game Reserve No. 2 and Etosha National Park boundaries.*

the decade and into the 1950s, Etosha's game warden maintained the park had a surplus of herbivores, particularly plains zebra and wildebeest (NAN NAO 066 1952; Berry *et al*. 1997). That same year Etosha's warden estimated the park contained 150 lions; a number he considered too few (Schalkwyk and Berry 2007, p. 57). During the 1950s an estimated 80 lions per year were killed on farms bordering Etosha (de la Bat 1982, p. 16). Peter Stark, who later served as Etosha's Chief Nature Conservator, claimed he personally killed 75 during this period, including many within the reserve's boundaries (Stark 2011, p. 38)

1953-1973: herbivores, infrastructure, and disease

In 1947, Kaokoveld and Etosha were formally separated; the former reclassified as a 'Native Reserve.' In 1958, the boundaries of the Etosha Reserve were altered to include a large swath of land to the south and west. Though boundary alterations would reduce Game Reserve No. 2 by approximately 55,000 km^2, wildlife still moved freely through an unfenced landscape (SWA 1947; de la Bat 1982).

The first estimates of Etosha's herbivore populations, based on consistent monitoring by professional park personnel, were made during the 1950s. Two management factors greatly affected Etosha's herbivores from the 1950s-1970s: the enclosure of Etosha by fences and the construction of artificial waterholes across the park. These dramatically altered the geography and numbers of herbivores within the park, leading to mixed effects for Etosha's lions. 1952 estimates for plains zebra (10,000-15,000) and blue wildebeest (7,000-10,000) in the Etosha area did not greatly differ from earlier estimates (Berry 1997), but dwarf later estimates. During the late 1950s-60s an estimated 25,000 plains zebra and 25-30,000 wildebeest maintained an anti-clockwise migration route within Etosha and beyond its borders to the north (Figures 4 and 5). Large herds typically departed the southern Etosha plains for the Grootvlakte and Adamax areas west of the pan, following the summer rains (Bigalke 1961; Ebedes 1976). Massive aggregations were also recorded within the Andoni plains in the northeast, and it was widely recognised that wildebeest migrated southwards from Owamboland into the park, and eland (*Taurotragus oryx*) entered from beyond the eastern border (Bigalke, 1961; Berry, 1980). In 1962,

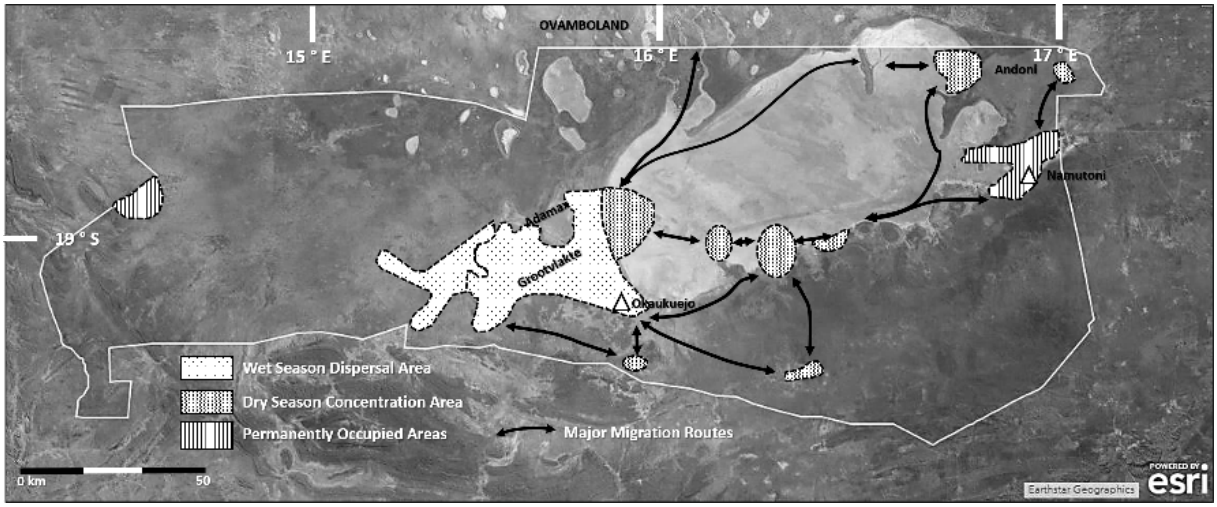

Figure 4: *Wildebeest distribution and migration, 1974-1978. Based on Berry (1981a, p. 257).*

an estimated 100,000 large herbivores inhabited Etosha (Berry 1997).

