Namibian Journal of Environment Volume 6

Section A: Peer-reviewed papers

Crawford RJM, Sydeman WJ, Tom DB, Thayer JA, Sherley RB, Shannon LJ, McInnes AM, Makhado AB, Hagen C, Furness RW, Carpenter-Kling T & Saraux C (2022) Food limitation of seabirds in the Benguela ecosystem and management of their prey base. *Namibian Journal of Environment* 6 A: 1-13

Pallett J, Simmons RE & Brown CJ (2022) Staggered towers on parallel transmission lines: a new mitigation measure to reduce collisions of birds, especially bustards. *Namibian Journal of Environment* 6 A: 14-21

Heydinger J, Packer C & Funston P (2022) The historical effects of infrastructure development on the lion population of Etosha National Park, Namibia. *Namibian Journal of Environment* 6 A: 22-36

Walters M & Hauptfleisch M (2022) An analysis of trophy size trends in popular hunting species in Namibia over five years. *Namibian Journal of Environment* 6 A: 37-46

Hamutenya J, Hauptfleisch M, De Cauwer V, Fennessy J, Fennessy S & Nzuma T (2022) Understanding community attitudes toward the Angolan giraffe (*Giraffa giraffa angolensis*) and its potential reintroduction into Iona National Park, Angola. *Namibian Journal of Environment* 6 A: 47-56

Shimhanda MN & Vivian B (2022) Media coverage of climate change in Namibia and South Africa: A comparative study of newspaper reports from October 2018 to April 2019. *Namibian Journal of Environment* 6 A: 57-66

Mbeha SL & Rutina LP (2022) Spatio-temporal functional diversity of large herbivores in Mudumu National Park, northeastern Namibia. *Namibian Journal of Environment* 6 A: 67-77

Périquet S, Crawford S, Naholo S, Stratford S & Stratford K (2022) At home or passing through? Leopard population and spatial ecology on a private game reserve. *Namibian Journal of Environment* 6 A: 78-91

Wenborn MJ, Nijman V, Kangombe D, Zaako RK, Tjimuine U, Kavita A, Hinu J, Huwe R, Ngarukue VJ, Kapringi KJ & Svensson MS (2022) Analysis of records from community game guards of human-elephant conflict in Orupupa Conservancy, northwest Namibia. *Namibian Journal of Environment* 6 A: 92-100

Section B: Research reports

Fischer H, Portas R & Edwards S (2022) A preliminary comparison of brown hyaena activity patterns at den sites located within a protected reserve and a commercial farmland. *Namibian Journal of Environment* 6 B: 1-5

Section C: Open articles

Kopij G (2022) Provisional atlas of breeding birds of Henties Bay in the coastal Namib Desert. *Namibian Journal of Environment* 6 C: 1-6

Theart F, Ping TJ, Engelking K & Becker FS (2022) Range extension of *Crotaphopeltis hotamboeia* (Laurenti, 1768) in Namibia. *Namibian Journal of Environment* 6 C: 7-9

Swanepoel W, Becker RW & De Cauwer V (2022) First records for Namibia of Lesser Masked Weaver *Ploceus intermedius* subsp. *beattyi*. *Namibian Journal of Environment* 6 C: 10-13

Section D: Monographs and Memoirs

Bryson U & Paijmans DM (2022) White-crowned Shrike (*Eurocephalus anguitimens*) A. Smith, 1836: comparative biometrics, moult data and criteria for the determination of age. *Namibian Journal of Environment* 6 D: 1-22

Food limitation of seabirds in the Benguela ecosystem and management of their prey base

RJM Crawford¹, WJ Sydeman², DB Tom³, JA Thayer², RB Sherley⁴, LJ Shannon⁵, AM McInnes⁶, AB Makhado¹, C Hagen⁶, RW Furness⁷, T Carpenter-Kling^{6,8}, C Saraux⁹

URL: http://www.nje.org.na/index.php/nje/article/view/volume6-crawford Published online: 2nd February 2022

Date received: 3rd December 2021; Date accepted: 13th January 2022.

ABSTRACT

Four of seven seabirds that are endemic to the Benguela ecosystem (African Penguin *Spheniscus demersus*, Cape Gannet *Morus capensis*, Cape Cormorant *Phalacrocorax capensis*, Bank Cormorant *P. neglectus*) compete with fisheries for prey and have an IUCN classification of Endangered. Prey depletion and food resource limitations have been major drivers of recent large population decreases of each of these species. As populations decrease, colony sizes also dwindle rendering them susceptible to Allee effects and higher probabilities of extinction. Therefore, it is necessary to maintain colonies at sizes that minimise their probability of extinction. Means to ensure an adequate availability of food to achieve this goal include closing important seabird foraging areas (often adjacent to key colonies) to relevant fishing, implementing ecosystem thresholds below which such fishing is disallowed (which are also expected to benefit forage resources) and, should there be an altered distribution of prey, attempting to establish seabird colonies close to the new location of forage resources.

Keywords: Allee effects; Benguela seabirds; conservation thresholds; food limitation; Namibia; spatial management

INTRODUCTION

This paper provides a brief review of food limitation of four Endangered (EN) seabirds that breed in the Benguela ecosystem, of the viability of seabird colonies and Allee effects, of forage and consumption thresholds and of potential management interventions that may enhance food availability. The locations of some of the system's important seabird colonies are shown in Figure 1.

STATUS OF THE BENGUELA'S SEABIRDS

Fifteen seabird species breed in the cool Benguela ecosystem, which extends from about Benguela in Angola to Woody Cape in South Africa, being bounded in the north and southeast by the warm Angola and Agulhas Currents, respectively (Figure 1). Seven of these are endemic to the ecosystem (Hockey *et al.* 2005). Of the endemic species, in terms of criteria of the International Union for Conservation of Nature (IUCN) four are EN

(African Penguin Spheniscus demersus, Cape Gannet Morus capensis, Cape Cormorant Phalacrocorax capensis, Bank Cormorant P. neglectus), one is Near-Threatened (NT, Crowned Cormorant Microcarbo coronatus) and two are Least Concern (LC, Damara Tern Sternula balaenarum and Hartlaub's Gull Larus hartlaubii, IUCN 2021). The non-endemic Leach's Petrel Hydrobates leucorous Oceanodroma leucorhoa) is Vulnerable (VU), whereas the other seven non-endemics are LC (IUCN 2021). Although substantial numbers of Leach's Storm Petrel migrate from the Northern Hemisphere into the Benguela system (Pollet et al. 2019), the breeding population of this species in South Africa is Critically Endangered (CR), as is that of Damara Tern (Taylor et al. 2015). In South Africa small, isolated populations of Great White Pelican Pelecanus onocrotalus, Caspian Tern Hydroprogne caspia and Roseate Tern Sterna dougallii are regarded as regionally VU (Taylor et al. 2015). Leach's Storm Petrel and Roseate Tern do not breed in Namibia, where Cape Gannet is considered CR

¹ Branch Oceans and Coasts, Department of Forestry, Fisheries and Environment, Cape Town, South Africa.

² Farallon Institute, Petaluma, CA, USA.

³ Ministry of Fisheries and Marine Resources, Lüderitz, Namibia.

⁴ Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn, UK.

⁵ Department of Biological Sciences, University of Cape Town, Cape Town, South Africa.

⁶ BirdLife South Africa, Cape Town, South Africa.

⁷ University of Glasgow, Glasgow, UK.

⁸ Institute for Coastal and Marine Research and Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa.

⁹ IPHC, CNRS, Université de Strasbourg, Strasbourg, France.

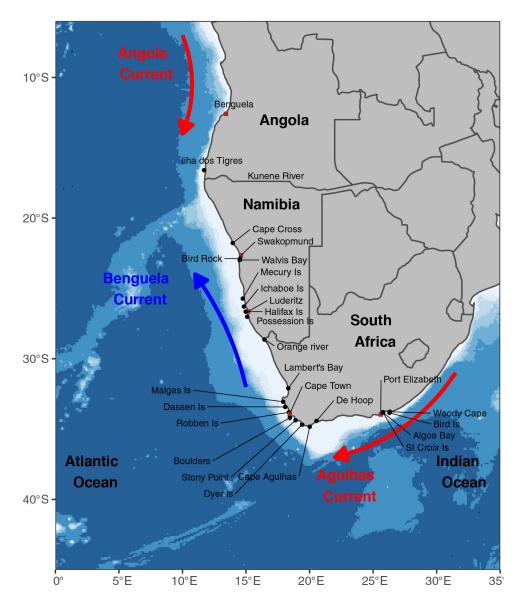


Figure 1: A map of the Benguela Current ecosystem showing locations of some of the region's important seabird breeding colonies and other localities mentioned in the text.

(Kemper 2015), Great White Pelican and Caspian Tern VU (Simmons 2015a, b) and Damara Tern NT (Simmons *et al.* 2015).

IMPORTANCE AND EVIDENCE OF FOOD LIMITATION

For a seabird population to be self-sustaining, mortality from its mature component must be balanced by recruitment or immigration. Recruitment is influenced by age at first breeding, breeding participation (proportion of mature birds electing to breed), breeding frequency (number of clutches produced annually), breeding success (chicks fledged per clutch) and survival from fledging to breeding. Insufficient food resources may negatively affect these demographic parameters leading to population

decreases, as is described below for the Benguela's four EN seabird species, which all feed mainly on three forage resources that are heavily exploited by fisheries when these are readily available. African Penguin, Cape Gannet and Cape Cormorant feed preferentially on sardine Sardinops sagax and anchovy Engraulis encrasicolus (Hockey et al. 2005). In South Africa, the intensively fished West Coast rock lobster Jasus lalandii is an important prey of Bank Cormorant (Dyer et al. 2019), whereas in Namibia the lightly-exploited but nutritionallydeficient bearded goby Sufflogobius birarbatus is one of its staple foods (Ludynia et al. 2010a). After the collapse of sardine in Namibia in the 1970s, bearded goby also replaced it as the dominant prey item for African Penguins breeding in Namibia (Ludynia et al. 2010b).

African Penguin

Large decreases of African Penguins at colonies between Lüderitz in Namibia and Dassen Island off west South Africa from the 1960s to the 1980s were recorded following the collapse of sardine stocks off Namibia and South Africa. North of Lüderitz, increases at Mercury and Ichaboe islands after the 1960s probably resulted from an increased local abundance of bearded (Crawford and Shelton 1978, Shelton et al. 1984, Crawford et al. 1985, 2001a). However, this did not prevent an overall decrease of 90% in penguins breeding in Namibia between 1956 and the early 2000s (Figure 2, Crawford 2007).

By contrast, an increase between the 1950s and 1970s and a later decrease in numbers of penguins at Dyer Island, southwest South Africa, coincided with an increase subsequent fluctuations in anchovy abundance (Crawford 1998). From 1989-2009 numbers of penguins breeding along west South Africa were significantly correlated with the overall biomass of sardine and anchovy in South Africa, as also was the case from 1999-2009 in Algoa Bay (Figure 2, Crawford et al. 2011). The formation of new penguin colonies at Stony Point and Boulders on South Africa's mainland and at Robben Island, and increases at these colonies and at Dassen Island, took place during a period of recovery of South Africa's sardine in the 1980s and 1990s and an increase in the biomass of anchovy at the start of the 21st century. This led to an overall increase in the numbers of penguins breeding in west South Africa (Underhill et al. 2006).

After 2004, large decreases in numbers of penguins breeding in west South Africa were associated with a shift to the south and east of adult anchovy and sardine and a collapse of

sardine (Crawford *et al.* 2011). Concomitant with the altered distribution of prey there were decreases in penguins at all South African colonies north of Cape Town (the northernmost colony at Lambert's Bay became extinct in 2006; Crawford *et al.* 2013). By contrast, in the south numbers increased or stabilised

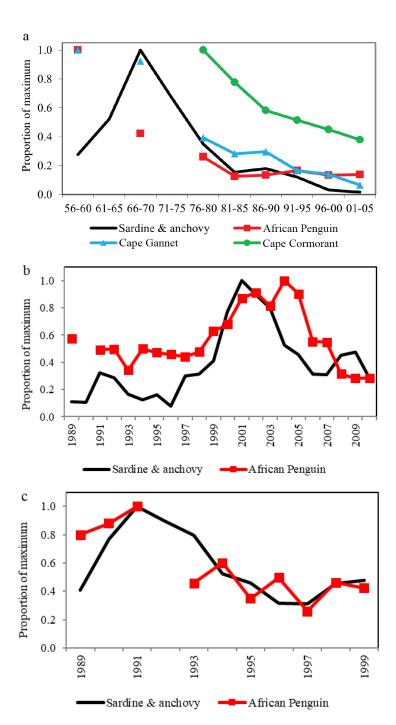


Figure 2: Comparison of trends in standardised estimates (maximum = 1) of the combined biomass of sardine and anchovy and breeding populations of seabirds that feed on these forage species for (a) Namibia 1956/60–2001/05 (redrawn from information in Crawford 2007), (b) west South Africa 1989–2010 and (c) Algoa Bay 1999–2009 (redrawn from information in Crawford et al. 2011). For west South Africa and Algoa Bay fish estimates are for the whole of South Africa.

at Boulders and Stony Point and penguins attempted to form a new colony at De Hoop Nature Reserve (Underhill *et al.* 2006, Crawford *et al.* 2011). Although trends in numbers of African Penguins at colonies are often regionally coherent (Underhill *et al.* 2006), at Dyer Island, also in the south, penguins

decreased in the 2000s. This may have resulted from heavy exploitation of sardine in its vicinity: 70,000 tonnes of sardine were caught within 30 km of Dyer Island in 2004 (Ludynia *et al.* 2014) and the exploitation rate of sardine west of Cape Agulhas increased to 30–44% in 2002 and from 2005–2007 (Coetzee *et al.* 2008). When the colony size at Dyer Island was > 3,500 pairs, numbers of penguins breeding there were negatively related to sardine catches made within 20 nautical miles of the island (Ludynia *et al.* 2014), suggesting an impact of catches on local food availability.

Local or regional abundances or availability of sardine and anchovy have been related to numbers of African Penguins breeding (Crawford 2007, Crawford *et al.* 2011, Sherley *et al.* 2013), to adult and immature survival (Crawford *et al.* 2011, 2019, Sherley *et al.* 2014, Robinson *et al.* 2015), to age at first breeding (Whittington *et al.* 2005), to breeding participation (Crawford *et al.* 1999b, Durant *et al.* 2010), to breeding success (Adams *et al.* 1992,

Crawford and Dyer 1995, Crawford *et al.* 1999b, 2006a, Cury *et al.* 2011, Sherley *et al.* 2013) and to foraging performance (Pichegru *et al.* 2010, 2012, Campbell *et al.* 2019, McInnes *et al.* 2019). Additionally, onset of breeding was probably delayed during a period of food scarcity (Crawford and Dyer 1995) and the chick fledging period was negatively correlated with prey abundance (Sherley *et al.* 2013). Delayed breeding and longer fledging periods may reduce the breeding frequency and cause abandonment of unfledged chicks when parents are constrained to leave colonies for pre-moult fattening (Crawford *et al.* 2018).

Cape Gannet

In Namibia, the Cape Gannet population decreased by 95% after the collapse of that country's sardine stock in the 1970s (Figure 2, Crawford 2007). However, at the same time the numbers of gannets in South Africa increased. Trends in the proportions of forage fish (sardine and anchovy) and gannets found

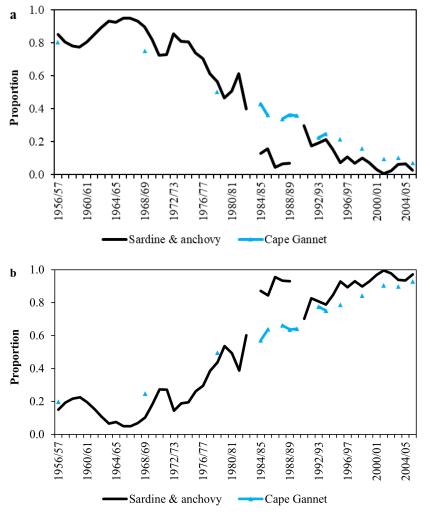


Figure 3: Trends in the proportions of the Benguela ecosystem's sardine and anchovy and Cape Gannet found in a) Namibia and b) South Africa, 1956/1957–2005/2006 (redrawn from information in Crawford et al 2007a).

in Namibia and in South Africa were similar (Figure 3) suggesting an impact of food. However, increases of gannets in South Africa did not offset losses in Namibia so that the overall abundance of Cape Gannets deceased (Crawford *et al.* 2007a).

In the 21st century, the movement of Cape Gannets to the south and east continued with a decrease in numbers breeding off west South Africa and an increase in Algoa Bay, matching a shift in the distribution of their prey (Crawford et al. 2015, Sherley et al. 2019). In the west, foraging effort of Cape Gannets increased and nest attendance decreased with reduced consumption of sardine and anchovy, and adult body condition was negatively impacted by increases in the dietary proportion of hake Merluccius sp. discarded by fisheries (Cohen et al. 2014). At Malgas Island, Cape Gannets had substantially reduced breeding success when they fed their chicks mainly low-quality fish discards (Grémillet et al. 2008). Between 2011 and 2014 there was a net deficit in energy expenditure during foraging for most Cape Gannets tracked from Malgas Island (Grémillet et al. 2016).

Cape Cormorant

In Namibia, numbers of Cape Cormorants decreased by 62% after the collapse of sardine in the 1970s (Figure 2). It was a lesser decrease and occurred later than those of African Penguins and Cape Gannets, possibly owing to Cape Cormorants benefitting from increased breeding space at Ichaboe Island and making use of alternative prey in the form of bearded goby (Crawford 2007, Crawford et al. 2007b, Erasmus et al. 2021). Additionally artificial nesting platforms constructed in central Namibia provided breeding habitat for Cape Cormorants closer to the reduced range of the sardine (Crawford 2007). By contrast, gannets and most penguins in Namibia bred in the south and suffered food shortages as the sardine's range contracted northwards (Crawford 2007). Cape Cormorants colonised Ilha dos Tigres in southern Angola in the 2000s and > 16,000 pairs bred there in 2017 (Mendelsohn and Haraes 2018).