Fences

During the 1950s, White farmers along Etosha's southern boundaries began erecting low-quality fencing to keep migrating wildlife off their lands and lions away from their livestock. From 1960-1963 a 'game-proof' fence was built along the park's southern boundary to combat the spread of foot-and-mouth disease between the park and neighbouring farmlands (Ebedes 1976). The blockage of wildlife migration led to greater pressure on grasses and may have contributed to a precipitous decline in wildebeest within Etosha, though the game fence appeared to have little short-term effect on the lion population. From 1953-1955, lion numbers within the park were estimated between 200-250 (Berry 1987), this was little changed by 1962, when the population was estimated at 260 (RSA 1964, p. 23).

Responding to international pressure to decolonise South West Africa, South Africa began implementing the recommendations of the so-called Odendaal Plan (RSA 1964) during the 1960s. As part of the apartheid government's policies for separating different races and land-uses, there was an emphasis on separating Etosha from the neighbouring Kaokoveld 'ethnic homeland' by further fencing the park (NAN LUKS 2.8 1966; Heydinger 2021a). By 1973, the park was enclosed by a high-quality 850-km game-proof boundary fence not only to keep wildlife inside, but also to ensure 'natives' could not graze their livestock or hunt within the park (Berry 1997; Dieckmann 2007; Hoole and Berkes 2010). Once the park was enclosed, a portion of the wildebeest population, normally considered "abundant" on lands north of the park during the dry season (Bigalke 1961), was now confined to the Ovamboland 'native reserve', where wildlife conservation was nominal at best. Herds stuck outside the fence diminished due to sport hunting and competition with livestock (Berry 1982). Herbivores

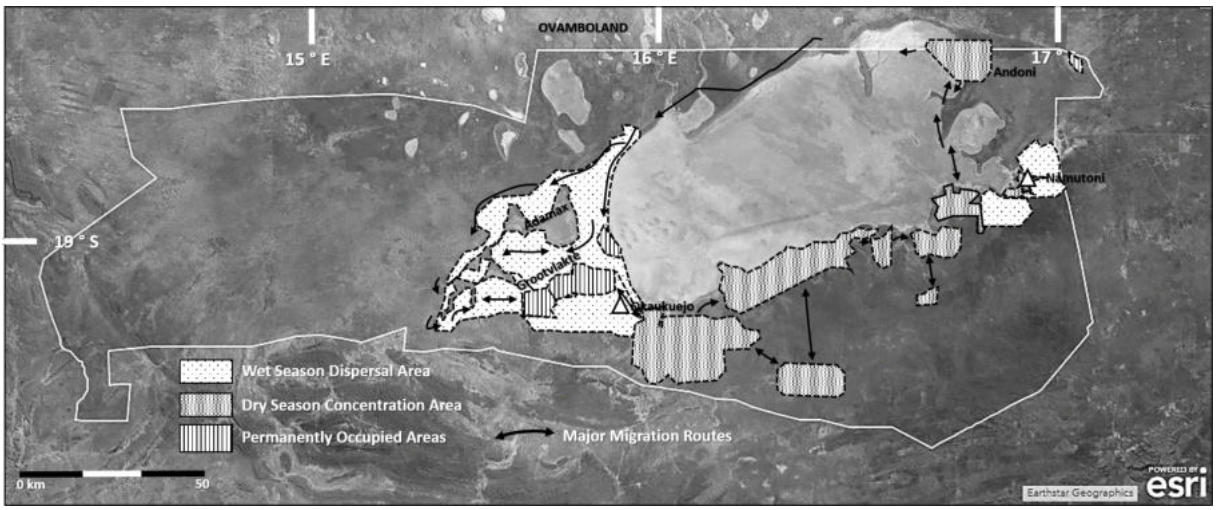

Figure 5: *Plains zebra distribution and migration. Based on Ebedes (1976, p. 103).*

confined within the park could no longer migrate to seasonal pastures beyond Etosha borders. However, this 'game-proof' fence was insufficient to keep lions within the park. Throughout the lifetime of the fence, lions have easily exploited holes, primarily created by the burrowing of warthogs (*Phacochoerus africanus*) and porcupines (*Hystrix cristata*), to move between Etosha and neighbouring farmland (Stander 1991; Trinkel *et al*. 2017; Heydinger and Vinjevold unpub. data).

Artificial waterholes

Beginning in 1951, Etosha staff constructed roads and a series of artificial waterholes centered along the 19th parallel in the park's western section. Prior to this, western Etosha was "poorly watered" and little game and few lions were encountered in the western woodlands (Bigalke 1961, p. 54; Stark 2011, p. 192). Road-building was meant to increase staff access to the western part of the park, enabling a more comprehensive picture of the wildlife and enhancing viewing opportunities for tourists. Waterhole construction was intended to reduce high concentrations of wildlife at existing waterholes. As many as 54 artificial waterholes were constructed during the 1950s (Berry and Siegfried 1991). Road-building also led to the creation of gravel pits, so-called 'mini-dams,' which would retain standing rainwater up to five weeks longer than naturally-occurring pans. This was considered a boon for Etosha herbivores: during the 1960s, the area's herbivore carrying capacity was thought to be primarily determined by the amount of water available (NAN LUKS 1.4 1964). As obligate drinkers (excluding gemsbok; *Oryx gazella*), Etosha's herbivores were able to exploit new grazing areas in the woodlands further west that had previously been poorly watered (Berry and Louw 1982). As a result, herbivores remained near these water points well into the dry season, overgrazing the nutrient-rich grasses. This was similar to what happened in Kruger National Park when gravel pits led to unwanted grazing concentrations in the 1960s (Ebedes 1976). Prior to the creation of these structures, lions were seldom seen in these areas, but the influx of herbivores subsequently attracted lions (Stander 1991). By 1970 at least 134 'mini-dams' had been created in the Okaukuejo area alone and hundreds were estimated to have been created throughout the park (Ebedes 1976; Berry and Siegfried 1991, p. 155).

Anthrax

The construction of new water sources, combined with the park's enclosure, led to cascading changes in herbivore numbers (Figure 6). Unable to depart Etosha for grazing, during the late 1960s and early 70s herbivores remained increasingly sedentary around mini-dams, overgrazing these areas, and suffering from anthrax outbreaks (Ebedes 1976). Anthrax had long been present in Etosha and on neighbouring farmlands but was not previously considered a serious threat to wildlife, until the work of Etosha veterinarian Hym Ebedes began

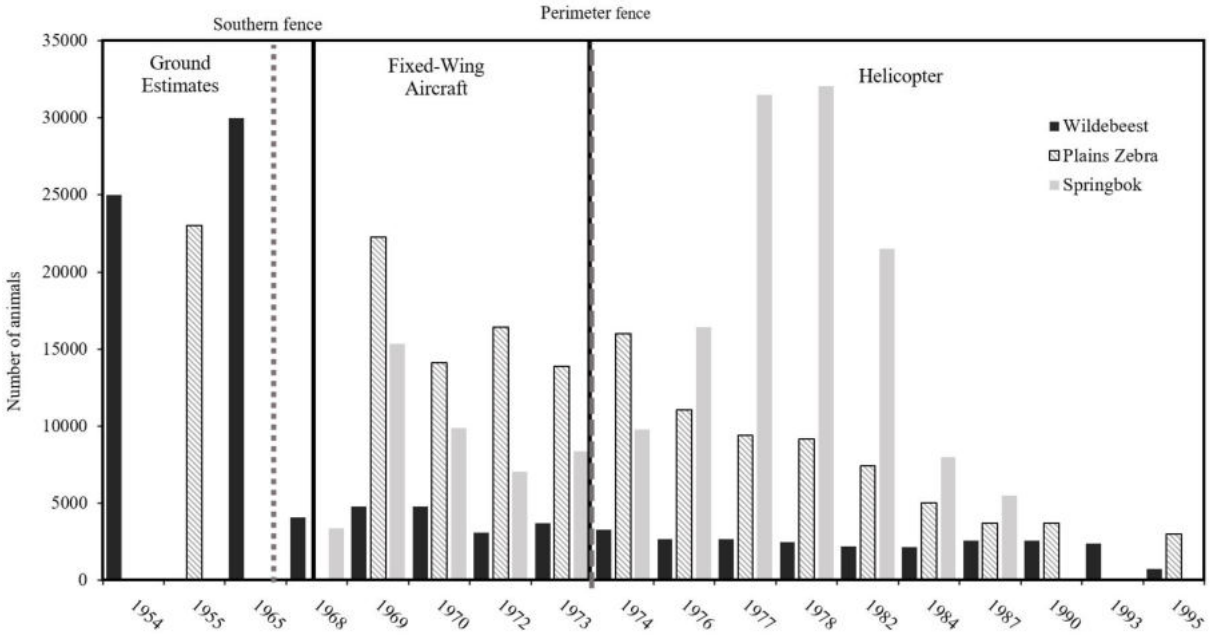

Figure 6: *Wildebeest, plains zebra, and springbok in central and eastern Etosha National Park Wildebeest data from Berry (1981a) [1954-1978]), Turnbull* et al. *(1989) [1982], and Gasaway* et al. *(1996) [1984-1990]. Plains zebra data from Gasaway* et al. *(1996) [1955; 1982-1990], Berry and Louw (1982) [1969-1978], and Turnbull* et al. *(1989) [1982]. Springbok data from Berry and Louw (1982) [1968-1978], Turnbull* et al. *(1989) [1982], and Gasaway* et al. *(1996) [1982-1987]. Left dashed line indicates when southern foot-and-mouth disease fencing was completed (1963). Right dashed line indicates when Etosha was enclosed by a high-quality game-proof fence (1973).*