Unlike in Namibia, numbers of Cape Cormorants breeding in west South Africa decreased in the mid-1990s *prior to* recent decreases in that region of African Penguins and Cape Gannets (Crawford *et al.* 2007b). There were substantial mortalities of adult Cape Cormorants at several colonies in west South Africa between 1991 and 2006 caused by avian cholera *Pasteurella multocida*, outbreaks of which may be triggered by stressful events such as food limitation (Crawford *et al.* 1992a, Ward and Williams 2004, Waller and Underhill 2007). The initial occurrence of avian cholera at Dassen Island may have been precipitated by a scarcity of forage fish during 1989 and 1990 (Crawford *et al.* 1992a).

Conforming to the recent shift in the distribution of sardine and anchovy, Cape Cormorants decreased off northwest South Africa but remained stable in the south, where new colonies formed (including at Robben Island and Stony Point) and some others increased (Crawford *et al.* 2016).

When food is scarce, as well as experiencing increases in adult mortality, Cape Cormorants, like some other cormorant species, often skip or abandon breeding or delay their first breeding attempt (Berry 1976, Crawford et al. 2001b, 2016, Crawford and Dyer 1995). They may also suffer extensive breeding failure (Duffy et al. 1984, Crawford et al. 1992b). In November 2008, Cape Cormorants brooding small chicks expended significantly greater foraging effort at Malgas and Dassen islands than at Dyer Island farther south (Hamann et al. 2012). During May and June 2014 Cape Cormorants north of Cape Town attempted to take bait from hand-lines used to fish for snoek Thyrsites atun, a behaviour not previously observed and that suggested poor food availability at that time (Crawford et al. 2016).

Bank Cormorant

In Namibia, Bank Cormorants decreased from 7,166 pairs in 1978-1980 to 3,735 pairs in 1995-1997; a severe reduction of bearded goby in central Namibia in 1994 was a probable cause of the decrease (Crawford et al. 1999a). In South Africa, Bank Cormorants decreased from 1,506 pairs in 1978-1980 to 846 pairs in 2010-2013 (Crawford et al. 2015). Total numbers breeding at 11 readily accessible localities between Lambert's Bay and Dyer Island fell from above 500 pairs during 1978-1987 to 350 pairs from 1995 to 2006. The most northern colony (Lambert's Bay) was extinct by 1999 and there were substantial decreases at the two largest colonies, Malgas and Dassen islands, which are north of Cape Town. There was fluctuating growth at Robben Island, near Cape Town, where birds were oiled by spills in 1994 (Apollo Sea) and 2001 (Treasure). Farther east numbers at two colonies increased. These trends are consistent with a reduced abundance of rock lobsters in the north and an expansion of this resource to the east (Crawford et al. 2008). As with other endangered species, fishing in the immediate vicinity of Malgas and Dassen islands may have reduced densities of lobsters below levels needed to sustain the larger colonies of Bank Cormorants. Where rock lobsters had not been severely depleted, Bank Cormorants showed a positive response to their local availability and modelling suggested that areas with no-take of lobsters at 20-30 km around Bank Cormorant colonies would benefit the conservation of this seabird (Sherley et al. 2017).

COLONY VIABILITY AND ALLEE EFFECTS

Traditionally, the Benguela's four Endangered seabirds bred in large colonies and those three that feed mostly on sardine and anchovy have often foraged in large multi-species flocks (Hockey *et al.* 2005). However, as populations have fallen, breeding colonies have decreased in size and on occasion fragmented into smaller units (e.g. Cordes *et al.* 1999, Crawford *et al.* 2016, Sherley *et al.* 2019).

The probabilities of extinctions of different-sized colonies of African Penguins over 40 years were obtained from empirical observations on the performance of 41 discrete colonies in southern Namibia from 1956–1996 (Crawford *et al.* 2001a). Only one (< 4 %) of 28 colonies that in 1956 had ≤ 50 pairs was extant in 1996, compared to 26% of those having 251–1,000 pairs, 67% of those having 1,001–5,000 pairs and 100% of those with > 5,000 pairs (Figure 4). Whereas three of the 30 breeding colonies extant in 2004 held > 5,000 pairs and, in terms of these probabilities, had no likelihood of extinction within 40 years, by 2019 none of the 25 remaining colonies had > 5,000 pairs so that all had some chance of extinction during such a period. In

2019, fifteen colonies had < 250 pairs and hence a 96% chance of extinction by 2059 (Figure 4). In 2019, only seven colonies held > 1,000 pairs and had a 67% probability of surviving to 2059: Mercury Island in Namibia; Dassen, Robben, Dyer, St Croix and Bird (Algoa Bay) islands and Stony Point in South Africa.

Fragmented seabird populations may suffer from Allee effects, i.e. reduced fitness at low population size increasing their likelihood of extinction (Ryan et al. 2012). African Penguins that feed in groups have a higher catch of prey per unit effort than solitary birds (McInnes et al. 2017), but colonies may become too small for sufficient foraging groups to form (Ryan et al. 2012). For example, in 2012 more penguins were documented foraging in a single flock of at least 158 birds (Ryan et al. 2012) than were breeding in 2019 at 10 of the 25 presumed extant African Penguin colonies. For plunge-diving Cape Gannets, highly-synchronised prey pursuits, which are likely contingent on their ability to locate an adequate number of conspecifics at sea, benefitted foraging efficiency when feeding on sardine schools (Thiebault et al. 2016). A lower number of individuals could also decrease the role of colonies as

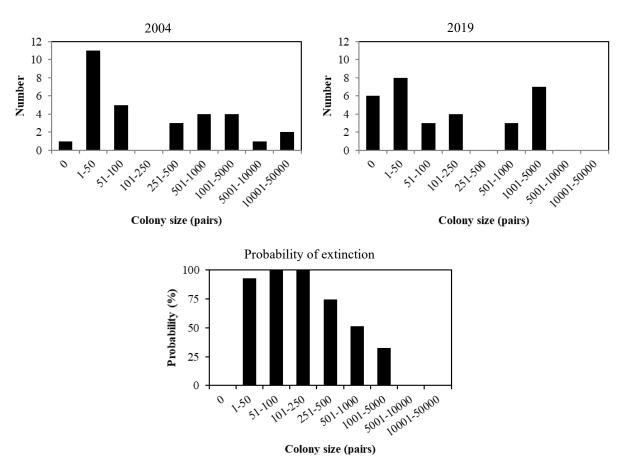


Figure 4: Top: numbers of African Penguin colonies of different sizes in 2004 (left) and 2019 (right). Numbers of colonies where breeding occurred since 1956 that were extinct in 2004 and 2019 are indicated by colony size = 0. Bottom: probabilities of extinction over a 40-y period of African Penguin colonies of different sizes derived from empirical information in Crawford et al. (2001a).

information centres, or the possibility to use conspecifics as cues to locate prey (e.g. Thiebault *et al.* 2016). Again smaller colonies have a larger proportion of birds nesting at colony edges, where eggs and chicks are at a greater risk to predation (e.g. Cordes *et al.* 1999), and sex-biased mortality (e.g. Pichegru and Parsons 2014) may decrease productivity of monogamous breeders at small colonies. The higher risks of extinction for small colonies make it imperative to maintain colony sizes above thresholds at which Allee effects are manifest. Furthermore, seabirds that have a late age at maturity may take substantial periods to recover from small numbers, even with fishery closures (e.g. Robinson *et al.* 2015).

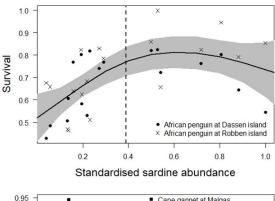
In 2010, Mercury Island held 72% of the global population of Bank Cormorants (Roux and Kemper 2015) and 73% of Namibia's African Penguins (Crawford et al. 2013). In 2018, c. 70% of the overall Cape Gannet population was at Bird Island, Algoa Bay at the eastern boundary of the Benguela ecosystem (Sherley et al. 2019). In the 2010s, 54% of South Africa's Cape Cormorants bred at Dyer Island (Crawford et al. 2016). Such congregations of large proportions of a species at a single locality may offset allee effects but render the species highly susceptible to local catastrophic events such as oil spills (e.g. Crawford et al. 2000), disease outbreaks (e.g. Waller and Underhill 2007), severe weather events (e.g. Randall et al. 1986) and reduced availability of resources.

FORAGE THRESHOLDS

Forage abundance thresholds

In a meta-analysis of long-term studies in seven marine ecosystems from around the globe, Cury *et al.* (2011) demonstrated key thresholds in prey (fish and krill) abundance, below which seabirds dependent on that food type suffered reduced and more variable breeding productivity. The threshold was equal to the long-term average biomass of prey and equivalent to one-third of the maximum observed prey biomass. Similar relationships were established for 13 of the 14 seabirds studied, including African Penguin and Cape Gannet from the Benguela ecosystem. The so-called "1/3 for the birds" rule provides a benchmark for management of forage fish fisheries at a level that would sustain seabird productivity over the long-term (Cury *et al.* 2011).

In a related study, Robinson *et al.* (2015) showed that annual mortality of adult African Penguins at Robben Island increased markedly when the biomass of sardine aged 1 y or older off west South Africa fell below 25% of its maximum value. The lower forage threshold observed for adult mortality (25%) than for breeding success (33%) confirmed the theoretical



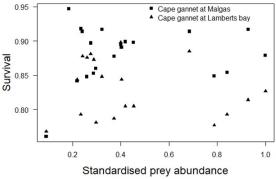


Figure 5: Estimated adult survival off west South Africa of (top) African Penguins at Dassen Island and Robben Island and (bottom) Cape Gannets at Lambert's Bay and Malgas Island compared with the standardised abundance of prey off west South Africa (i.e. centered and scaled by dividing by the standard deviation). Estimates of survival were from Sherley et al. (2014) for African Penguins and Distiller et al. (2012) for Cape Gannets. Estimates of prey abundance were updated from Cury et al. (2011). The prediction (and 95% confidence interval) of the GAM is indicated with the black curve (and grey polygon) for African Penguins. The vertical dashed line represents the threshold below which adult survival decreased markedly with decreasing sardine abundance. For Cape Gannets, no significant relationship was found between adult survival and prey (sum of anchovy and sardine) abundance.

prediction of Cairns (1987) that decreases in forage abundance would influence seabird breeding success ahead of survival. When data for African Penguins at Dassen and Robben islands were grouped, a generalised additive model (GAM) showed that adult survival decreased when standardised (i.e. centred and scaled) sardine abundance off west South Africa fell below a threshold of zero (Figure 5).

It is noteworthy that off west South Africa, Cape Gannets were better able to buffer effects of reduced prey abundance than African Penguins (Distiller *et al.* 2012, Sherley *et al.* 2014, Robinson *et al.* 2015). After an eastward displacement of the main forage resources and the collapse of sardine (Coetzee *et al.* 2008), adult gannets, due to their movement capabilities, were able to feed on alternative food,

such as saury *Scomberesox saury* and hake offal (Grémillet *et al.* 2008, 2019, Crawford *et al.* 2014, 2019). Consequently, their survival was unrelated to standardised estimates of the overall abundance of sardine and anchovy (Figure 5).

Forage consumption thresholds

Saraux et al. (2021) investigated thresholds for the consumption of forage fish stocks by seabirds in five marine ecosystems: off Norway, South Africa, Peru, in the Baltic Sea (Sweden) and at Shetland (Scotland). In each of these systems, the predation pressure, estimated as the proportion of a forage fish stock consumed by seabirds, was generally small (median = 1% of biomass) but increased sharply when prey biomass decreased below a threshold of 15 to 18% of its maximum recorded value. A threshold of 18% was considered a limit not to be reached in order to avoid a sharp rise in the natural mortality rate of forage fish resources, and below which extra cautious management of fisheries would be required (Saraux et al. 2021). Similarly, Essington et al. (2015) advised that a risk-based management scheme that reduces fishing when populations become scarce would protect both forage fish and their predators from collapse, with little effect on long-term average catches.

OTHER FORAGE CONSIDERATIONS

Forage quality

Condition of prey may influence its ability to sustain predator populations in addition to its abundance (e.g. Grémillet et al. 2008). For example, poor food quality likely caused unprecedented breeding failures at many seabird colonies on the east coast of Great Britain in 2004 (Wanless et al. 2005), decreased mass at fledging of Common Guillemots (Murres) Uria aalge in the Baltic Sea and brought about breeding failures and mass mortality of this species in the Northeast Pacific in 2015-2016 (Osterblom et al. 2006, Piatt et al. 2020). In South Africa, the condition of sardine deteriorated in the 2000s (Ndjaula et al. 2013), possibly contributing to some of the seabird population decreases. As also mentioned above, reliance on fish offal as a food source reduced Cape Gannet chick survival (Grémillet et al. 2008).

Fisheries mortality

In addition to contributing to collapses of forage resources (e.g. Essington *et al.* 2015), fishing may cause localised depletion of prey; as such, the fisheries mortality rate (F) can be employed as another management threshold. For example, the performance of three species of *Pygoscelis* penguins breeding near the Antarctic Peninsula was reduced when local harvest rates of Antarctic krill *Euphausia*

superba were $\geq 10\%$ of the estimated biomass (Watters et al. 2020). By comparison, the exploitation rate of South Africa's sardine west of Cape Agulhas increased substantially after 1999 and reached 44% in 2006 (Coetzee et al. 2008). Spatially explicit thresholds in fishing mortality need to be carefully defined to assist in management of fish stocks so as to support viable seabird populations in the Benguela system.

Forage availability

It is not only the absolute abundance of prey but also its availability that impacts energy acquisition, demography and population trends of seabirds. For example, Crawford et al. (2019) used long-term information on the diet of Cape Gannets off west South Africa to derive an index of the availability of anchovy and sardine per unit biomass to seabirds in that region, terming it a Forage Availability Index (FAI). The study demonstrated a substantial decrease in the availability of anchovy and sardine to seabirds in the 2000s compared to the 1990s. Breeding numbers of Cape Gannets and Cape Cormorants and survival of adult African Penguins at both Dassen and Robben islands were significantly related to the FAI. For gannets, the numbers breeding increased when the FAI, which increases as anchovy and sardine contribute more to the diet, was > c. -1 and for cormorants when it was > c. 1. The higher threshold for Cape Cormorants than Cape Gannets at which numbers breeding were predicted to increase probably resulted from the fact that, unlike Cape Gannets but similarly to African Penguins, Cape Cormorants are mostly unable to access alternative food such as saury and hake offal (Crawford et al. 2019). Notably, frequent aggregations of anchovy close to the seabed were thought to have reduced their availability to purse-seiners, and were suggested as a reason for a large under-catch of the total allowable catch (TAC) of anchovy in recent years (DAFF 2016).

The importance of prey depth was highlighted in a modelling study from the Humboldt upwelling system off western South America, where it primarily determined foraging success of Peruvian Boobies *Sula variegata* and Guanay Cormorants *P. bougainvilliorum*, which feed mainly on Peruvian anchoveta *Engraulis ringens* (Boyd *et al.* 2017). Peruvian Boobies and Guanay Cormorants are the ecological equivalents in that system of Cape Gannets and Cape Cormorants in the Benguela system (Crawford *et al.* 2006b).

African Penguins and other diving piscivores may herd prey shoals upwards, thereby facilitating their availability to surface-feeding predators (e.g. McInnes and Pistorius 2019). Hence their loss will influence ecosystem functioning.

POSSIBLE INTERVENTIONS TO ENHANCE FOOD AVAILABILITY

Various international agreements participating parties to implement an ecosystembased approach to fisheries management (EAF). For example, the Code of Conduct for Responsible Fisheries of the United Nations' Food and Agriculture Organisation, adopted in 1995, stated that Management measures should not only ensure the conservation of target species but also of species belonging to the same ecosystem or associated with or dependent upon the target species (http://www. fao.org/3/v9878e/v9878e00.htm). The sixth Aichi Target of the Convention on Biological Diversity's Strategic Plan for Biodiversity 2011–2020 reads: By 2020 all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species and ecosystems are within safe ecological limits (https://www.cbd.int/convention/text/default.shtml). In South Africa, the Marine Living Resources Act of 1988 attempts to provide legislative support for the EAF but is in urgent need of updating and further amendment better to achieve this (Cochrane et al. 2015).

One tool available to manage fisheries so as to avoid harmful impacts on associated or dependent species (ADS) is marine spatial planning, for example the implementation of fishing closures around important seabird colonies (e.g. Ludynia et al. 2012, Sherley et al. 2015, 2018). In northeast Scotland, Black-legged Kittiwakes Rissa tridactyla benefitted from closure of fishing for sandeels Ammodytes marinus, an important prey for kittiwakes, around breeding colonies (Daunt et al. 2008, Furness 2020). In the Californian upwelling ecosystem off west North America, a precautionary ecosystem approach that avoids localised depletion of forage resources (including anchovy and sardine) near predator concentrations is deemed necessary. In 1983, nearshore (within 3 to 6 km of the coast) fishing for anchovy was prohibited, the main objectives being to protect pre-recruit anchovy, live bait and recreational fisheries, and predator forage (Pacific Fisheries Management Council 1983, Thayer and Sydeman 2020). At the time, the anchovy-dependent Brown Pelican Pelecanus occidentalis was listed as Federally Endangered in USA (Anderson et al. 1982). In the Humboldt upwelling ecosystem off west South America, fishing for Peruvian anchoveta close to a Peruvian Booby colony increased the birds' foraging effort. The more the fishery reduced the quantity of anchoveta in the area, the farther the breeding boobies needed to forage from the colony to find food (Bertrand *et al.* 2012). In the Benguela system, in which similarly to the California and Humboldt systems sardine and anchovy are key forage resources, short-term fishery closures around African Penguin colonies, even though not matched to the late age at recruitment and high mate and site fidelity of the penguins (Crawford *et al.* 2013), have increased breeding productivity and deceased parental foraging costs (Pichegru *et al.* 2010, Sherley *et al.* 2015, 2018, Sydeman *et al.* 2021).

A second means to account for the foraging requirements of marine predators is the identification and implementation of ecosystem thresholds, below which fishing would be prohibited. Ecosystem thresholds have already been widely applied to minimise by-catch mortality of ADS in fisheries (e.g. Rollinson *et al.* 2017, Da Rocha *et al.* 2021) and are increasingly proposed as means to ensure sufficient quantities of prey for predators, such as seabirds (e.g. Cury *et al.* 2011, Smith *et al.* 2011, Sydeman *et al.* 2017, Hill *et al.* 2020). In the Californian upwelling ecosystem, a harvest rule disallows fishing of sardine when its biomass is below 150,000 metric tonnes (Pacific Fisheries Management Council 2003, Thayer and Sydeman 2020).

A third mechanism to achieve adequate food for seabirds is to offset mismatches in the distributions of the breeding localities and the prey of seabirds through establishment of colonies nearer to the food supply. Guano platforms in Namibia served this purpose for Cape Cormorants (Crawford 2007) and an attempt to establish a new African Penguin colony in South Africa closer to the present distributions of sardine and anchovy has been initiated (BirdLife South Africa 2016).

Recommendations from the 2020 AEWA Benguela Current Forage Fish Workshop

In November 2020, a *Benguela Current Forage Fish* (BCFF) Workshop, organised by the African-Eurasian Migratory Waterbird Agreement (AEWA), in collaboration with the Benguela Current Convention (BCC) and BirdLife South Africa, recommended actions to be undertaken as a matter of urgency under the auspices of BCC, AEWA and the AEWA Benguela Coastal Seabird International Working Group, as well as by the national governments of Angola, Namibia and South Africa. These included:

 developing tools to increase the availability of sufficient forage [fish] for threatened endemic Benguela seabird species, such as setting ecosystem thresholds (i.e. sizes of forage resource populations below which a range of precautionary measures relating to fishing would be implemented at various spatial scales)

- and closing key foraging areas to fishing, adjacent to major seabird colonies;
- ensuring the existence or creation of suitable seabird breeding habitat within the contracted or altered distributions of forage fish species to partially alleviate the impact of an altered distribution of prey on affected seabird species;
- and facilitating and prioritising the recovery of seabird colonies to sufficient sizes to minimise known and potential Allee effects, thus reducing the probability of colony extinctions (AEWA 2020).

CONCLUSION

In conclusion, it is apparent that food limitation has been a major driver of adverse trends in the population sizes and conservation status of four Benguela seabirds that compete with fisheries for food. Hence it will be important to manage the impact of fisheries on the availability of prey to these seabirds, including through the use of measures that were successfully applied elsewhere or that have empirical support for use in the Benguela ecosystem.

ACKNOWLEDGEMENTS

We are grateful to F Dakwa for drawing Figure 1, to W Froneman and a second reviewer for constructive comments on a draft manuscript, and to all persons and organisations who contributed to collecting and analysing data used in this paper. The paper is an output of the BCC's marine top predator working group (BECUMATOP).

REFERENCES

- Adams NJ, Seddon PJ, van Heezik YM. 1992. Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment? *South African Journal of Marine Science* 12: 959–974.
- AEWA. 2020. Benguela Current Forage Fish Workshop recommendations: 4 pp.
- Anderson DW, Gress F, Mais KF. 1982. Brown Pelicans: influence of food supply on reproduction. *Oikos* 39: 23–31
- Berry HH. 1976. Physiological and behavioural ecology of the Cape cormorant *Phalacrocorax capensis*. *Madoqua* 9: 5–55.
- Bertrand S, Joo R, Arbulu C, Tremblay Y, Barbraud C, Weimerskirch H. 2012. Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology* 49: 1168–1177.
- BirdLife South Africa. 2016. Proposal to re-establish an African Penguin colony at De Hoop Nature Reserve. BirdLife South Africa, Cape Town: 18 pp.
- Boyd C, Grünbaum D, Hunt GL, Punt AE, Weimerskirch H, Bertrand S. 2017. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. *Journal of Applied Ecology* 54: 1362–1372.
- Cairns DK. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.

- Campbell KJ, Steinfurth A, Underhill LG, Coetzee JC, Dyer BM, Ludynia K, Makhado AB, Merkle D, Rademan J, Upfold L, Sherley RB. 2019. Local forage fish abundance influences foraging effort and offspring condition in an endangered marine predator. *Journal of Applied Ecology* 13409: 1365–2664.
- Cochrane KL, Joyner J, Sauer WHH, Swan J. 2015. An evaluation of the Marine Living Resources Act and supporting legal instruments as a framework for implementation of an ecosystem approach to fisheries in South Africa. *African Journal of Marine Science* 37: 437–456.
- Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP. 2008. Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science* 65: 1676–1688.
- Cohen LA, Pichegru L, Grémillet D, Coetzee J, Upfold L, Ryan PG. 2014. Changes in prey availability impact foraging behaviour and fitness of Cape gannets over a decade. *Marine Ecology Progress Series* 505: 281–293.
- Cordes I, Crawford RJM, Williams AJ, Dyer BM. 1999. Decrease of African Penguins at the Possession Island group, 1956–1995 contrasting trends for colonial and solitary breeders. *Marine Ornithology* 27: 117–126.
- Crawford RJM. 1998. Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. *South African Journal of Marine Science* 19: 355–364.
- Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* 148 (Suppl 2): S253–S260.
- Crawford RJM, Dyer BM. 1995. Responses by four seabirds to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.
- Crawford RJM, Shelton PA. 1978. Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. *Biological Conservation* 14: 85–109.
- Crawford RJM, Cruickshank RA, Shelton PA, Kruger I. 1985. Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. South African Journal of Marine Science 3: 215–228.
- Crawford RJM, Allwright DM, Heyl CW. 1992a. High mortality of Cape Cormorants (*Phalacrocorax capensis*) off western South Africa in 1991 caused by *Pasteurella multocida*. *Colonial Waterbirds* 15: 236–238.
- Crawford RJM, Underhill LG, Raubenheimer CM, Dyer BM, Martin J. 1992b. Top predators in the Benguela ecosystem implications of their trophic position. *South African Journal of Marine Science* 12: 675–687.
- Crawford RJM, Dyer BM, Cordes I, Williams AJ. 1999a. Seasonal pattern of breeding, population trend and conservation status of bank cormorants *Phalacrocorax neglectus* off southwestern Africa. *Biological Conservation* 87: 49–58.
- Crawford RJM, Shannon LJ, Whittington PA. 1999b. Population dynamics of the African Penguin at Robben Island. *Marine Ornithology* 27: 135–143.
- Crawford RJM, Davis SA, Harding R, Jackson LF, Leshoro TM, Meÿer MA, Randall RM, Underhill LG, Upfold L, Van Dalsen AP, Van der Merwe E, Whittington PA, Williams AJ, Wolfaardt AC. 2000. Initial impact of the *Treasure* oil spill on seabirds off western South Africa. South African Journal of Marine Science 22: 157–176.
- Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux J-P, Underhill LG, Ward VL,

- Williams AJ, Wolfaardt AC. 2001a. African Penguins as predators and prey coping (or not) with change. *South African Journal of Marine Science* 23: 435–447.
- Crawford RJM, Dyer BM, Upfold L, Ward VL. 2001b. Age at first breeding of Bank, *Phalacrocorax neglectus*, and Cape Cormorants, *P. capensis. Ostrich* 72: 145–148.
- Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L. 2006a. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation* 132: 119–125.
- Crawford RJM, Goya E, Roux J-P, Zavalaga CB. 2006b. Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems. *African Journal of Marine Science* 28: 553–560.
- Crawford RJM, Dundee BL, Dyer BM, Klages NTW, Meÿer MA, Upfold L. 2007a. Trends in numbers of Cape gannets (*Morus capensis*), 1956/57–2005/06, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science* 64: 169–177.
- Crawford RJM, Dyer BM, Kemper J, Simmons RE, Upfold L. 2007b. Trends in numbers of Cape Cormorants (*Phalacrocorax capensis*) over a 50-year period, 1956–57 to 2006–07. *Emu* 107: 253–261.
- Crawford RJM, Cockroft AC, Dyer BM, Upfold L. 2008. Divergent trends in bank cormorants *Phalacrocorax neglectus* breeding in South Africa's Western Cape consistent with a distributional shift of rock lobsters *Jasus lalandii*. *African Journal of Marine Science* 30: 161–166.
- Crawford RJM, Altwegg R, Barham BJ, Barham PJ, Durant JM, Dyer BM, Geldenhuys D, Makhado AB, Pichegru L, Ryan PG, Underhill LG, Upfold L, Visagie J, Waller LJ, Whittington PA. 2011. Collapse of South Africa's penguins in the early 21st century: a consideration of food availability. *African Journal of Marine Science* 33: 139–156.
- Crawford RJM, Kemper J, Underhill LG. 2013. African Penguin (*Spheniscus demersus*). In: Garcia Borboroglu P, Boersma PD (eds), Penguins Natural History and Conservation. University of Washington Press, Seattle and London: 211–231.
- Crawford RJM, Makhado AB, Waller LJ, Whittington PA. 2014. Winners and losers responses to recent environmental change by South African seabirds that compete with purse-seine fisheries for food. *Ostrich* 85: 111–117.
- Crawford RJM, Makhado AB, Whittington PA, Randall RM, Oosthuizen WH, Waller LJ. 2015. A changing distribution of seabirds in South Africa the possible impact of climate and its consequences. *Frontiers in Ecology and Evolution* 3: 10, 1–10.
- Crawford RJM, Randall RM, Cook TR, Ryan PG, Dyer BM, Fox R, Geldenhuys D, Huisamen J, McGeorge C, Upfold L, Visagie J, Waller LJ, Whittington PA, Wilke CG, Makhado AB. 2016. Cape cormorants decrease, move east and adapt foraging strategies following eastward displacement of their main prey. *African Journal of Marine Science* 38: 373–383.
- Crawford RJM, Makhado AB, Oosthuizen WH. 2018. Bottom-up and top-down control of the Benguela ecosystem's seabirds. *Journal of Marine Systems* 188: 133–141.
- Crawford RJM, Sydeman WJ, Thompson SA, Sherley RB, Makhado AB. 2019. Food habits of an endangered seabird indicate recent poor availability of abundant

- forage resources. *ICES Journal of Marine Science* 76: 1344–1352.
- Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T, Crawford RJM, Furness RW, Mills JA, Murphy EJ, Österblom H, Paleczny M, Piatt JF, Roux J-P, Shannon L[J], Sydeman WJ. 2011. Global seabird response to forage fish depletion one-third for the birds. *Science* 334: 1703–1706.
- Da Rocha N, Oppel S, Prince S, Matjila S, Shaanika TM, Naomab C, Yates O, Paterson JRB, Shimooshili K, Frans E, Kashava S, Crawford R. 2021. Reduction in seabird mortality in Namibian fisheries following the introduction of bycatch regulation. *Biological Conservation* 253: 108915.
- DAFF (Department of Agriculture, Forestry and Fisheries). 2016. Status of the South African Marine Fishery Resources 2016. Cape Town, DAFF.
- Daunt F, Wanless S, Greenstreet SPR, Jensen H, Hamer KC, Harris MP. 2008. The impact of the sandeel fishery closure on seabird food consumption, distribution, and productivity in the northwestern North Sea. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 362–381.
- Distiller G, Altwegg R, Crawford RJM, Klages NTW, Barham B. 2012. Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape Gannet. *Marine Ecology Progress Series* 461: 245–255.
- Duffy DC, Berruti A, Randall RM, Cooper J. 1984. Effects of the 1982–3 warm water event on the breeding of South African seabirds. *South African Journal of Science* 80: 65–69.
- Durant JM, Crawford RJM, Wolfaardt AC, Agenbag CJ, Visagie J, Upfold L, Stenseth NC. 2010. Influence of feeding conditions on breeding of African penguins importance of adequate local food supplies. *Marine Ecology Progress Series* 420: 263–271.
- Dyer BM, Cooper J, Crawford RJM, Sherley RB, Somhlaba S, Cockcroft A, Upfold L, Makhado AB. 2019. Geographical and temporal variation in the diet of Bank Cormorants *Phalacrocorax neglectus* in South Africa. *Ostrich* 90: 373–390.
- Erasmus VE, Currie B, Roux J-P, Elwen SH, Kalola MS, Tjizoo B, Kathena JN, Iitembu JA. 2021. Predatory species left stranded following the collapse of the sardine *Sardinops sagax* (Pappe, 1854) stock off the northern Benguela upwelling system: a review. *Journal of Marine Systems* 224: 103623.
- Essington TE, Moriarty PE, Froehlich HE, Hodgson EE, Koehn LE, Oken KL, Siple MC, Stawitz CC. 2015. Fishing amplifies forage fish population collapses. *PNAS* 112: 6648–6652.
- Furness RW. 2020. Sandeel stocks and seabirds in the North Sea. *AEWA Doc. BCFF Inf.* 6: 12 pp.
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society of London B: Biological Sciences* 275: 1149–1156.
- Grémillet D, Péron C, Kato A, Amélineau F, Ropert-Coudert Y, Ryan PG, Pichegru L. 2016. Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem. *Marine Biology* 163: 35.
- Grémillet D, Collet J, Weimerskirch H, Courbin N, Ryan PG, Pichegru L. 2019. Radar detectors carried by Cape

- gannets reveal surprisingly few fishing vessel encounters. *PLoS ONE* 14: e0210328.
- Hamann MH, Grémillet D, Ryan PG, Bonadonna F, van der Lingen CD, Pichegru L. 2012. A hard-knock life: the foraging ecology of Cape cormorants amidst shifting prey resources and industrial fishing pressure. *African Journal of Marine Science* 34: 233–240.
- Hill SL, Hinke J, Bertrand S, Fritz L, Furness, RW, Ianelli JN, Murphy M, Oliveros-Ramos R, Pichegru L, Sharp R, Stillman RA, Wright PJ, Ratcliffe N. 2020. Reference points for predators will progress ecosystem-based management of fisheries. *Fish and Fisheries* 21: 368–378
- Hockey PAR, Dean WRJ, Ryan PG (eds). 2005. Roberts Birds of Southern Africa, 7th edn. John Voelcker Bird Book Fund, Cape Town.
- IUCN. 2021. IUCN Red List version 2021-1. https://www.iucnredlist.org. Downloaded on 17 January 2021.
- Kemper J. 2015. Cape Gannet Morus capensis. In: Simmons RE, Brown CJ, Kemper J (eds), Birds to watch in Namibia. Red, rare and endemic species. Windhoek, Namibia: Ministry of Environment and Tourism and Namibia Nature Foundation. pp 149–151.
- Ludynia K, Jones R, Kemper J, Garthe S, Underhill LG. 2010a. Foraging behaviour of bank cormorants in Namibia: implications for conservation. *Endangered Species Research* 12: 31–40.
- Ludynia K, Roux JP, Jones R, Kemper J, Underhill LG. 2010b. Surviving off junk: low-energy prey dominates the diet of African penguins Spheniscus demersus at Mercury Island, Namibia, between 1996 and 2009. African Journal of Marine Science 32: 563–572.
- Ludynia K, Kemper J, Roux J-P. 2012. The Namibian Islands' Marine Protected Area: using seabird tracking data to define boundaries and assess their adequacy. *Biological Conservation* 156: 136–145.
- Ludynia K, Waller LJ, Sherley RB, Abadi F, Galada Y, Geldenhuys D, Crawford RJM, Shannon LJ, Jarre A. 2014. Processes influencing the population dynamics and conservation of African penguins on Dyer Island, South Africa. African Journal of Marine Science 36: 253–267.
- McInnes AM, Pistorius PA. 2019. Up for grabs: prey herding by penguins facilitates shallow foraging by volant seabirds. *Royal Society open science* 6: 190333.
- McInnes AM, McGeorge C, Ginsberg S, Pichegru L, Pistorius PA. 2017. Group foraging increases foraging efficiency in a piscivorous diver, the African penguin. *Royal Society open science* 4: 170918.
- McInnes AM, Ryan PG, Lacerda M, Pichegru L. 2019. Targeted prey fields determine foraging effort thresholds of a marine diver: important cues for the sustainable management of fisheries. *Journal of Applied* Ecology 56: 2206–2215.
- Mendelsohn JM, Haraes L. 2018. Aerial census of Cape Cormorants and Cape Fur Seals at Baía dos Tigres, Angola. *Namibian Journal of Environment* 2 Section A: 1–6.
- Ndjaula HO, Gerow KG, van der Lingen CD, Moloney CL, Jarre A. 2013. Establishing a baseline for evaluating changes in body condition and population dynamics of sardine (*Sardinops sagax*) in the southern Benguela ecosystem. *Fisheries Research* 147: 253–263.
- Osterblom H, Casini M, Olsson O, Bignert A. 2006. Fish, seabirds and trophic cascades in the Baltic Sea. *Marine Ecology Progress Series* 323: 233–238.