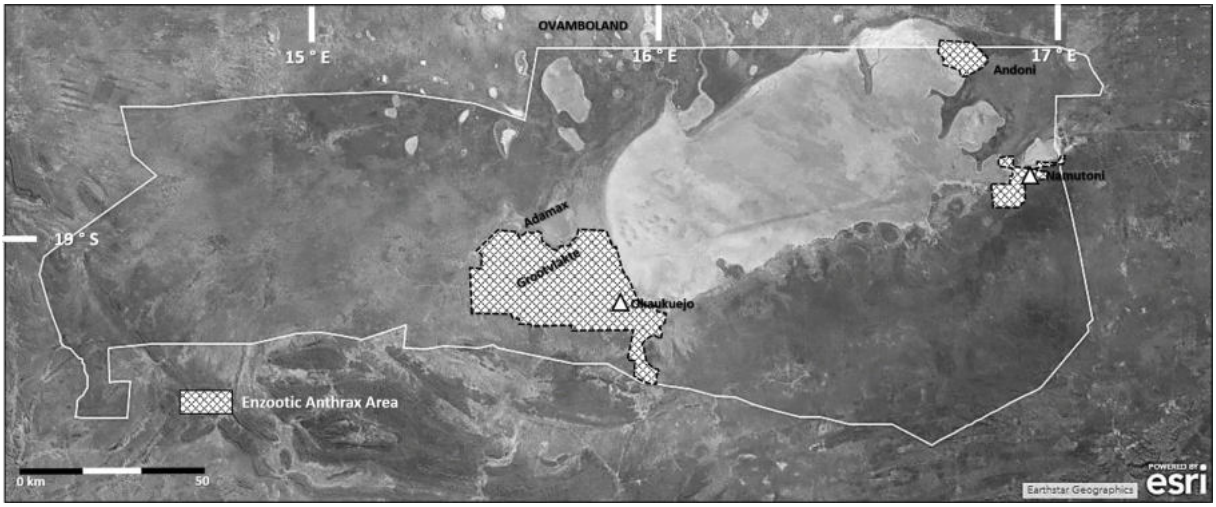

Figure 7: *Enzootic anthrax areas. Based on Ebedes (1976, p. 106).*

uncovering the effects of anthrax in the 1970s. Once areas around Namutoni and west of the pan became more intensively grazed further into the rainy season, and even into the dry season, they became enzootic anthrax areas, with the Adamax-Grootvlakte-Okaukuejo triangle being the most seriously affected (Figure 7). Between 1966-74 at least 1,635 animals, 89% of which were plains zebra and wildebeest, were recorded as dying of anthrax in Etosha (Ebedes 1976). From 1974-78, 76% of recorded wildebeest mortalities were the result of anthrax (Berry 1982). From 1967-87, anthrax was the primary recorded cause of death in 11 different species (Berry 1987). During the 1970s, a period of higher-than-average rainfall, Etosha's plains zebra and wildebeest populations failed to bounce back from their declining numbers following Etosha's enclosure.

Coinciding with increased anthrax and fencing, lion numbers increased within the park. Between 1965-1976, Etosha lions were estimated between 320-450. During this period, Etosha ecologists attributed the rise in lion numbers to the combined effects of limited herbivore migration, the increased construction of artificial waterholes, and a surplus of anthrax-infected carcasses (Berry 1982). Lions were largely immune to the effects of anthrax (Turnbull *et al*. 1992). Data on other Etosha carnivores, including spotted hyaena (*Crocuta crocuta*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*), are limited, though Berry (1987) estimated that during the late 1970s, cheetah (highly susceptible to anthrax) and wild dog numbers (soon to be extirpated from Etosha) decreased dramatically while hyaena increased. Etosha ecologist Hu Berry summarised the relationship between these factors and the increase in Etosha's lion population during this period,

> "Initially, the boundary fence around Etosha and veterinary barriers outside the park eliminated the ability of the [herbivore] species to migrate. This severely decimated the original [herbivore] population. Subsequently, the residual population remaining within Etosha has been subjected to elevated levels of anthrax caused by 'incubator areas' in gravel pits used for road building. The abundant supply of anthrax-infected carcasses during an epidemic favours lions and other carnivores which are immune to anthrax. Man has further stabilised the environment for predators by constructing artificial water points" (Berry 1982, p. 156).

The result was the highest estimated lion population yet recorded for Etosha, which peaked at about 500 for the plains areas between 1978-1980 (Berry, 1987).