- Pacific Fisheries Management Council. 1983. Northern Anchovy Fishery Management Plan Amendment 5. Portland, Oregon, 229 pp.
- Pacific Fisheries Management Council. 2003. Allocation of the Pacific Sardine Harvest Guideline – Coastal Pelagic Species Fishery Management Plan Amendment 11. Portland, Oregon, 48 pp.
- Piatt JF, Parrish JK, Renner HM, Schoen SK, Jones TT, Arimitsu ML, Kuletz KJ, Bodenstein B, García-Reyes M, Duerr RS, Corcoran RM, Kaler RSA, McChesney GJ, Golightly RT, Coletti HA, Suryan RM, Burgess HK, Lindsey J, Lindquist K, Warzybok PM, Jahncke J, Roletto J, Sydeman WJ. 2020. Extreme mortality and reproductive failure of common murres resulting from the northeast Pacific marine heatwave of 2014-2016. *PLoS ONE* 15: e0226087.
- Pichegru L, Parsons NJ. 2014. Female-biased mortality in African penguins. *African Journal of Marine Science* 36: 279–282
- Pichegru L, Grémillet D, Crawford RJM, Ryan PG. 2010. Marine no-take zone rapidly benefits Endangered penguin. *Biology Letters* 6: 498–501.
- Pichegru L, Ryan PG, van Eeden R, Reid T, Grémillet D, Wanless R. 2012. Industrial fishing, no-take zones and endangered penguins. *Biological Conservation* 156: 117–125.
- Pollet IL, Ronconi RA, Leonard ML, Shutler D. 2019. Migration routes and stopover areas of Leach's Storm Petrels *Oceanodroma leucorhoa*. *Marine Ornithology* 47: 55–65.
- Randall RM, Randall BM, Erasmus T. 1986. Rain-related breeding failures in Jackass Penguins. *Gerfaut* 76: 281–288.
- Robinson WML, Butterworth DS, Plaganyi EE. 2015. Quantifying the projected impact of the South African sardine fishery on the Robben Island penguin colony. *ICES Journal of Marine Science* 72: 1822–1833.
- Rollinson DP, Wanless RM, Ryan PG. 2017. Patterns and trends in seabird bycatch in the pelagic longline fishery off South Africa. *African Journal of Marine Science* 39: 9–25.
- Roux J-P, Kemper J. 2015. Bank Cormorant *Phalacrocorax neglectus*. In: Simmons RE, Brown CJ, Kemper J (eds). Birds to watch in Namibia: red, rare and endemic species. Ministry of Environment and Tourism and Namibia Nature Foundation, Windhoek: 155–157.
- Ryan PG, Edwards L, Pichegru L. 2012. African penguins *Spheniscus demersus*, bait balls and the Allee effect. *Ardea* 100: 89–94.
- Saraux C, Sydeman W, Piatt J, Anker-Nilssen T, Hentati-Sundberg J, Bertrand S, Cury P, Furness RW, Mills JA, Österblom H, Passuni G, Roux J-P, Shannon LJ, Crawford RJM. 2021. Seabird-induced natural mortality of forage fish varies with fish abundance: evidence from 5 ecosystems. *Fish and Fisheries* 22: 262–279.
- Shelton PA, Crawford RJM, Cooper J, Brooke RK. 1984. Distribution, population size and conservation of the Jackass penguin *Spheniscus demersus*. *South African Journal of Marine Science* 2: 217–257.
- Sherley RB, Underhill LG, Barham BJ, Barham PJ, Coetzee JC, Crawford RJM, Dyer BM, Leshoro TM, Upfold L. 2013. Influence of local and regional prey availability on breeding performance of African penguins *Spheniscus demersus*. *Marine Ecology Progress Series* 473: 291–301.
- Sherley RB, Abadi F, Ludynia K, Barham BJ, Clark AE, Altwegg R. 2014. Age-specific survival and movement

- among major African penguin *Spheniscus demersus* colonies. *Ibis* 156: 716–728.
- Sherley RB, Winker H, Altwegg R, van der Lingen CD, Votier SC, Crawford RJM. 2015. Bottom-up effects of a no-take zone on endangered penguin demographics. *Biology Letters* 11: 20150237: 1–4.
- Sherley RB, Botha P, Underhill LG, Ryan PG, van Zyl D, Cockcroft AC, Crawford RJM, Dyer BM, Cook TR. 2017. Defining ecologically-relevant scales for spatial protection using long-term data on an endangered seabird and local prey availability. *Conservation Biology* 31: 1312–1321.
- Sherley RB, Barham BJ, Barham PJ, Campbell KJ, Crawford RJM, Grigg J, Horswill C, McInnes A. Morris TL, Pichegru L, Steinfurth A, Weller F, Winker H, Votier SC. 2018. Bayesian inference reveals positive but subtle effects of experimental fishery closures on marine predator demographics. *Proceedings of the Royal Society* B: 285: 20172443: 1–9.
- Sherley RB, Crawford RJM, Dyer BM, Kemper J, Makhado AB, Masotla M, Pichegru L, Pistorius PA, Roux J-P, Ryan PG, Tom D, Upfold L, Winker H. 2019. The status and conservation of Cape Gannets *Morus capensis*. Ostrich 90: 335–346.
- Simmons RE. 2015a. Caspian Tern *Hydroprogne caspia*. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds to watch in Namibia. Red, rare and endemic species*. Windhoek, Namibia: Ministry of Environment and Tourism and Namibia Nature Foundation. pp 88–90.
- Simmons RE. 2015b. Great White Pelican. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds to watch in Namibia. Red, rare and endemic species.* Windhoek, Namibia: Ministry of Environment and Tourism and Namibia Nature Foundation. pp 173–175.
- Simmons RE, Braby RJ, Braby SJ. 2015. Damara Tern *Sternula balaenarum*. In: Simmons RE, Brown CJ, Kemper J (eds), *Birds to watch in Namibia. Red, rare and endemic species*. Windhoek, Namibia: Ministry of Environment and Tourism and Namibia Nature Foundation. pp 91–95.
- Smith ADM, Brown CJ, Bulman CM, Fulton EA, Johnson P, Kaplan IC, Lozano-Montes H, Mackinson S, Marzloff M, Shannon LJ, Shin Y-J, Tam J. 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science* 333: 1147–1150.
- Sydeman WJ, Thompson SA, Anker-Nilssen T, Arimitsu M, Bennison A, Bertrand S, Boersch-Supan P, Boyd C, Bransome N, Crawford RJM, Daunt F, Furness R,

- Gianuca D, Gladics A, Koehn L, Lang J, Logerwell E, Morris T, Phillips EM, Provencher J, Punt A, Saraux C, Shannon L, Sherley R, Simeone A, Wanless R, Wanless S, Zador S. 2017. Best practices for assessing forage fish fisheries seabird resource competition. *Fisheries Research* 194: 209–221.
- Sydeman WJ, Hunt GL, Pikitch EK, Parrish JK, Piatt JF, Boersma PD, Kaufman L, Anderson DW, Thompson SA, Sherley RB. 2021. South Africa's experimental fisheries closures and recovery of the endangered African penguin. *ICES Journal of Marine Science* 78: 3538–3543.
- Taylor MR, Wanless RM, Peacock F (eds). 2015. The Eskom red data book of birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg.
- Thayer J, Sydeman W. 2020. Implementing ecosystem considerations in California Current forage fisheries. Presentation to AEWA Benguela Current Forage Fish Workshop: 20 pp.
- Thiebault A, Semeria M, Lett C, Tremblay Y. 2016. How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. *Journal of Animal Ecology* 85: 157–167.
- Underhill LG, Crawford RJM, Wolfaardt AC, Whittington PA, Dyer BM, Leshoro TM, Ruthenberg M, Upfold L, Visagie J. 2006. Regionally coherent trends in colonies of African penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987–2005. *African Journal of Marine Science* 28: 697–704.
- Waller LJ, Underhill LG. 2007. Management of avian cholera *Pasturella multocida* outbreaks on Dyer Island, South Africa, 2002–2005. *African Journal of Marine Science* 29: 105–111.
- Wanless S, Harris MP, Redman P, Speakman JR. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.
- Ward VL, Williams AJ. 2004. Coastal killers: causes of seabird mortality. *Bird Numbers* 13: 14–17.
- Watters GM, Hinke JT, Reiss CS. 2020. Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. *Nature Scientific Reports* 10: 2314.
- Whittington, P[A], Klages N[TW], Crawford R[JM], Wolfaardt A[C], Kemper J. 2005. Age at first breeding of the African Penguin. *Ostrich* 76: 14–20.

Staggered towers on parallel transmission lines: a new mitigation measure to reduce collisions of birds, especially bustards

J Pallett¹, RE Simmons², CJ Brown³

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-pallett Published online: 9th February 2022

- ¹ FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town. Present address Southern African Institute for Environmental Assessment, P O Box 6322, Ausspannplatz, Windhoek, Namibia. john.pallett@saiea.com
- ² FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, South Africa
- ³ Namibian Chamber of Environment, P O Box 40723 Ausspannplatz, Windhoek, Namibia

Date received: 31st August 2021; Date accepted: 7th December 2021.

ABSTRACT

Significant numbers of birds are killed annually by flying into power lines across Africa, and numerous attempts have been made to mark lines to make them more conspicuous, to reduce these collisions. Results from surveys reported in this paper and many others indicate that bustards (family Otidae) are most susceptible. Bustard fatalities are not greatly reduced by adding bird diverters to earth wires. Here we propose a new mitigation measure that may reduce the number of mortalities by two-thirds where two power lines run in parallel: staggered towers. Power line surveys in Namibia and South Africa indicate that 87% of 134 bird collisions occurred in and near the middle sections of a span, while only 13% of collisions occurred near the towers themselves. Despite the skull morphology of bustards creating a blind spot immediately ahead of them, it appears that the towers are big enough to be seen (or heard) and avoided. Thus, by aligning power lines of similar size in parallel and as close as technically feasible and staggering the towers such that each tower is aligned with the mid-span of the neighbouring line, the lines may become more visible. This should allow collision-prone birds to gain altitude and fly over the lines. Theoretically, this method is expected to reduce power line fatalities by 67% for each new line. We call for experimental validation of this novel mitigation measure.

Keywords: bird mortalities; Namibia; power lines; span position; South Africa

INTRODUCTION

Power lines strung across the landscape inadvertently create problems for birds, through collisions, electrocutions and displacement from their preferred habitat (Bevanger 1998, Jenkins et al. 2010, Silva et al. 2010, Uddin et al. 2021). Collisions have been identified as particularly problematic for large birds, effectively making the power line grid a network of traps, running to tens of thousands of kilometres of lines in southern Africa alone. By 2007, South Africa's power utility Eskom had 27 770 km of high voltage transmission lines and 325 000 km of distribution lines (Eskom 2007), and in Namibia the current figure is 34 000 km of transmission and distribution lines (Wagner pers. com. 2021). The electricity network will continue to expand, increasing the level of concern for those large birds that are susceptible and known to be threatened by this infrastructure.

An estimated 47 000 Ludwig's Bustards (*Neotis ludwigii*) are killed annually in South Africa by power lines, at a rate of about one bustard per kilometre of line per year (Shaw *et al.* 2018), with the potential for population level effects. Other species of conservation concern killed in large numbers

include flamingos, storks, other bustards, vultures, Secretarybirds (*Sagittarius serpentarius*) and cranes (Jenkins *et al.* 2010, Shaw *et al.* 2018), both in Namibia (Pallett in prep.) and South Africa (Shaw *et al.* 2021). Bustards are particularly prone to collisions, partly due to their skull and eye morphology which makes them blind in the direction of flight (Martin & Shaw 2010). In an evolutionary sense this was never a disadvantage because they are open-country birds with no need to navigate through a three-dimensional landscape that savanna or woodland species inhabit.

Globally reducing collision mortality has proven particularly intractable. When new power lines are to be constructed, careful routing may help to minimise the risks to susceptible birds (APLIC 2012). The most widespread method is marking the lines with static or dynamic bird flight diverters to make them more visible (Bernardino *et al.* 2018). Attempts to reduce the high rate of collision with power lines have shown good success for Blue Cranes (*Grus paradisea*) (92% reduction in fatalities) and other large birds (51% reduction) in South Africa (Shaw *et al.* 2021). This was achieved by affixing such bird diverters to the earth wire – the thin top-most conductor that protects the line from lightning strikes. While such

methods have reduced fatalities by 40-94% in various experimental set-ups in high-strike areas (Janss 2000, Jenkins et al. 2010, Barrientos et al. 2011, Bernadino et al. 2019) the heavy-flying bustards show little decrease in collision rate compared to lines with no diverters, both here in Africa and elsewhere in the world (Jenkins et al. 2010, Shaw et al. 2015, Shaw et al. 2021). In Namibia and South Africa, Ludwig's and Kori Bustards experience a heavy toll from collisions with power lines, while the smaller korhaans (also Otidae) are impacted to a lesser extent. Both Ludwig's and Kori Bustards are threatened red data species in both Namibia (Simmons et al. 2015) and in South Africa (Taylor et al. 2015) with the main cause of mortality being collisions with power lines. Solutions are clearly needed to protect all bustard populations from further decline.

The idea presented here arose from work trying to mitigate a 460 km length of 400 kV line that Namibia's power utility, NamPower, proposes to construct through prime bustard, vulture and raptor habitat. The daunting task of mitigating this line with bird diverters to avoid fatalities of threatened birds, but with the knowledge that collisions were still certain to occur, prompted the consultants (Sustainable Solutions Trust 2015, Birds and Bats Unlimited 2018) to look for novel alternatives. In this way we could not only test a new mitigation, but also test it against the efficacy of traditional diverters to understand if they are required at all. If bird flight diverters are found to be unnecessary then utility companies may opt to use the methods proposed here. Our aim is to describe a novel method to reduce bustard collision mortalities that is likely to benefit other collision-prone species too, to give theoretical reasons why we believe it will work, and to request researchers and environmental specialists to test our method with unmitigated lines.

METHODS

Data for this analysis were drawn from two sources: (i) power line surveys on four different capacity power lines conducted in southern Namibia over 15 months in 2012-13 (Pallett in prep.); (ii) mortalities recorded on two power line surveys in the Western and Northern Cape, South Africa in 2014 and 2017. The objective was to assess the distribution of collisions within a span, relative to the total span length of any power line. We therefore selected incidents with the following criteria:

a) Certainty that the incident was a collision. Any dead large bird found close to a power line was assumed to have collided with it. In some cases, a collision could be confirmed by the presence of broken wing or leg bones, and occasionally the exact site of the collision could be verified by one or two small body feathers stuck to an overhead conductor where the impact had occurred;

- b) Presence of a relatively fresh carcass or a single concentration of body feathers snagged in the vegetation in one place. We assumed that the location of the carcass or main concentration of feathers was close to where it hit the conductor, fell and died, and represented the best estimate of where the collision occurred. Bird remains that were scattered over a wide area without any noticeable concentration in one spot, or that were only a small part of the bird such as a wing or a leg, were not included in the data set, as these could have been carried away from the main carcass by scavengers;
- c) Lateral distance from the centre of the power line less than 30 m. Carcasses further away were rejected on the basis that they could have been moved there by crippling (where an injured bird had fallen to the ground and moved away before dying) or by scavengers carrying the carcass to a new location. The further away from the power line, the more likely this was a factor, and the less confidence we could place in the location of the actual collision;
- d) Incidents that could be attributed to one power line only. Collisions that occurred in places where there were two or more power lines closer than 0.5 km together were rejected, as it was impossible to identify which power line caused the incident.

Namibian surveys

The systematic surveys in southern Namibia were conducted by JP on 81-95 km sections of four voltages of power lines (Pallett in prep.). The lines had capacities of 66, 132, 220 and 400 kV, and surveys were carried out every three months over a 15-month period, with the first survey used as a clearing survey.

South African surveys

These data derived from a repeat survey of a 50 km section of power line by RES and M Martins along the 400 kV Aries-Helios power line near Kenhardt, and a once-off 7 km power line survey of the Aurora-Juno 400 kV line near Strandfontein on the west coast.

Monitoring protocol

The monitoring protocol on all the surveys was as follows: the survey routes traversed relatively even ground (not deeply broken or rocky, where carcasses could easily be missed) over open plains with low and/or sparse vegetation, where detectability was relatively constant. While some carcasses of small birds were found, the searching method was directed at birds larger than a Pied Crow (*Corvus albus*) (mass 500 g, total length 50 cm) – which would usually

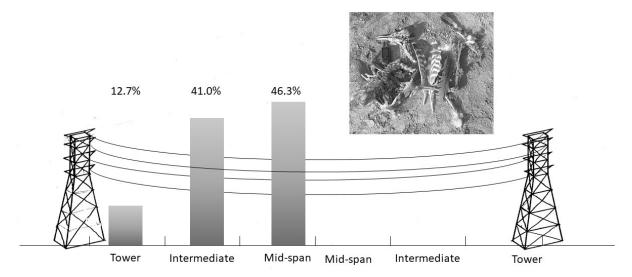


Figure 1: Percentage of large bird collisions in relation to position within the span on power lines. Records combine those for southern Namibia (n = 100) and the Northern and Western Cape, South Africa (n = 34) and indicate that most large bird deaths (87.3%) occur away from towers

produce enough evidence to be visible within the search zone. The observers drove slowly (10-20 km/h) on the track beneath the power line, with the driver and passenger searching ahead and approximately 30 metres to left and right. All bird carcasses or other evidence of a power line-related incident were recorded, noting the species as far as it could be identified. The coordinates were recorded on a GPS device and photographed at the place where the majority of the body feathers were found. All bird remains were cleared away to prevent recounting on future surveys in Namibia or left *in situ* to judge permanency of remains in South Africa.

Note that while most surveys were repeat surveys, no adjustment for scavenger removal was required as our aim was to record where the carcass was found relative to the towers, not the rate of mortality per kilometre for the species located.

Data analysis

Transmission lines and their towers are visible on Google Earth images, so we measured the span where each collision occurred and noted the location of the collision within the span. Each collision in the data set was categorised according to its position within the span, divided into thirds (Figure 1): the central third forming the Mid-span, the two sixths closest to the towers forming another third, labelled Tower, and the two sixths in between labelled Intermediate.

We compared the ratio of selected versus rejected incidents to test whether the selection criteria introduced any bias into the results. A chi-square test with Yates correction (for more than two categories) was used.

RESULTS

Of the 327 mortalities that were recorded, 134 (41.0%) were noted as confirmed collisions with accurate locality coordinates (Table 1). The overall proportions of Mid-span: Intermediate: Tower for those carcasses which were selected for this analysis, were not significantly different from those which were rejected [$\chi 2$ (df = 2, n = 327) = 1.376, p > 0.1]. Under all the transmission lines surveyed we found a bias towards more large bird collisions in the midspan of the lines and on either side of the mid-span. In our samples, 87.3% of 134 carcasses occurred under the mid-span and intermediate sections, and only 12.7% occurred around the towers (Figure 1 and Table 1). Even though the length of an average span differs widely when comparing lines of lower versus higher capacity, smaller proportions of collisions occurred at the towers, for all the power line types.

The diversity of birds making up the collision fatalities is shown in Appendix 1. The dominant victims were Ludwig's Bustard and Kori Bustard, which together comprised 83.6% of all the collisions. The proportion of their collisions occurring in the middle sections compared to the tower rose to 90.2:9.8% when considering only these two bustards.

DISCUSSION

The results from this study are very clear: bustards and other large collision victims on Namibian power lines are more likely to hit the central sections of the line but tend to avoid colliding with the towers. This is mirrored by a 3-year study in South Africa's Karoo where bustards were also much more likely to collide with the mid-span of transmission lines (72%) and

Table 1: Distribution of collision carcasses among different sections of power line spans in Namibia and South Africa.

D P	Number of collisions along different sections of the power line span			
Power lines surveyed	Average span length (m)	Mid-span	Inter-mediate	Tower
66 kV line between Lüderitz and Rosh Pinah, southern Namibia (5 surveys, 95 km each)	198.5	3 (37.5%)	4 (50.0%)	1 (12.5%)
132 kV line west and east of Warmbad, southern Namibia (5 surveys, 81 km each)	321.2	9 (50.0%)	4 (22.2%)	5 (27.8%)
220 kV line south of Keetmanshoop, southern Namibia (5 surveys, 91 km each)	414.5	16 (42.1%)	19 (50.0%)	3 (7.9%)
400 kV line south-east of Keetmanshoop, southern Namibia (5 surveys, 81 km each)	453.4	17 (47.2%)	14 (38.9%)	5 (13.9%)
400 kV line near Kenhardt, Northern Cape, RSA (2 surveys, 56 km each)	360.7	8 (57.1%)	5 (35.7%)	1 (7.1%)
400 kV line near Strandfontein, Western Cape, RSA (1 survey, 7.1 km)	334.0	9 (45.0%)	9 (45.0%)	2 (10.0%)
Total (134 collisions)		62	55	17
Overall percentages		46.3%	41.0%	12.7%

did so at a very high rate of approximately 1.0 bustard/km/year (Shaw 2013).

The collision fatalities in the two countries indicate the same trend: that bustards and other collisionprone species likely fail to see the mid-sections of power lines, but do avoid the towers supporting the lines, most of the time.

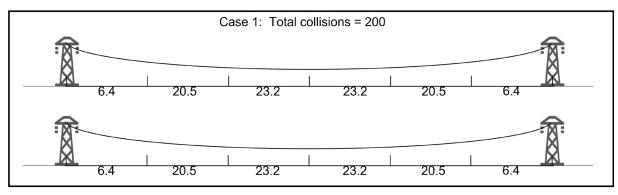
It is this ability to see (or hear) the tower and avoid it that is the core of the new mitigation proposed here. By aligning two power lines close together in parallel and staggering the tower of one line to align with the mid-span of the adjacent line, bustards will more likely detect and avoid both power lines.

We suggest that bustards are more likely to detect the towers, because (i) they are larger than the conductors and (ii) we noted in our extensive surveys that the wind often whistled through the lattice structure and, for some towers, loose plates or fittings often vibrated with considerable noise. If the birds are detecting the sound rather than the structure itself, this in itself could be exploited to increase the signature of the structure (or the bird diverter) to get around the poor vision of these collision-prone species.

No precise predictions can be made from this idea but the theoretical reduction in collision rate can be calculated by referring to Figure 2. Assuming two separate power lines cause 100 collisions each, the proportion of collisions per section of line will be as shown in Case 1, as deduced from our distribution of collision incidents amongst the span sections. If the power lines are arranged close together with the towers optimally staggered as illustrated in Case 2, the total collisions will be reduced to 66.6. This is because bundling the two power lines close together theoretically creates the effect of only one power line, and the tower of each line should help to mutually reduce the fatalities in the worst section of the adjacent line. The total collision rate on both lines is 33.3% of the total in Case 1.

Is there any field evidence for this effect? A small sample with "naturally" staggered towers was sampled in two surveys of a section of 220 kV and 400 kV lines running parallel and 58 m apart in South Africa's Karoo region in 2018 (Figure 3). No avian fatalities were recorded in 14 km of either the 220 kV or the 400 kV line, compared to one bustard fatality in 11 km of a nearby non-staggered 400 kV line in the same habitat. This provides a hint that bundling lines together and staggering the towers could help to reduce bird collision rates. This principle is best suited to lines of similar height. Evidence is needed from other situations, where unequal power lines run in parallel, as it is conceivable that an approaching bird might first see the shorter line, fly over it then collide with the higher line behind it.

If this novel mitigation proves successful it will be especially useful for proposed power lines that cross large areas known to be inhabited by highly collision-prone groups such as bustards, Secretarybird and flamingos. To our knowledge it has not been proposed before and has never been tested.



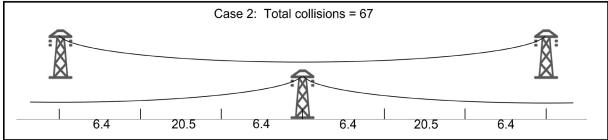


Figure 2: Schematic representation of the theoretical reduction in collision rate from bundling power lines together and staggering the towers. The number of collisions in each section of the span is shown, derived from the proportions recorded under power lines sampled in Namibia and South Africa. Case 1 represents the situation of two separate power lines, causing 200 collisions. Case 2 represents two power lines bundled close together with staggered towers.

Wherever new power lines are to be erected, mitigation measures should include bundling lines together in a narrow corridor, irrespective of design or size, rather than distancing them apart in separate lines. Secondly, where two types of power line are the same (as in the case that prompted this initiative) every effort should be made to position the towers in a maximally staggered arrangement. A similar but reduced benefit of fewer collisions is expected even on lines of different sizes (such as a 220 and a 400 kV line together, as in Figure 3), but logically the amount of staggering will vary due to the different span lengths of the two lines. That is, some parts will have their towers closely aligned, and other parts will have them staggered with the mid-span of one line adjacent to the tower of the other. There will also be

practical elements on the ground which might make it difficult to achieve optimum staggering in hilly terrain, but the principle is to aim for the maximum offset of one tower against the other.

What we presently do not know is (i) whether this theoretical prediction will work in practice and (ii) whether the bustards approaching the mid-span of one line will see the tower of the adjacent line behind the mid-span and take evasive action. If they do take evasive action, then this method has the potential to reduce bustard deaths by 67%. Individual circumstances, such as the angle of approach toward the lines, and the distance between two parallel lines, are expected to contribute to the efficacy of the staggering effect.



Figure 3: An example of a 400 and a 220 kV power line in parallel with staggered towers showing the greater visibility of the lines with a tower placed opposite the mid span.

To test these ideas, we propose to set up a monitoring programme on target power lines in Namibia over 460 km before and after construction of a parallel staggered line (with a control line of equal size) to compare collision and fatality rates. We expect *a priori* that fatality rates will be about two-thirds lower compared with the pre-staggered line and the controls.

We also expect that the staggered towers idea will mitigate avian collisions better than simply two lines of equal voltage bundled together with their towers aligned. This is because the conductors are still equally unlikely to be seen by collision-prone birds whether there are two or more (Shaw 2013).

We request researchers and environmental avian specialists to collect systematic data on bustard and other collision-prone bird fatalities along power lines that by chance exhibit the staggered tower effect outlined here. Ideally the fatality rate should be compared with simultaneously collected avian fatalities along un-staggered lines of the same voltage in similar habitat. This will give a first order assessment of the efficacy of this potential new mitigation measure.

Already these methods are being discussed and recommended in South African power-supply circles. It is our hope that staggered towers on adjacent lines will reduce the need for any other form of avian collision-mitigation and thereby be favoured by power utilities to reduce start-up costs involved with affixing spirals or dynamic markers and the maintenance of such mitigations.

ACKNOWLEDGEMENTS

We thank all those with whom this idea was discussed or field work assistance provided including Dr Jessica Shaw, Peter Bridgeford and Marlei Martins. Max Weylandt and Dr Colleen Seymour assisted with the statistics. We are also grateful to NamPower employees Pierre van Niekerk, Hansie Peens, Bertie Steyn, Johnny Nanyome, Ebro Kooper and David Plaatz, and Karl-Heinz Wagner for the personal communication. Their sharing of knowledge and ideas helped greatly in our own thoughts. JP thanks the NamPower-Namibia Nature Foundation Strategic Partnership, and the Namibian Chamber of Environment for logistical and financial support. RES was supported by various Independent Power producers during survey work for renewable energy facilities. We thank reviewers Jessica Shaw, Holger Kolberg and Peter Ryan for valuable comments.

REFERENCES

Anderson MD (2002) The effectiveness of two different marking devices to reduce large terrestrial bird collisions with overhead electricity cables in the eastern Karoo, South Africa. Unpublished report: Eskom, Johannesburg.

- APLIC (2012) Reducing avian collisions with power lines: the state of the art in 2012. Edison Electric Institute and Avian Power Line Interaction Committee, Washington DC
- Barrientos R, Alonso J, Ponce C, Palacín C (2011) Metaanalysis of the effectiveness of marked wire in reducing avian collisions with power lines. *Conservation Biology* 25(5): 893–903.
- Bernadino J, Bevanger K, Barrientos R, Dwyer J, Marques A, Martins R, Shaw J, Silva J, Moreira F (2018) Bird collisions with power lines: State of the art and priority areas for research. *Biological Conservation* 222: 1–13.
- Bernadino J, Martins R, Bispo R, Moreira F (2019) Reassessing the effectiveness of wire-marking to mitigate bird collisions with power lines: a meta-analysis and guidelines for field studies. *Journal of Environmental Management* 252: 109651.
- Bevanger K (1998) Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biological Conservation* 86: 67–76.
- Birds and Bats Unlimited (2018) Avifaunal Assessment. Input to the Scoping Report of Proposed Kokerboom – Auas 400kV Transmission Line Environmental Impact Assessment Report. Unpublished report: NamPower, Windhoek.
- Eskom (2007) *Eskom Annual Report 2007*. Unpublished report: Eskom, Johannesburg.
- Janss G (2000) Avian mortality from power lines: a morphologic approach of a species-specific mortality. *Biological Conservation* 95: 353–359.
- Jenkins A, Smallie J, Diamond M (2010) Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. *Bird Conservation International* 20: 263–278.
- Martin G, Shaw J (2010) Bird collisions with power lines: failing to see the way ahead. *Biological Conservation* 143: 2695–2702.
- Pallett J (in prep.) Large bird collision mortalities on power lines in southern Namibia. Contact author for preprint.
- Shaw J (2013) Power line collisions in the Karoo: Conserving Ludwig's Bustard. PhD, University of Cape Town.
- Shaw J, van der Merwe R, van der Merwe E, Ryan P (2015) Winter scavenging rates under power lines in the Karoo, South Africa. *African Journal of Wildlife Research* 45(1): 122–126.
- Shaw J, Reid T, Gibbons B, Pretorius M, Jenkins A, Visagie R, Michael M, Ryan P (2021) A large-scale experiment demonstrates that line marking reduces power line collision mortality for large terrestrial birds, but not bustards, in the Karoo, South Africa. *Ornithological Applications* 123: 1–10.
- Shaw J, Reid T, Schutgens M, Jenkins A, Ryan P (2018) High power line collision mortality of threatened bustards at a regional scale in the Karoo, South Africa. *Ibis* 160: 431–446.
- Silva J, Santos M, Queirós L, Leitão D, Moreira F, Pinto M, Leqoc M, Cabral J (2010) Estimating the influence of overhead transmission power lines and landscape context on the density of little bustard *Tetrax tetrax* breeding populations. *Ecological Modelling* 221: 1954–1963.
- Simmons R, Brown C, Kemper J (2015) *Birds to watch in Namibia: red, rare and endemic species.* Ministry of Environment and Tourism, and Namibia Nature Foundation, Windhoek.
- Sustainable Solutions Trust (2015) Avifaunal Scoping Report. Input to the Scoping Report of Proposed

- Kokerboom Auas 400kV Transmission Line Environmental Impact Assessment Report. Unpublished report: NamPower, Windhoek.
- Taylor M, Peacock F, Wanless R (2015) *The Eskom Red Data book of birds of South Africa, Lesotho and Swaziland*. Birdlife South Africa, Johannesburg.
- Uddin M, Dutta S, Kolipakam V, Sharma S, Usmani F, Jhala Y (2021) High bird mortality due to power lines invokes urgent environmental mitigation in a tropical desert. *Biological Conservation* 261: 109262.

Appendix 1

Numbers of birds that collided with sampled power lines in Namibia and South Africa, with the relative position within a span where the collisions occurred. Data from the power line surveys described in Methods.

	Mid-span	Intermediate	Tower	Total
Ludwig's Bustard Neotis ludwigii	37	34	9	80
Kori Bustard Ardeotis kori	14	8	2	24
Unidentified large bustard	3	5	0	8
Karoo Korhaan Eupodotis vigorsii	2	0	1	3
Northern Black Korhaan Afrotis afraoides	2	1	1	4
Southern Black Korhaan Afrotis afra	0	1	0	1
Lappet-faced Vulture Torgos tracheliotos	0	1	0	1
White-backed Vulture Gyps africanus	1	0	1	2
Secretarybird Sagittarius serpentarius	0	2	1	3
Martial Eagle Polemaetus bellicosus	1	1	0	2
Greater Kestrel Falco rupicoloides	0	0	1	1
Lesser Flamingo Phoeniconaias minor	1	0	0	1
Unidentified flamingo	0	1	0	1
Pied Crow Corvus albus	0	1	1	2
Unidentified duck	1	0	0	1
Total	62	55	17	134

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

J Heydinger¹, C Packer¹, P Funston²

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-heydinger Published online: 15th February 2022

¹ University of Minnesota, 1479 Gortner Avenue, St Paul, MN, 55108, USA. heydingerj@gmail.com

Date received: 23rd August 2021; Date accepted: 20th January 2022.

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 km²). Since that time Etosha's size has been dramatically reduced (currently 22,700 km²), yet it remains an essential refuge for many of Namibia's threatened large mammals, such as blackfaced 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

² African Lion Conservation, Cape Town, South Africa

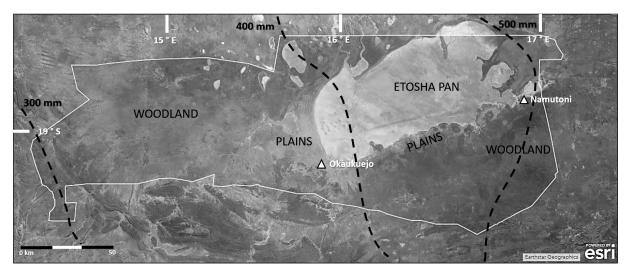


Figure 1: Etosha National Park with major habitats and rainfall isohyets. Based on Berry & Siegfried (1991).

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 underresourced. 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 km² 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 km² 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).

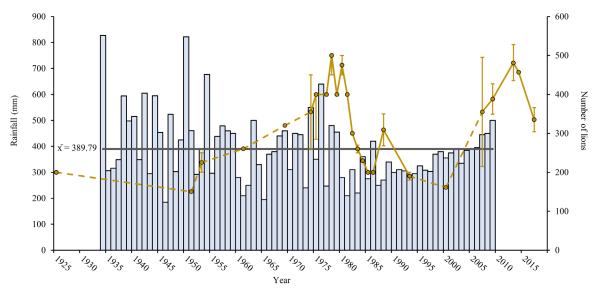


Figure 2: Historical rainfall and lion numbers for Etosha National Park. All rainfall measurements were taken at Okaukuejo; data are from Bigalke (1961) [1934-1957], Berry and Siegfried (1991) [1958-1989], and Trinkel (2013) [1990-2009]. Dashed lines between lion population data points indicate where 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. Limitedcirculation 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 <i>et al.</i> (1988)	Range: 450-500	
1982	400	Berry (1987)		
1983	300	Berry (1987)		
1984	260	Berry (1987); Orford <i>et al.</i> (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 km²; 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

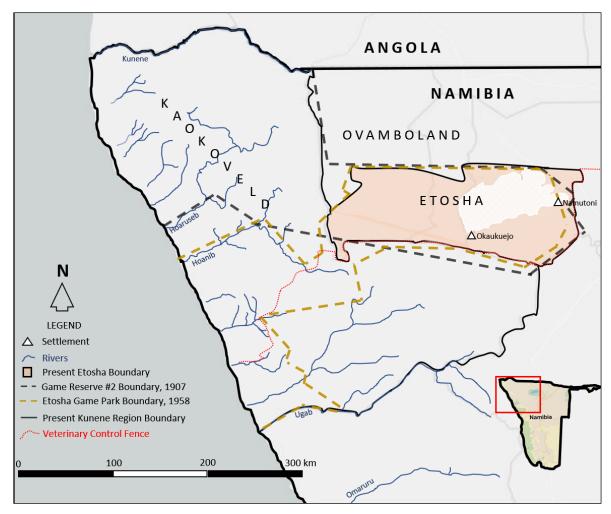


Figure 3: Historical Game Reserve No. 2 and Etosha National Park boundaries.

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 km², 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 anticlockwise 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,

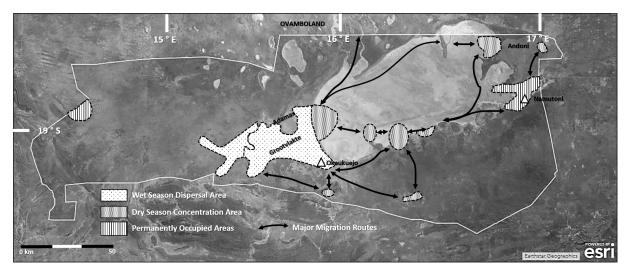


Figure 4: Wildebeest distribution and migration, 1974-1978. Based on Berry (1981a, p. 257).