1974-1980: herbivore declines and peak lion numbers

In 1974 the effort invested in lion monitoring in the park increased, though research still focused on the central and eastern plains areas (Berry 1997). From 1974-78, 21 areas were known to have resident prides or nomadic groups, and the park's population was estimated between 285-400 lions (Berry 1981b, p. 242). Though it was thought that few lions inhabited the woodlands, park staff were unable to intensively monitor these areas. Known lion territories overlapped with plains zebra and wildebeest range (Figure 8): these two species comprised 80% of recorded lion prey items (Berry 1980). Rising recorded lion numbers, combined with the effects of anthrax, conspired to drive down plains zebra and wildebeest populations, which reached 9,000 and 3,000 respectively by 1980 (Owen-Smith 2010, p. 322). In the late 1970s Etosha's lion:prey ratio measured at 1 kg of lion to 107-153 kg of prey; this was on par with Kruger's lion:prey ratio, where lion control measures were being implemented (Berry 1981b).

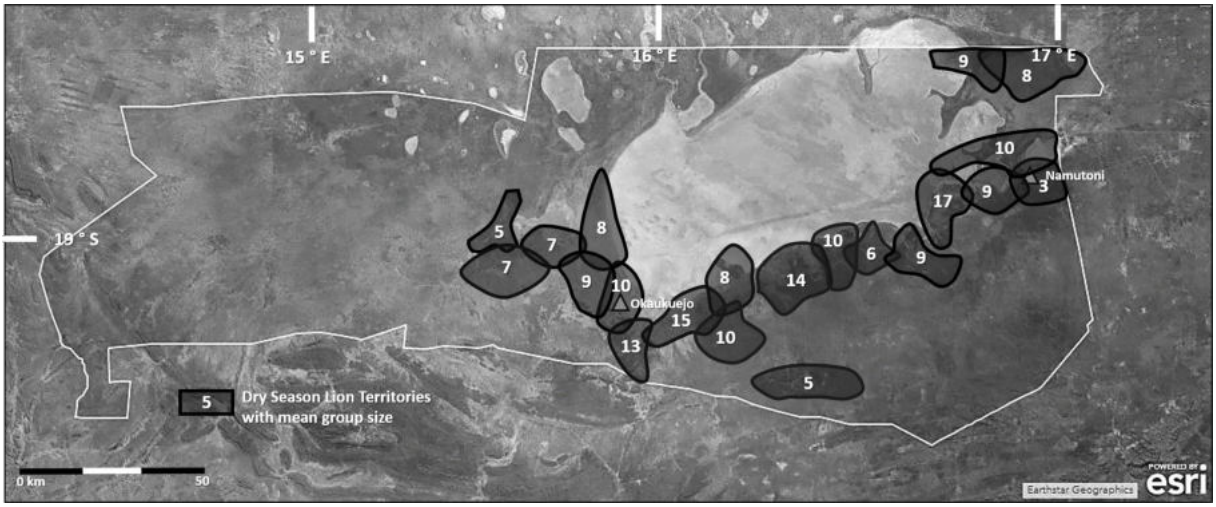

Figure 8: *Dry season ranges for the 21 known lion groups in plains habitat (1974-1978). Based on Berry (1981b, p. 244).*

Whether a surplus of carcasses from anthrax, resulting from the changing geography of available water, led to an increase in lion numbers cannot be confidently inferred from available data. Though, what Berry called the "stabiliz[ation] of the environment for predators" due to the construction of artificial waterpoints, coincides with an increase in lion numbers and accords with evidence from other areas. Contrasting lion population density, cub survival, and subadult dispersal rates in the Ngorongoro Crater ("high-quality habitat") and Serengeti ("low-quality habitat"), Hanby *et al*. (1995) found lion population density was most closely correlated with "poor season" prey availability. They also found cub survival was limited when food was scarce and water widely scattered. In Ngorongoro, where lions only moved two-thirds as much per night as lions inhabiting Serengeti, immature lions made up a greater proportion of groups (61% versus 48%). Packer *et al*. (1988) have also shown reproductive success and cub recruitment are greater where prey availability is greater. During the 1970s, Smuts (1976) found a > 50% increase in the lion population of Kruger National Park, following the construction of artificial waterholes, leading to lions settling in previously unoccupied areas. In Etosha, groups of lions maintained discrete territories during the dry season, but during the rainy season territorial boundaries become more fluid (Berry 1981b). Based on these findings linking lion density to "poor season" prey availability, we infer that as mini-dams opened up new grazing areas for herbivores further into the dry season, lions could have more reliably exploited new dry season territories, giving rise to increased densities, increased dispersal, and leading to greater lion numbers across the park. During his intensive study of Etosha lions during the 1980s, Stander (1991) found lion densities were highest in areas with a greater number of artificial waterpoints, presumably owing to higher prey densities. Across Etosha, the creation of new artificial waterholes could have led to higher concentrations of prey in new areas, thus allowing lions to thrive in areas that were previously water-limited, well into the dry season.