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-andmouth 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 Africa, South Africa West 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 population, wildebeest 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

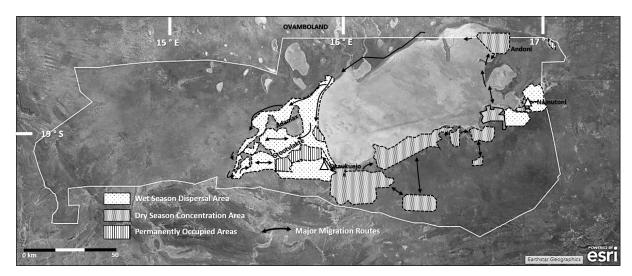


Figure 5: Plains zebra distribution and migration. Based on Ebedes (1976, p. 103).

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 intended construction was to reduce concentrations of wildlife at existing waterholes. As many as 54 artificial waterholes were constructed during the 1950s (Berry and Siegfried 1991). Roadbuilding also led to the creation of gravel pits, socalled 'mini-dams,' which would retain standing rainwater up to five weeks longer than naturallyoccurring 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

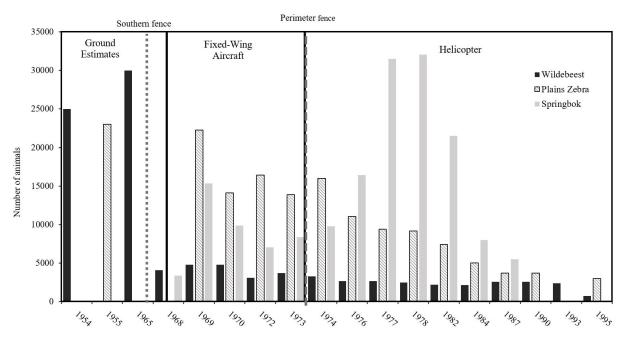


Figure 6: Wildebeest, plains zebra, and springbok in central and eastern Etosha National Park Wildebeest data from Berry (1981a) [1954-1978]), Turnbull et al. (1989) [1982], and Gasaway et al. (1996) [1984-1990]. Plains zebra data from Gasaway et al. (1996) [1955; 1982-1990], Berry and Louw (1982) [1969-1978], 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).

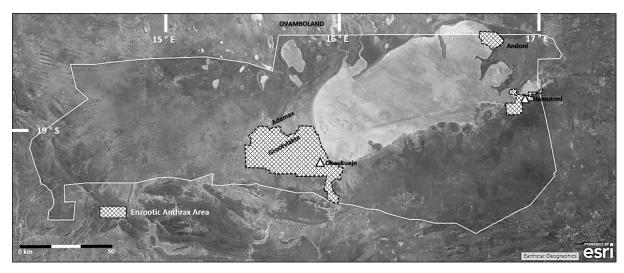


Figure 7: Enzootic anthrax areas. Based on Ebedes (1976, p. 106).

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 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).

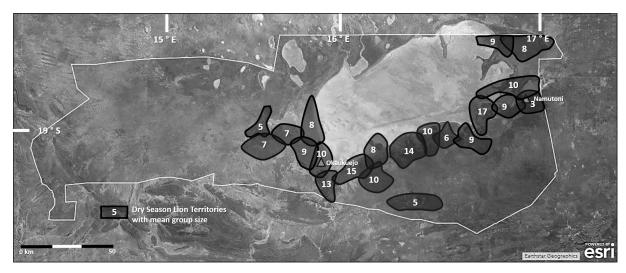


Figure 8: Dry season ranges for the 21 known lion groups in plains habitat (1974-1978). Based on Berry (1981b, p. 244).

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

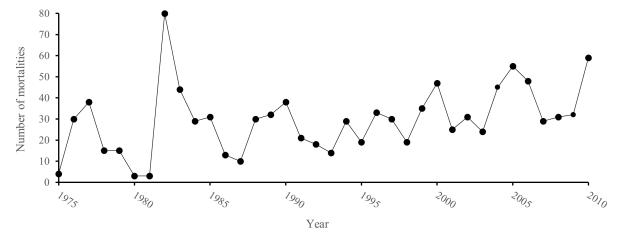


Figure 9: Records of lion mortalities on farms bordering Etosha National Park (Funston unpub. data).

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 dving 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 '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 prev. 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 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.

ACKNOWLEDGEMENTS

Thanks to staff at the Ministry of Environment, Forestry and Tourism and Ongava Research Center for providing supporting documentary evidence. Thanks to National Geographic for supporting Heydinger's *in situ* work. Thanks to the National Archives of Namibia staff. Thanks to Alicia Robey.

REFERENCES

- Andersson CJ (1861) *The Okavango River: a narrative of travel, exploration, and adventure.* Harper and Brothers, New York, NY.
- Andersson CJ (1856) Lake Ngami; or, explorations and discoveries during four years' wanderings in the wilds of southwestern Africa. Harper and Brothers, New York, NY
- Bauer H, Chapron G, Nowell K, Henschel P, Funston P, Hunter LTB, Macdonald DW, Packer C (2015) Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proc. Natl. Acad. Sci.* 112, 14894-9.
- Bennett B, van Sittert L (2019) Historicising perceptions and the national management framework for invasive alien plants in South Africa. *J. Env. Manag.* 229, 174-181.
- Berry H (1980) Behavioural and Eco-physiological Studies on Blue Wildebeest (*Connochaetes taurinus*) at the Etosha National Park, PhD thesis, University of Cape Town, 611 pp.
- Berry H (1981a) Population structure, mortality patterns and a predictive model for estimating future trends in wildebeest numbers in the Etosha National Park. *Madoqua* 12, 255-266.
- Berry H (1981b) Abnormal levels of disease and predation as limiting factors for wildebeest in the Etosha National Park. *Madoqua* 12, 242-253.
- Berry H (1982) The wildebeest problem in the Etosha National Park: a synthesis. *Madoqua* 13, 151-157.
- Berry H (1987) Ecological Background and Management Application of Contraception in Free-Living African Lions. Okaukuejo.
- Berry H (1996) Lions in Namibia. Cat News 24, 13-14.
- Berry H (1997) Historical review of the Etosha Region and its subsequent administration as a National Park. *Madoqua* 20, 3-12.
- Berry H (2003) Survival of lion cubs in Etosha. *Travel News Namibia Spec. Ed. Conserv. Environ*. Namibia 36-37.
- Berry H, Louw GN (1982) Nutritional balance between grassland productivity and large herbivore demand in the Etosha National Park. *Madoqua* 13, 141-150.
- Berry H, Rocher CJV, Paxton M, Cooper T, (1997) Origin and meaning of place names in the Etosha National Park, Namibia. *Madoqua* 20, 13-35.
- Berry H, Siegfried WR (1991) Mosaic-Like Events in Arid and Semi-Arid Namibia, *in* Remmert, editor. *The Mosaic-Cycle Concept of Ecosystems*. Springer, Berlin, pp. 147-160.

- Bigalke RC (1961) Some observations on the Ecology of the Etosha Game Park, South West Africa. *Annu. Cape Prov. Museum* 1, 49-67.
- Bollig M, Olwage E (2016) The political ecology of hunting in Namibia's Kaokoveld: from Dorsland Trekkers' elephant hunts to trophy-hunting in contemporary conservancies. *J. Contemp. African Stud.* 34, 1-19.
- Bollig M (2020) Shaping the African Savannah: From Capitalist Frontier to Arid Eden in Namibia, Cambridge, Cambridge University Press.
- Brockington D (2002) Fortress Conservation. Oxford University Press, Oxford, UK.
- Creel S, Becker MS, Durant SM, M'Soka J, Matandiko W, Dickman AJ, Christianson D, Droge E, Mweetwa T, Pettorelli N, Rosenblatt E, Schuette P, Woodroffe R, Bashir S, Beudels-Jamar RC, Blake S, Borner M, Breitenmoser C, Broekhuis F, Cozzi G, Davenport TRB, Deutsch J, Dollar L, Dolrenry S, Douglas-Hamilton I, Fitzherbert E, Foley C, Hazzah L, Henschel P, Hilborn R, Hopcraft JGC, Ikanda D, Jacobson A, Joubert B, Joubert D, Kelly MS, Lichtenfeld L, Mace GM, Milanzi J, Mitchell N, Msuha M, Muir R, Nyahongo J, Pimm S, Purchase G, Schenck C, Sillero-Zubiri C, Sinclair ARE, Songorwa AN, Stanley-Price M, Tehou CA, Trout C, Wall J, Wittemyer G, Zimmerman A (2013) Conserving large populations of lions the argument for fences has holes. *Ecol. Lett.* 16, 1-4.
- Cumming GS (2016) The relevance and resilience of protected areas in the Anthropocene. *Anthropocene* 13, 46-56.
- de la Bat BJG (1982) Etosha: 75 years. South West Africa Annu. Suppl. 11-22.
- Dieckmann U (2007) Hai||om in the Etosha Region: A History of Colonial Settlement, Ethnicity and Nature Conservation. Basler Afrika Bibliographien, Basel, Switzerland.
- Dlamini J (2020) Safari Nation: A Social History of the Kruger National Park. Ohio University Press, Athens.
- Durant SM, Becker MS, Creel S, Bashir S, Dickman AJ, Beudels-Jamar RC, Lichtenfeld L, Hilborn R, Wall J, Wittemyer G, Badamjav L, Blake S, Boitani L, Breitenmoser C, Broekhuis F, Christianson D, Cozzi G, Davenport TRB, Deutsch J, Devillers P, Dollar L, Dolrenry S, Douglas-Hamilton I, Droge E, FitzHerbert E, Foley C, Hazzah L, Hoperaft JGC, Ikanda D, Jacobson A, Joubert D, Kelly MJ, Milanzi J, Mitchell N, M'Soka J, Msuha M, Mweetwa T, Nyahongo J, Rosenblatt, E, Schuette P, Sillero-Zubiri C, Sinclair ARE, Price MRS, Zimmerman A, Pettorelli N (2015) Developing fencing policies for dryland ecosystems. *J. Appl. Ecol.* 52, 544-551.
- Di Minin E, Slotow R, Fink C, Bauer H, Packer C (2021) A pan-African spatial assessment of human conflicts with lions and elephants. *Nature Communications*, 12:2978, 1-10.
- Ebedes H (1976) Anthrax epizootics in Etosha National Park. *Madoqua* 10, 99-118.
- Gaerdes J (1975) Löwen in Südwest Afrika. Wissenschaftliche Gesellschaft, Newsl. Supplment XVI, 5-6.
- Galton F (1853) The Narrative of an Explorer in Tropical South Africa. John Murray, London.
- Gasaway WC, Gasaway KT, Berry HH (1996) Persistent low densities of plains ungulates in Etosha National Park, Namibia: Testing the food-regulating hypothesis. *Can. J. Zool.* 74, 1556-1572.

- Goelst C, Moeller M, Killian W (2018) Etosha National Park Carnivore Monitoring Project Update, Unofficial Report, Re: Lion GPS-Monitoring, 2018 Lion Population Call-Up Survey. Etosha Ecological Institute.
- Green LG (1952) Lords of the Last Frontier: The Story of South West Africa and its People of all Races. Howard B. Timmins, Cape Town.
- Hanby JP, Bygott JD, Packer C (1995) Ecology, Demography, and Behavior of Lions in Two Contrasting Habitats: Ngorongoro Crater and the Serengeti Plains, in Sinclair and Arcese, editors. Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. University of Chicago Press, 315-331.
- Harrington R, Owen-Smith N, Viljoen PC, Biggs HC, Mason DR, Funston P (1999) Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biol. Conserv.* 90:1, 69-78.
- Hayward MW, Kerley G (2009) Fencing for conservation: Restriction of evolutionary potential or a riposte to threatening processes? *Biol. Conserv.* 142, 1-13.
- Heydinger J (2020a) 'Vermin': Predator Eradication as an Expression of White Supremacy in Colonial Namibia, 1921-1952. *J. South. Afr. Stud.* 46, 91-108.
- Heydinger J (2020b) Humans, Livestock, and Lions in northwest Namibia. PhD thesis, Macquarie/University of Minnesota. 259 pp.
- Heydinger J (2021a) A More-Than-Human History of Apartheid-Era Planning in Etosha-Kaokoveld Namibia, c. 1960-1970s. *So. Afr. Hist. J.*, 73:1, 64-94.
- Heydinger J (2021b) Human-Lion Conflict and the Reproduction of White Supremacy in Northwest Namibia. *Afr. Stud. Rev.* 64:4, 909-937.
- Hoole A, Berkes F (2010) Breaking down fences: recoupling social-ecological systems for biodiversity conservation in Namibia. *Geoforum* 41, 304-317.
- IUCN SSC Cat Specialist Group, 2018. Guidelines for the Conservation of Lions in Africa, Version 1.0 - December 2018. Muri/Bern, Switzerland.
- Jacobson A, Riggio J (2018) Big Cats in Africa: status update on the African lion, cheetah and leopard, with recommendations for effective big cat conservation funding. National Geographic.
- Jones B, Murphree, M (2001) The Evolution of Policy on Community Conservation in Namibia and Zimbabwe, in Hulme and Murphree, editors. African Wildlife & Livelihoods: The Promise and Performance of Community Conservation. James Currey, Oxford, 38-58.
- Jones B, Weaver LC (2008) CBNRM in Namibia: Growth, trends, lessons and constraints, in Suich, Child, and Spenceley, editors. Evolution and Innovation in Wildlife Conservation: Parks and Game Ranches to Transfrontier Conservation Areas. Earthscan, London and Sterling, VA, 223-242.
- Joubert E, Mostert PKN (1975) Distribution patterns and status of some mammals in South West Africa. *Madoqua* 9, 5-44.
- Kilian W, Moeller CH (2015) Etosha National Park Lion (*Panthera leo*) Survey Report. Windhoek, Namibia.
- le Roux CJG, Grunow JO, Morris JW, Bredenkamp GJ, Scheepers JC (1988) A classification of the vegetation of the Etosha National Park. *South African J. Bot.* 54, 1-10.
- Lindsey PA, Miller JRB, Petracca LS, Coad L, Dickman AJ, Fitzgerald KH, Flyman MV, Funston PJ, Henschel P, Kasiki S, Knights K, Loveridge AJ, Macdonald DW, Mandisodza-Chikerema RL, Nazerali S, Plumptre AJ, Stevens R, Van Zyl HW, Hunter LTB 2018. More than \$1 billion needed annually to secure Africa's protected

- areas with lions. *Proc. Natl. Acad. Sci.* 115, E10788-E10796.
- Lindsey PA, Petracca LS, Funston PJ, Bauer H, Dickman A, Everatt K, Flyman M, Henschel P, Hinks AE, Kasiki S, Loveridge A, Macdonald DW, Mandisodza R, Mgoola W, Miller SM, Nazerali S, Siege L, Uiseb K, Hunter LTB (2017) The performance of African protected areas for lions and their prey. *Biol. Conserv.* 209, 137-149.
- Massey, AL, King, AA, Foufopoulos J (2014) Fencing protected areas: A long-term assessment of the effects of reserve establishment and fencing on African mammalian diversity. *Biol. Conserv.* 176, 162-171.
- (MET) Namibia Ministry of Environment and Tourism, 2008. A draft of lion conservation management Plan. Windhoek, Namibia.
- (MET) Namibia Ministry of Environment and Tourism, 2017. Human-Lion Conflict Management Plan for North West Namibia. Windhoek, Namibia.
- Miescher G (2012) Namibia's Red Line: The History of a Veterinary and Settlement Border. Palgrave Macmillan, New York, NY.
- Möller P (1899) Journey in Africa through Angola, Ovampoland and Damaraland. Struik, Cape Town.
- Namibia National Archives (NAN) Odendaal Liasion Committee (LUKS) 1.4 (1964) Vorderingsverslag in Sake Wersaamhede van Skakelkomitee vir Tydperk, 30 Junie-30 Oktober 1964.
- NAN LUKS 2.8 (1966) Memorandum aan Uitvoerende Komitee Insake Notul en Aanbevelings van de Skakelkomitee (Vergadering gehou te Windhoek op 9 Junie 1966).
- NAN Native Affairs Ovamboland (NAO) 066 (1948) Game Control: Game Reserve No. 2; Native Commissioner, Ovamboland to Secretary of South West Africa. 12 January 1948.
- NAN NAO 066 (1952) Reasons for shooting game at Etosha Pan, newspaper article, unknown newspaper cl, 12 March 1952.
- NAN South West Africa Administration (SWAA) 1331 (1924) The Third Percy Sladen and Kaffrarian Museum Expedition "Ovambloland", 7 July-9 Dec. 1924.
- NAN SWAA 2328 (1922) Outjo Magistrate to Secretary South West Africa, Telegram No. 161, 16h40, 27 June 1922.
- NAN SWAA 2328 (1938a) Protection of Vermin and Wild Life in Namutoni Game Reserve. Secretary South West Africa, 30 August, 1938.
- NAN SWAA 2328 (1938b) Protection of Vermin and Wild Life in Namutoni Game Reserve. Official Correspondence: Secretary South West Africa and Commissioner South West Africa Police, 11 July, 1938.
- NAN SWAA 2329 (1952) Proposed Extermination of Lions, Etosha Pan Game Reserve, Secretary South West Africa to Magistrate, Grootfontein. 21 April 1952.
- NAN SWAA 2230 (1934) Vermin Killed, Statistical Year 1934.
- NAN SWAA 2331 (1952) A.510/1 Destruction of Lions; Letter from Mr. R. Bohme, Onguma, Tsumeb. 7 March 1952.
- Neumann RP (1998) *Imposing Wilderness: struggles of livelihood and nature preservation in Africa*. University of California Press, Berkeley, California.
- Orford HJL, Perrin MR, Berry HH (1988) Contraception, reproduction and demography of free-ranging Etosha lions (*Panthera leo*). J. Zool. Soc. London 216, 717-733.