The notable increase in the Etosha lion population during the 1970s, from an estimated 320 to 500 (keeping in mind this was before lions in Etosha's woodlands were comprehensively monitored) took place during a period when rainfall was 10% higher than average, peaking in 1976 when rainfall was 61% above average. The creation of new mini-dams prior to this relatively wet period would have enabled herbivores and dispersing lions to occupy new areas well into the dry season. As Packer *et al*. (2005) have shown, lion populations go through periods of stasis followed by sudden transitions to new equilibriums following habitat transformations: an expanding food supply in the Serengeti only allowed lion populations to grow when pre-existing groups could split to form viable new groups that were large enough to defend new territories. The evidence from Etosha during the 1970s suggests when herbivores remained in areas that were no longer water-limited this also opened these areas for lions to maintain new dry season territories. As lion range expanded, lions would have been able to form new groups, leading to a growing lion population even as plains zebra and wildebeest numbers declined.

During the late 1970s lions adjusted their diets accordingly. Though they continued to primarily select plains zebra and wildebeest, springbok – susceptible to anthrax, though not to the extent of plains zebra and wildebeest – increased from 9,800 to 32,000 during the 1970s (Berry 1981b; Ebedes 1976). Subsequently, lions increasingly selected springbok and gemsbok as prey (Berry and Siegfried 1991; Stander 1991b). As Berry summarised, "lion numbers probably reach[ed] their peak in 1979, which coincided with the end of a wet cycle of 10

years" (1987, p. 8). By 1980, lions in Etosha were considered so numerous that ecologists piloted a contraception program in five groups near Okaukuejo; culling having proven ineffective and disruptive to group dynamics in Kruger (Smuts, 1978; Orford *et al*. 1988).

1980s-early 1990s: drought and intensive monitoring

The early 1980s proved to be the driest years on record (Gasaway *et al*. 1996). From 1980-1985 rainfall was 30% below average, resulting in herbivore population declines and subsequent declines in the lion population. From 1980-1986 the Etosha lion population dropped from an estimated 500 to 200. Lions declined during this period not only because of their elevated numbers, but also due to earlier changes in available prey. Whereas from 1974-1978 plains zebra and wildebeest formed a combined 80% of lion prey items while springbok formed 11% (Berry 1981b), from 1984 to 1988 springbok made the greatest contribution to lion diet, both in terms of prey items (62%) and biomass consumed (37%). In contrast, during this period zebra and wildebeest comprised a total of 21% of prey items and 52% of biomass consumed (Stander 1991b). Though these changing values can be partially attributed to new data collection methods (Stander 1991b), they also indicate a transformation in Etosha's herbivore population – with subsequent effects for lions. As we have shown, during the 1970s plains zebra and wildebeest numbers declined markedly. A reliance on springbok would have constrained lions during the drought: a 1996 study of the effects of drought on four Etosha species (plains zebra, wildebeest, springbok, and gemsbok), found springbok were most affected. From 1978-1987 springbok declined from 32,000 to 5,000 (Berry 1981b; Gasaway *et al*. 1996).

From 1984-1989, Etosha lions were intensively monitored, and lions in the woodlands were monitored for the first time (Stander 1991). Research technician and later scientist, Dr. Philip Stander, provided more precise population estimates and densities for Etosha's different habitats. His studies showed lion numbers declined during the worst of the drought (1980-1986), then quickly rebounded in the late 1980s – though Etosha experienced below average rainfall throughout the 1990s. Elevated cub survival following the drought indicated heightened levels of recruitment, similar to the 1970s when the lion population was growing rapidly. Whereas Berry (1981b) recorded 37% immature (0-3 years) lions on the plains from 1974-1978, in January 1987 Stander (1991a) recorded a similar 49% (0-4 years) in the woodlands, dropping to 36% by February 1989. For 1989, Stander (1990, 1991) estimated between 268-351 lions in Etosha. Population gains occurred even as an average of 27 lions were killed annually on neighbouring farmlands from 1982 to 1989 (Figure 9; Funston unpub. data). However, lion numbers in Etosha did not return to the heights of the late 1970s throughout the remainder of the twentieth century.

1994-2010s: Limited data and persistent conflict

Since the mid-1990s, lion population surveys have been irregular. Thus, less is known about Etosha lions presently than during the 1970s and 80s. While groups in the plains area were monitored regularly until 1997, there has been no comprehensive lion monitoring across Etosha since 2000 (Trinkel *et al*. 2017). Available estimates indicate the population remained relatively low during the 1990s – including suffering relatively high cub mortality (54%) (Berry 2003) – but increased during the moderately rainy 2000s.