- Owen-Smith G (2010) An Arid Eden: A Personal Account of Conservation in the Kaokoveld. Jonathan Ball, Johannesburg and Cape Town.
- Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ, Mulder MB (1988) Reproductive success of lions, in Clutton-Brock, editor. Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems. University of Chicago Press, 363-383.
- Packer C, Hilborn R, Mosser A, Kissui B, Borner M, Hopcraft G, Wilmshurst J, Mduma S, Sinclair ARE (2005) Ecological Change, Group Territoriality, and Population Dynamics in Serengeti Lions. *Science* 307, 390-393.
- Packer C, Loveridge A, Canney S, Caro T, Garnett ST, Pfeifer M, Zander KK, Swanson A, MacNulty D, Balme G, Bauer H, Begg CM, Begg KS, Bhalla S, Bissett C, Bodasig T, Brink H, Burger A, Burton AC, Clegg B, Dell S, Delsink A, Dickerson T, Dloniak SM, Druce D, Frank L, Funston P, Gichohi N, Groom R, Hanekom C, Heath B, Hunter L, Delongh, Joubert CJ, Kasiki SM, Kissui B, Knocker W, Leathem B, Lindsey PA, Maclennan SD, McNutt JW, Miller SM, Naylor S, Nel P, Ng'weno C, Nicholls K, Ogutu JO, Okot-Omoya E, Patterson BD, Plumptre A, Salerno J, Skinner K, Slotow R, Sogbohossou EA, Stratford KJ, Winterbach C, Winterbach H, Polasky S (2013) Conserving large carnivores: Dollars and fence. *Ecol. Lett.* 16, 635-641.
- Pekor A, Miller JRB, Flyman MV, Kasiki S, Kesch MK, Miller SM, Uiseb K, van der Merwe V, Lindsey PA (2019) Fencing Africa's protected areas: Costs, benefits, and management issues. *Biol. Conserv.* 229, 67-75.
- (RSA) Government of South Africa (1964) Report of the Commission of Enquiry into South West Africa Affairs. Government Printer, Republic of South Africa, Pretoria, South Africa.
- van Schalkwyk R, Berry HH, editors. 2007a. *Etosha 100:* Celebrating a Hundred Years of Conservation. Venture Publications, Windhoek, Namibia.
- Shortridge GC (1934) The mammals of South west Africa; a biological account of the forms occurring in that region. Heinemann, London.
- Smuts GL (1978) Interrelations between Predators, Prey, and Their Environment. *Bioscience* 28, 316-320.
- Smuts GL (1976) Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe* 19, 153-164.
- Stander P (1990) A suggested management strategy for stock-raiding lions in Namibia. *South African J. Wildl. Res.* 20, 37-43.
- Stander P (1991a) Demography of lions in the Etosha National Park, Namibia. *Madoqua* 18, 1–9.
- Stander P (1991b) Foraging dynamics of lions in a semiarid environment. *Can. J. Zool.* 70, 8–21.
- Stander P (1999) Conservation of lions and other large carnivores in Etosha National Park and Khorixas District, Namibia. Windhoek.
- Stander P (2001) Research Progress Report Population ecology and long term monitoring of free-ranging populations in Namibia's marginal and aid environments. Windhoek.
- Stander P (2004) An analyses of the spatial, temporal, and demographic patterns of lions destroyed along the borders of Etosha National Park over a 20-year period, 1982 to 2001. Unpublished report, Etosha Ecological Institute, Okaukuejo.
- Stander P (2018) Vanishing Kings: Lions of the Namib Desert. HPH Publishing, Johannesburg.

- Stark P (2011) *The White Bushman*. Protea, Pretoria. Stassen N (2016) *The Thirstland Trek*, 1874-1881. Protea, Pretoria
- (SWA) Government of South West Africa (1947) Native Reserve Proclamation.
- Trinkel M (2013) Climate variability, human wildlife conflict and population dynamics of lions *Panthera leo*. *Naturwissenschaften* 100, 345-353.
- Trinkel M, Fleischmann PH, Slotow, R (2017) Electrifying the fence or living with consequences? Problem animal control threatens the long-term viability of a free-ranging lion population. *J. Zool.* 301, 41-50.
- Turnbull PCB, Carman JA, Lindeque PM, Joubert F, Hubschle OJB, Snoeyenbos GH (1989) Further Progress

- in Understanding Anthrax in the Etosha National Park. *Madoqua* 16, 93-104.
- Turnbull PCB, Doganay M, Lindeque PM, Aygen B, McLaughlin J (1992) Serology and anthrax in humans, livestock and Etosha National Park wildlife. *Epidemiol. Infect.* 108, 299-313. World Bank. 2021. Data Commons Place Explorer: Namibia. https://datacommons.org/place/country/NAM. Accessed: 7 July 2021.
- Xinhua. 2021. Namibia's tourism industry loses 220 mln USD due to COVID-19 pandemic. Xinhuanet.com. http://www.xinhuanet.com/english/africa/2021-02/17/c 139748473.html. Accessed: 7 July 2021.

An analysis of trophy size trends in popular hunting species in Namibia over five years

M Walters¹, M Hauptfleisch²

URL: http://www.nje.org.na/index.php/nje/article/view/volume6-walters Published online: 15th April 2022

¹ PO Box 80724, Olympia, Windhoek. matthew.walters94@gmail.com

Date received: 15th June 2021; Date accepted: 1st April 2022.

ABSTRACT

Within the last twenty years, Namibia has developed a leading alternative model of biodiversity conservation, largely due to its Community-Based Natural Resource Management (CBNRM) programme and its allocation of large areas of land towards biodiversity conservation. The CBNRM model is based on the rights of communal conservancies to benefit from the wildlife that is present on their land; one such right is to receive meat and revenue from trophy hunting. However, the marketability of desirable trophy animals is dependent on the consistent presence of quality trophy individuals within local wildlife populations, which can, through over-hunting, lead to an unsustainable operation. This study considered trends in numbers, locations and sizes of trophies hunted over a five-year period. Three sought-after high-value species, namely buffalo (Syncerus caffer), roan (Hippotragus equinus), and sable (Hippotragus niger), along with the iconic and frequently hunted trophy species kudu (Tragelaphus strepsiceros), were considered in this study. Buffalo and roan trophy sizes showed signs of a non-significant increase over time. Sable trophy measurements indicated a non-significant negative size trend, while kudu trophy measurements significantly declined across Namibia over the 5 years. It is speculated that large kudu bulls have become less common, possibly due to a combination of overhunting and the impact of rabies. Most roan, sable and kudu were hunted on freehold farms, while buffalo were exclusively hunted in national parks and communal conservancies in the north-east. Despite commercial game farmers breeding roan and sable selectively, there were no significant positive trends in trophy size on freehold farms. This study paves the way for further research into the effect of environmental and socio-economic variables that could be factored into determining the influence on trophy measurement trends, and for more effective monitoring and management of popular hunting wildlife species.

Keywords: buffalo; hunting; kudu; Namibia; roan; sable; trophy

INTRODUCTION

Hunting has been recognised as a useful natural resource management tool across the globe in terms of its economics, its ecological influences, and its sociological benefits (Gallo and Pejchar 2016). Trophy hunting can be a viable economic activity that adds value to the presence of wildlife; a fact made clear by trophy hunting drawing more income per client than non-consumptive tourism (PACEC 2006; Lindsey et al. 2007; Munn et al. 2010). The reinvestment of hunting revenue into wildlife protection and the contribution towards antipoaching efforts by hunters has contributed towards species conservation in many of the countries where sport hunting is practiced (Lindsey et al. 2007; Arnett and Southwick 2015) and considerably so in Namibia (Humavindu and Barnes 2003; Erb 2004; Schalkwyk et al. 2010).

Ecologically, hunting can have a lesser impact on the environment, when compared with other development opportunities, in terms of disturbance, fossil fuel use, and infrastructure development; also, trophy hunting (if well managed) utilises no more than 2-5% of the male population in a designated

area, making it mostly a sustainable industry (Lindsey *et al.* 2007). To take advantage of the economic opportunity that trophy hunting offers, private landowners have re-established and protected wildlife species which were previously eradicated (Bond *et al.* 2004; Bothma *et al.* 2016). A great determinant of the success of the trophy hunting industry, from a financial point of view, is the variety of species on offer, along with high quality trophies (Von Brandis and Reilly 2007). The creation of measuring systems and record books has led to competitiveness within the trophy hunting community, as some hunters strive to find a large trophy animal that might be recorded in the Rowland Ward or SCI Record Books.

In Namibia specifically, wildlife population numbers in Kunene and Zambezi Regions have increased due to the incentives that were created for sustainable wildlife utilisation by residents on communal land since the 1990s (Jones and Weaver 2009; MET/NACSO 2020). As a means of unlocking wildlife value to communities, trophy hunting is permitted, which generates the highest cash revenue to communal conservancies throughout the country (MET/NACSO 2020).

² Namibia University of Science and Technology Biodiversity Research Centre, Private Bag 13388, Windhoek

There are however growing negative sentiments towards trophy hunting, which are based mainly on the perceived threats towards the populations of rare or endangered species; these negative sentiments are further compounded by concerns around the ethics of sport hunting of any animal (Lindsey *et al.* 2007; Di Minin *et al.* 2016; Sheikh and Bermejo 2019). Besides concerns regarding the ecological impacts of trophy hunting, there are additional concerns regarding corruption in developing nations that might siphon off funds (from trophy fees) from their intended beneficiaries (Packer *et al.* 2011).

Multiple studies have been conducted to ascertain the sustainability of hunting and its influence on trophy size. A study on roe deer (Capreolus capreolus) in the Baltic region (Balčiauskas et al. 2017) concluded that smaller trophy size in certain areas could be attributed to the hunting of individuals that had not yet matured, which motivated the need for a minimum age limit. A study of bighorn sheep (Covis canadensis) in Arizona (Pigeon et al. 2016) attributed a decline in trophy sizes to the hunting of younger individuals with faster-growing or longer horns, or overall overharvesting (Festa-Bianchet et al. 2004). Similarly, a 40-year study of trophy size trends of Stone's sheep (Ovis dalli) in Canada indicated that there was a decline in early horn growth and males harvested in areas where there was a strong selective hunting pressure (Douhard et al. 2016).

Various studies of trophy hunting (with a specific emphasis on trophy sizes and trends) and its effects, especially upon wild ungulate species, have been conducted in Africa. One study in Tanzania (Wilfred

2012), using data from 2006 to 2010 showed that mean trophy size, with the exception of (Phacochoerus warthog africanus), showed only slight changes, with most species remaining just above the threshold of acceptable trophy size. Studies within the Selous Game Reserve of Tanzania confirmed that trophy size of buffalo, lion (Panthera leo), leopard (Panthera pardus), elephant (Loxodonta africana), hippo (Hippopotamus and amphibius) had significantly declined largely due unrestricted trophy hunting since poaching incidents were relatively few (Songorwa and du Toit 2007). A similar study in Zimbabwe (Crosmary et al. 2013), determined that the trophy sizes of commonly hunted species revealed some

form of decline; but a 6% decrease in sable could mainly be attributed to hunting pressures associated with their high-value status. Another study in Zimbabwe's Sengwa Wildlife Research Area revealed that the trophy size of elephant, buffalo, and lion had declined (Patmore *et al.* 2015). With buffalo, roan, sable, and kudu being high value and sought-after trophy hunting species in Namibia, trophy size measurements for these species were chosen in this study. The study considered numbers and locations of trophy hunts, and trophy size trends over a five-year period between 2011 to 2015.

METHODS

Study area

The initial analysis of the database of trophy records primarily focused on the communal conservancies and national parks situated within the north-eastern regions of Namibia (i.e., the Namibian component of the Kavango-Zambezi Transfrontier Conservation Area) (MET/NACSO 2020). However, since the focus of the study includes the hunting of animals on all available wildlife land-types, freehold farmland was included as a part of the study (Figure 1).

The hunting of the four study species - buffalo, roan, sable, and kudu - within national parks is very limited and takes place mostly within the Bwabwata National Park and the Waterberg Plateau Park (where all four species are present). Communal conservancies do have higher quota allocations in comparison to national parks, but most of the hunting of roan, sable, and kudu takes place on privately owned farmland.

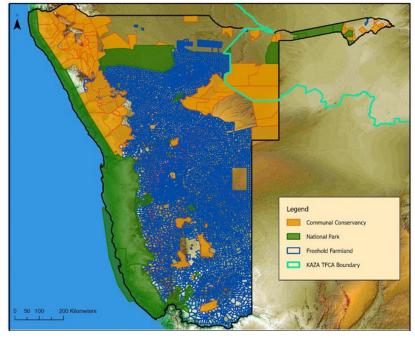


Figure 1: Land use in Namibia, subdivided into national parks, communal conservancies and freehold farmland. Target conservancies were located within the KAZA TFCA boundary.

Buffalo occur almost exclusively in the north-eastern national parks and communal conservancies; with Waterberg Plateau Park being the only exception (Kasiringua *et al.* 2017). Roan and sable occur naturally in the north-eastern national parks and communal conservancies and have been introduced to freehold farmland for hunting and live sales (Blackmore 2017). Kudu are present naturally throughout the country (Skinner and Chimbimba 2005).

Data source

Data were sourced from the Ministry of Environment, Forestry and Tourism's database of annual hunter's return forms. The forms were gathered during 2011-2015, containing details of 11,665 data entries for trophy hunts of the four species considered in this study. The forms are required to be completed by law (Nature Conservation Ordinance 1975) following each successful trophy hunt. Each of the return forms gives specific information regarding the locality of the hunt, land tenure type, the year, the nationality and name of the hunter, the permit number, the species hunted and the measurements of the trophy hunted.

There are three official methods for trophy measurement in Southern Africa which can be used to determine trophy size (van Rooyen *et al.* 2016).

These are the Rowland Ward system, the Safari Club International (SCI) system, and the South African system. Each measurement system makes use of specific measurements such as horn length, horn circumference and skull size to produce a trophy score (Figure 2). Any trophy which is considered a record-sized trophy can be added to either the Rowland Ward or the SCI record books. The publication of these records is considered essential in marketing a region, as international hunters are more likely to hunt in areas where the largest trophies were shot (du Toit *et al.* 2016).

The SCI measuring system (Schwabland and Barnhart 2016) is the most commonly used system and forms the foundation for hunter return forms submitted to the Namibian Ministry of Environment, Forestry and Tourism (Schwabland and Barnhart 2016). Records using this system were used in the analyses for this study.

To investigate whether the perception of hunting trends by hunters corresponded with the data analysis, interviews were conducted with 38 professional hunters, who have operated within several of the communal conservancies and freehold farms. Most questions were directed towards understanding their perceptions on the trends in the trophy size and to compare their perceptions with the quantitative analysis of the trophy measurements.

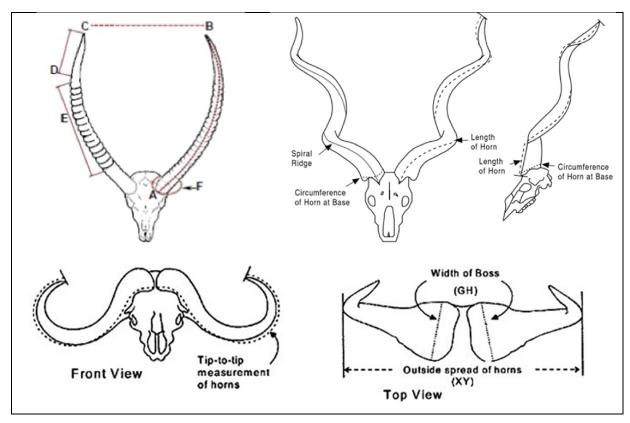


Figure 2: SCI measuring system for simple-horned antelope, spiral-horned antelope, and African buffalo (Schwabland and Barnhart 2016).

There are currently over 350 registered members of NAPHA (NAPHA, 2019); hence the sample size of 11% was considered adequate since this was not the primary focus of the overall study.

Data preparation and analysis

For each of the four study species, a quantitative assessment of annual trends of the number of animals hunted was conducted. The Kruskal-Wallis Analysis of Variance (ANOVA) test (Katz and McSweeney 1980) was used to test for any statistical significance in the annual variation per species using Statistica® Version 10 for Windows (StatSoft 2011); but only after the Shapiro-Wilks test for normality (Shapiro *et al.* 1968) was conducted on the total scores. None of the data analysed were normally distributed.

Any statistical analysis of trophy size that yielded a significant difference (p > 0.95) for a dataset was subsequently tested using the Tukey post hoc test (Tukey 1949) to determine specific significance between variables.

RESULTS AND DISCUSSION

Numbers hunted

Table 1 presents the numbers of each species hunted. Across the study area, buffalo were the only species hunted mostly in communal conservancies with a total of 237 out of 330 individuals (Figure 3a) being trophy hunted during the years 2011-2015. In the north-eastern communal conservancies. Bwabwata National Park, and the Waterberg Plateau Park, buffalo accounted for 21.95% of all trophies. Though buffalo are the 25th most commonly hunted of all species within Namibia, they are considered to be one of the most popular trophy animals to hunt in other African countries, especially among American hunters (Lindsey et al. 2006), due to it being classed as a dangerous game species (Lindsey et al. 2007), with considerable adventure and prestige being associated with a buffalo hunt (Gandy and Reilly 2004). Private ownership of buffalo is prohibited within Namibia to prevent disease transfer to cattle in accordance with European Union (EU) beef import requirements (Tekleghiorghis *et al.* 2016). Therefore, the national parks and communal conservancies have an exclusive market for hunting of this species.

Roan, alongside sable, tends to be a popular trophy species due to its attractive trophy qualities and relative rarity (Van der Merwe et al. 2004). Roan and sable populations have recovered from historical lows in the 1980s (Harrington et al. 1999; McLoughlin and Owen-Smith 2003; Owen-Smith et al. 2012) largely due to being intensively bred by commercial farmers for lucrative auction prices and hunting demand for the species (Bothma et al. 2016; Palazy et al. 2012; Rethman et al. 1996; Van der Merwe and Saayman 2005). This was followed by a period when both species were bred selectively for increased horn sizes mostly in South Africa (Nel 2015; Taylor et al. 2020), but also in Namibia (Blackmore 2017). As an example, during the study period, a roan trophy bull was sold for N\$ 1,000,000 at a commercial wildlife auction (New Era 2015). Roan is still regarded as a rare antelope in Namibia (Havemann et al. 2016; IUCN 2019b; Martin 2003), even though the recent range expansion onto freehold farmland has made the species a relatively common sight throughout Namibia. Roan was the 34th most commonly hunted species during the study period and was the 16th most popular animal to hunt in northeastern parks and conservancies (mainly within Waterberg Plateau Park and Nyae Nyae Conservancy).