What has been more comprehensively recorded is the problem of human-lion conflict along Etosha's borders. From 1975-2010, at least 1,059 lions were destroyed on farms bordering Etosha, primarily on privately-owned (White) farms to the south and east (Funston unpub. data; Stander 2004) (Figure 9). The

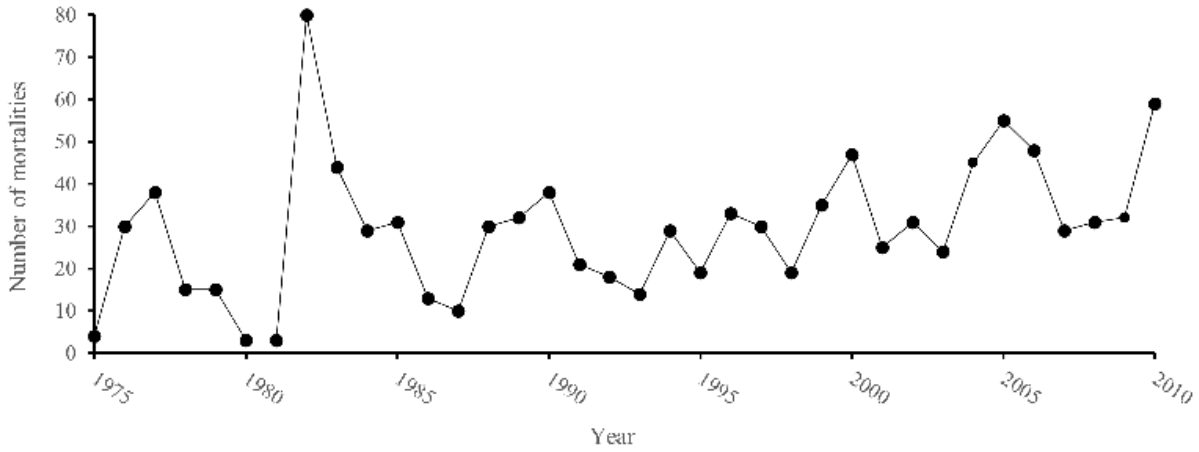

Figure 9: *Records of lion mortalities on farms bordering Etosha National Park (Funston unpub. data).*

relatively stable number of average annual mortalities ($\mu = 29.4$, std dev = 15.78) throughout this period is further stabilised when outlying data from 1982 (80 mortalities) are removed ($\mu = 27.97$, std dev = 13.53), as has been suggested by Stander (2004), who felt 1982 records, based on farmer surveys, likely included incidents from previous years. Though these records are less than the 80 mortalities per year suggested for the 1950s (de la Bat 1982) (above), they underscore the permeability of Etosha's fence for lions. In two reviews of stock raiding lions along Etosha's borders, Stander (1989, 2004) emphasised the regularity, even predictability of lions dying on neighbouring farms, primarily within farmland to the east, south, and southwest of the park where livestock farming, and more recently game farming, is most heavily concentrated. Though mortality records since 2010 are not available, the challenge of human-lion conflict persists. The contemporary picture is one of lions either dispersing from Etosha or surreptitiously exiting the park to prey on farmers' livestock at night, only to return to Etosha's safe confines during the day. A typical incident, reported from along Etosha's western border in January 2019 reads, "[the] lions came from Etosha and fle[d] back after killing and feeding on Mr. _____'s six livestock at Okatutu [farm]" (Heydinger and Vinjevold unpub. data). Such incidents affect farmers' livelihoods, leading to lions being shot or poisoned.

DISCUSSION: HISTORICAL INSIGHTS

Changes to Etosha's infrastructure preceded changing lion numbers in the park during the second half of the twentieth century. There is circumstantial evidence that infrastructure changes contributed to a temporary increase in the lion population, though it is difficult to separate signal from noise. With disparate historical sources, comparing data, such as lion and herbivore numbers, anthrax incidents, or lion mortalities, across eras, where methods, sample sizes, and efforts have changed, engenders difficulties for subsequent analysis. Explanations of historical causation are necessarily tentative. Our approach highlights interwoven social and ecological factors leading to changes in lion and herbivore numbers within Etosha.

During the 1970s and 80s Etosha ecologists emphasised the effect of fencing and waterpoint construction, as well as subsequent anthrax outbreaks, on the park's herbivores (Ebedes 1976; Berry 1981b, 1982). They further hypothesised these changes directly contributed to the growth of Etosha's lion population. While the erection of game-proof perimeter fencing is thought to have led to the dramatic reduction of plains zebra and wildebeest, there is insufficient evidence to conclude whether fencing alone either greatly benefited or limited Etosha lions. While plains zebra and wildebeest numbers decreased in the 1960s-70s, lion numbers increased. Limited prey mobility and increasing availability of carcasses due to anthrax likely benefited lions. However, the decline in available prey coinciding with the rising lion population throughout the 1970s suggests lion numbers were not limited by the total amount of prey. As in Kruger (Smuts 1976), the increasing size of the lion population is positively correlated with the construction of artificial waterholes which opened up new areas for prey. Harrington *et al*. (1999) have shown that the construction of new waterholes attracts herbivores, and subsequently lions, to previously water-limited areas. Consonant with evidence from Serengeti (Packer *et al*. 2005), lions were able to occupy new territories when prey was redistributed to areas that were previously only seasonally inhabited by herbivores. However, the dramatic increase in Etosha lions during the 1970s was temporary. During the 1970s-80s the composition of Etosha's herbivore guild was transformed (Figure 6). Previously dominated by plains zebra and wildebeest, springbok predominated by the 1980s, and lions changed their foraging habits accordingly (Stander 1991b). When drought struck (1980-1986), springbok numbers declined dramatically, and lion numbers followed.

In the Kaokoveld 'ethnic homeland' to the west, livestock and wildlife numbers collapsed during this same period. This has been primarily attributed to the development of water infrastructure and the subsequent transformations in landscape use among grazers (Bollig 2020). As artificial waterholes were developed in previously water-limited areas of Kaokoveld, livestock and wildlife made year-round use of new areas. During the drought, livestock and grazers died in large numbers, not for want of water, but for want of grass. Lions in Kaokoveld also struggled during this period (Heydinger 2021b). When rains failed in Kaokoveld, lions struggled to find adequate prey, resulting in increasing amounts of human-lion conflict and the subsequent destruction of lions by local farmers. As in Kaokoveld, the construction of artificial waterholes in Etosha transformed the geography of prey species, with downstream effects for lions.

Etosha lion population estimates do not include the park's woodlands until the 1980s (Berry 1996). Due to a lack of information concerning survey methods we have not adjusted earlier estimates, but it is reasonable to assume lions in woodland areas were undercounted. Researchers and staff in Etosha throughout the 1950s-70s noted little information was available concerning wildlife in Etosha woodlands, though they uniformly felt lions were not common in these areas (e.g. Bigalke 1961; Berry 1981b; Stark 2011). In contrast, during the 1980s

Stander rigorously monitored lions in Etosha's woodlands, finding high lion densities correlated with the number of artificial waterpoints and prey densities (Stander 1991a). Stander's emphasis on the effect of artificial waterpoints and areas of high prey density provides further evidence that infrastructure led to increasing lion numbers in the woodland areas. Stander's late 1980s' estimate of lion numbers for Etosha (268-351) may thus undersell the decline in lion numbers during the 1980s.

While Etosha's perimeter fence has proven successful at enclosing the park's herbivores and excluding pastoralists' livestock, the fence has proven consistently ineffective for enclosing the park's lions. This is evident in the persistent challenge of human-lion conflict, and relatively stable number of human-caused lion deaths, along Etosha's border. Clearly all fences are not created equal, and fences have differentiated effects for different species. The development of conservation infrastructure is also bound-up with social and political considerations, which can have long-lasting effects. The fencing which enclosed Etosha during the apartheid era was constructed primarily for political and secondarily for veterinary purposes, but it had and continues to have wildlife survival implications.

CONCLUSION

The history of protected areas and neighbouring lands is a growing topic in environmental history and can provide important insights for managers (Dlamini 2020; Neumann 1998). These histories can also provide perspective on scientific and management debates surrounding issues such as conservation infrastructure and add to the recognition that infrastructure development does not take place in isolation from other conservation actions (Massey *et al*. 2014).

Protected areas are human-created entities, which impose certain politics, economics, and values on wildlife, landscapes, and people (Brockington 2002; Cumming 2016). For protected area managers this history demonstrates the long-term effects of politics as it pertains to infrastructure development. The social and political history driving the erection of fencing and construction of waterpoints in Etosha has been examined elsewhere (Heydinger 2021a); this is the first examination of their effects on Etosha's wildlife. This provides new avenues for researchers to examine the effects of other human activities on lions and other wildlife within protected areas. Clearly Etosha is a social and ecological system in which human and environmental factors feedback on one another across multiple time scales. There is no reason to think this case is unique. Historical methods, including, but not limited to, archival and textual analysis, such as those performed here, can augment field-based scientific approaches to better contextualise long-term wildlife population trends.

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