In comparison to other high-value species, roan trophy hunt quotas were conservatively allocated within the north-eastern communal conservancies of Namibia. There was a slight decrease in the number of roan allocated on trophy hunting quotas within communal conservancies coinciding with an increase in the number of roan hunted - with the total amount not exceeding the newly adjusted quotas (Figure 3b), probably influenced by population counts and subsequent quota readjustments for those respective years. In 2012, the estimated number of roan in

	National Park				Communal Conservancy				Freehold Farmland						
	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015	2011	2012	2013	2014	2015
Buffalo	22	18	16	16	21	28	46	47	53	63	N/A	N/A	N/A	N/A	N/A
Roan	2	3	2	3	4	5	8	9	8	9	12	16	22	12	20
Sable	3	8	5	7	8	1	0	5	1	1	44	51	58	47	64
Kudu	3	7	9	10	12	41	50	45	28	37	2,222	2,243	2,140	1,540	1,446
Total	30	36	32	36	45	75	104	106	90	110	2,278	2,310	2,220	1,599	1,550

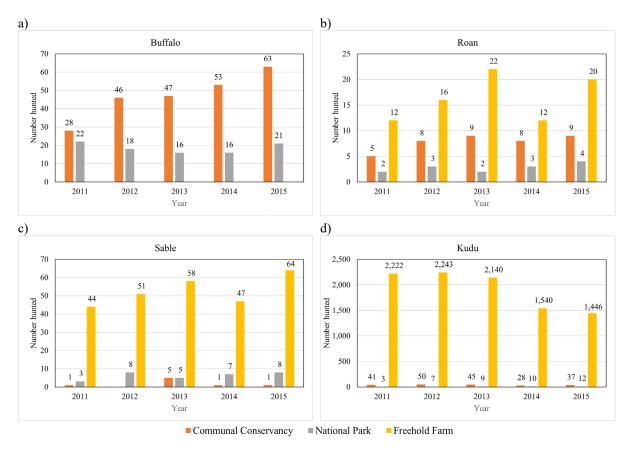


Figure 3: Total number of a) buffalo, b) roan, c) sable, and d) kudu hunted nationally during the study period on each land use. Noticeably, there was an increase in the number of buffalo and sable hunted within communal conservancies and freehold farms respectively. There was a decline in the number of kudu hunted during the study period.

Bwabwata National Park and the Zambezi conservancies were 1,789 (NACSO 2012a) and in 2015 it was 1,192 (NACSO 2015a, 2015b).

Sable was not as commonly hunted during the study period, both nationally (26th on the list of hunted animals within Namibia) and within the north-eastern national parks and communal conservancies (23rd on the list of hunted animals in north-eastern parks and communal conservancies). This contrasts with other countries where the popularity of sable-hunting (i.e. Zambia and Zimbabwe) is unquestionably high (Crosmary et al. 2013; Lindsey et al. 2007). Generally, the low numbers hunted in communal conservancies can be attributed to the limited availability of suitable habitat (Bothma et al. 2016; Martin 2003; NNF 2008) and consequently the low population numbers. Since intensive breeding of sable for huntable animals became popular later than in South Africa, far fewer individuals were hunted on Namibia's commercial hunting farms. Intensive breeding is also not as popular as in South Africa, since Namibia mostly markets hunting of animals in extensive natural landscapes as opposed to small land units with artificially bred specimens (Nel 2018).

Despite the increase in communal conservation land in the north-east, sable hunting did not increase proportionally. This is possibly due to most new conservancies being proclaimed on the Chobe East floodplains while sable tends to prefer open woodland (Skinner and Chimbimba 2005). The quota being allocated is probably a response to the number of sable observed on game counts (estimated at 1,494 in 2012 and 2,355 in 2015) (NACSO 2012a, 2015a, 2015b) or via other means of counting methodology (e.g. aerial wetland surveys and fixed foot patrols) (MET/NACSO 2020). There was no observable trend in the number of sable hunted (Figure 3c) since hunting within communal conservancies and parks was somewhat sporadic, while there was a noticeable increase in the number hunted on freehold farmland.

In terms of the desirability of kudu as trophy animal, it was the 4th most commonly hunted trophy animal in Namibia, preceded only by gemsbok, warthog, and springbok. The desirability of kudu as a huntable species in Namibia is probably linked to it being common and the appeal of the large horn size that sets it apart as a charismatic species (Crosmary *et al.* 2013), and its distribution across most parts of the country (Mendelsohn *et al.* 2002).

The number of kudu made available for trophy hunting within communal conservancies across the country increased despite the declining population

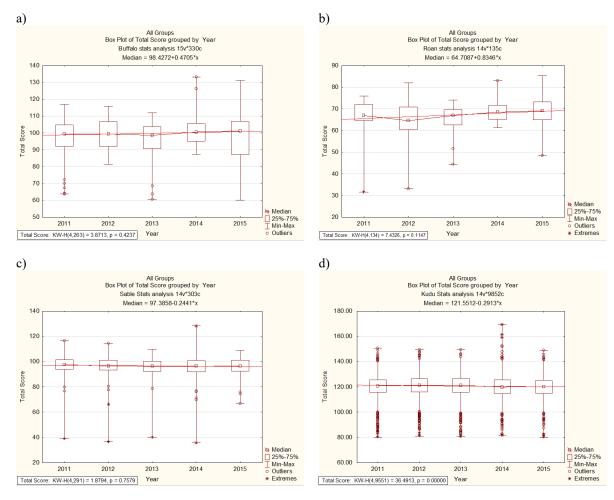


Figure 4: Trophy size over five years (2011-2015) in all land-use types for a) buffalo, b) roan, c) sable, and d) kudu. There were no statistically significant trends in trophy size for buffalo, roan, and sable over the study period. Kudu showed a statistically significant (p < 0.05) decline in horn size.

estimates for the north-western and north-eastern communal conservancies (Figure 3d), nevertheless, the percentage of the total quota for kudu was less than 5% of the estimated population (NACSO 2015a, 2015c). There was a 16.4% decrease in kudu numbers based on the 2012 and 2015 game counts in northwestern (NACSO 2015c, 2012b) and north-eastern Namibia (NACSO 2015a, 2015b, 2012a). However, it is evident that kudu is a highly utilised and popular species for trophy hunting in Namibia (Lindsey et al. 2007; MacLaren et al. 2019). The endemic presence of rabies within kudu and the ease of transmissibility within kudu herds has episodically caused a substantial decline in the kudu population in some areas of Namibia (Scott et al. 2012). During the study period, 17% (n = 271) of the reported mammal rabies cases were kudu, preceded only by cattle (n = 472)and domestic dogs (n = 494) (Rainer Hassel, personal communication, 2018).

Three of the four species showed stable or increasing trophy sizes over the five-year period (Figure 4). Considering the principle that a reduction in trophy sizes over time may indicate overhunting of trophy

animals by selectively removing animals with desirable traits (Von Brandis and Reilly 2007), this study indicates no overhunting of buffalo, roan or sable. This will allow for a sustained marketability of these species for international hunters.

Trophy size trends

Kudu

Based on the statistical significance (p < 0.05) presented by the kudu data (Figure 4d), (Table 2) kudu trophy sizes were significantly larger in 2012 and 2013 than in 2014 and 2015. This suggests an overall decline in trophy size.

The experience of wildlife veterinarians suggests that rabies affects both kudu bulls and cow-calf herds equally (Tübbesing 2016); which suggests that availability of larger trophies will be more severely impacted with reccurring rabies outbreaks (affecting the trophy bulls and influencing the reproductive rate of the population).

Buffalo

Despite the increased year-on-year trends for numbers of buffalo hunted (Figure 3a), overall trophy size was found to be stable or increasing (Figure 4a). This may be influenced by the fact that although the resident population of buffalo in the Zambezi is approximately 5,000 (Chase 2007; NACSO 2015a), in comparison to northern Botswana's estimated population of 40,000 buffalo (Chase 2017), there is a high level of dispersal and migration between Botswana and Namibia (Naidoo et al. 2014); evidenced by a collared buffalo that migrated over 100 km between the two countries in a one-year period. The total source population for buffalo is therefore extremely large and hunting at current levels is unlikely to influence trophy sizes. An advantage is that most communal wildlife areas are unfenced open systems where immigration and emigration of wildlife can occur uninterrupted and where the genetic diversity is large as a result (Naidoo et al. 2014; MET/NACSO 2020).

However, it should be noted that even though the appearance of trophy measurements during the study period indicates a non-significant (p > 0.05) positive growth trend, care should be taken to assess whether the measurement size is linked to the age of the individual animals – the increase in larger trophies might be a product of the hunting of younger individuals or bulls that are in their prime (Gandy and Reilly 2004; Jeke *et al.* 2019) since horn sizes tend to decrease after 67-72 months of age (Lepori *et al.* 2019).

Since buffalo horn size is often correlated to the openness of the environment and the nutrition available (du Toit 2016), along with the health of the individual animals (Ezenwa and Jolles 2008) the largely unfenced system of north-eastern Namibia, Zambia, Botswana, and Angola, known as the Kavango-Zambezi Transfrontier Conservation Area (KAZA) (Naidoo *et al.* 2014), will likely house a healthy number of trophy animals.

The increase of the average trophy measurements within the communal conservancies and the national parks stands in contrast to what is being observed elsewhere in Africa (e.g. Zimbabwe and Tanzania) (Wilfred 2012; Ngorima and Mhlanga 2015).

Roan

There was a marginal, but statistically nonsignificant, increase in roan trophy size over the fiveyear period (Figure 4b). Roan hunts were mostly on freehold farmland (60.7% throughout the study period), and it was expected that the increase would be more noteworthy since roan are one of the most popular intensively bred species on freehold farmland, where selection for animals with large horn sizes is practiced commonly (Blackmore 2017; Nel

Table 2: Tukey post hoc test for the kudu national trophy size data for the years 2011-2015. Statistical significance for the corresponding years is indicated as follows: p < 0.05; **p < 001; ***p < 0.005.

Year	{2011}	{2012}	{2013}	{2014}	{2015}
	(120.35)	(121.02)	(120.90)	(119.98)	(119.84)
2011		0.0746	0.2263	0.6976	0.3998
2012	0.0746		0.9904	0.0026	0.0005
				***	***
2013	0.2263	0.9904		0.0129	0.0028
				*	***
2014	0.6976	0.0026	0.0129		0.9916
		***	*		
2015	0.3998	0.0005	0.0028	0.9916	
		***	***		
l					

2015). Roan trophies were only marginally larger on freehold farmland than in communal conservancies. Although the largest trophies were consistently hunted in the national parks where they occur naturally, there was a significant decline in the sizes of roan trophies in the national parks.

Sable

There was an overall decline in the trophy size for sable (Figure 4c), but based on the further in-depth statistical analysis, there was a steeper decline in the sable trophy horn measurements in the national parks than in any of the other land-uses - however, there was no significant difference (p > 0.05) in sable trophy sizes over the five-year period. If trophy size is therefore truly an indication of population health, the trends might be similar to those of the greater Hwange conservation area, where the sable population did not seem to thrive in the national parks (Crosmary et al. 2015). Some studies mention that sable is reliant on open woodlands and grasslands for reproduction (Bothma et al. 2016; Capon 2012; Crosmary et al. 2015; Skinner and Chimbimba 2005), but, if sable are under hunting pressure, they will relocate to the safety of closed woodlands where they are difficult to locate and hunt (Ndaimani et al. 2014).

Hunter perception

Hunter perception seemed to closely mirror the quantitative trends found in Figures 4a to 4d within conservancies and national parks (Figure 5). Of the hunters questioned (n=15) 26% felt that buffalo trophy size was increasing, 47% claimed that the trophy size trends were stable, and the remaining 26% felt that trophy sizes were decreasing. In terms of roan, 38% of the hunters felt that the trophy sizes had increased, and the remaining 62% perceived that trophy sizes were stable. For sable, 25% of the hunters felt that the trophy sizes were increasing and

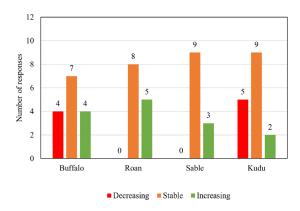


Figure 5: Hunter perceptions of trophy size within communal conservancies and national parks show mostly stable to increasing trophy size trends for all four species.

the remaining 75% claimed that the trophy sizes were stable. In contrast to the other species, it was felt by only 13% of the hunters that the kudu trophy sizes had increased, 56% believed that the trophy sizes were stable, and the remaining 31% perceived that the trophy sizes had decreased.

On private land hunter perception tended to overestimate trophy size trends for sable over time (e.g. Figure 4c versus Figure 6). For buffalo, roan, and kudu, the perceived trends were similar to the reported measurements.

CONCLUSION AND RECOMENDATIONS

This study indicated that trophy measurements for buffalo and roan were stable to increasing. This was found across all areas indicating that hunting of these species for the study period was indeed sustainable. Sable trophy measurements declined mostly in national parks, which indicates that adaptive management is needed to ensure the sustainability of hunting sable in these areas. Of most concern is the significant decline in kudu trophy sizes, where the combination of rabies and overhunting seems to be affecting the numbers of large trophies and possibly the national population of the species negatively.

The largest buffalo trophies were found in the northeastern conservancies (specifically Balyerwa) and Bwabwata National Park – since this is where the species is commonly hunted in Namibia and where it occurs in larger numbers. For roan, the largest trophies for Namibia were recorded mainly on freehold farmland. In terms of sable, the reported top trophy was recorded in Bwabwata National Park, but a majority of the largest trophies were hunted on freehold farmland. The largest trophies for kudu were all hunted on freehold farmland, mainly in central Namibia.

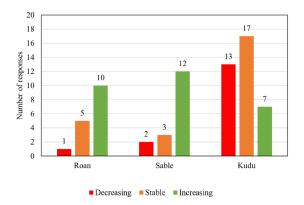


Figure 6: Hunter perceptions of trophy size within freehold farmland show mostly stable to increasing trophy size trends for roan and sable and stable to decreasing trophy size trends for kudu.

The study also found that hunters' perceptions of trophy sizes are a good indication of trends, indicating that their opinions are important to use when considering trophy hunting sustainability. Regular structured surveys should therefore be conducted in addition to the trophy return forms to provide input into adaptive setting of trophy quotas for the future.

Additional studies of age-related trophies would provide additional value in assessing the true value of conservation hunting (hunting post-reproductive males rather than the males with the highest trophy score).

This study mainly sought to discover the trends in the high-value species of the north-eastern regions of Namibia, and the possible influences on these trends between the different land uses. More detailed studies should be conducted to link the trends with other important variables (e.g. rainfall, trends in poaching, the vegetation type that allows for visibility, fire frequency, trophy trends in other native ranges, the human population density in the local and international ranges, the density of large carnivores in home ranges of the study species, the hunting experience of the professional hunters involved, the movement of species in open systems, and the economic drivers in trophy desirability).

The impact of commercial farmers relocating sable and roan to private farms on unsuitable habitat and in areas where they did not previously occur needs further investigation. This impact relates to the impact on trophy sizes with selective breeding, the impact on habitats and the reputational impact of hunting trophies in unnatural conditions, which contrasts with Namibia's reputation of natural hunting conditions.

ACKNOWLEDGEMENTS

A special thanks is offered to the colleagues of the World Wildlife Fund in Namibia, the NACSO Natural Resource Working Group and the Ministry of Environment, Forestry and Tourism. Their knowledge of the hunting industry and species that were a subject of the study proved invaluable. Furthermore, I would like to thank the members of the Namibian Professional Hunter's Association and other members of the hunting community for providing valuable insights regarding the role of hunting and the observed trends in the data. I would like to thank Peter Erb and Florian Weise for aiding with the improvement of the manuscript during the review process. My appreciation should be expressed to the Deutscher Akademischer Austauschdienst (German Academic Exchange Service) for funding this project. The financial aid provided was well spent and helped in the advancement of natural resource management.

REFERENCES

- Arnett EB, Southwick R. 2015. Economic and social benefits of hunting in North America. *International Journal of Environmental Studies* 72:734–745.
- Balčiauskas L, Varanauskas R, Bukelskis E. 2017. Impact of selective hunting on the trophy size of roe deer: Baltic example. *North-Western Journal of Zoology* 13:118-127.
- Blackmore A. 2017. Selective breeding and the intensive management of wildlife: a legal challenge for Namibian conservation. *African Journal of Wildlife Research* 47:65–78.
- Bond I, Child B, de la Harpe D, Jones B, Barnes J, Anderson H. 2004. Private land contribution to conservation in South Africa. In: *Parks in transition: Biodiversity, rural development and the bottom line*. Earthscan, London, UK. pp 29-61.
- Bothma J du P, Sartorius von Bach HJ, Cloete PC. 2016. Economics of the wildlife industry in Southern Africa. In *Game ranch management*, 6th edition. Van Schaik Publishers, Pretoria, South Africa. pp 85-94.
- Crosmary WG, Loveridge AJ, Ndaimani H, Lebel S, Booth V, Côté SD, Fritz H. 2013. Trophy hunting in Africa: long-term trends in antelope horn size. *Animal Conservation* 16:648–660.
- Di Minin E, Leader-Williams N, Bradshaw CJ. 2016. Banning trophy hunting will exacerbate biodiversity loss. *Trends in Ecology & Evolution* 31:99–102.
- Douhard M, Festa-Bianchet M, Pelletier F, Gaillard JM, Bonenfant C. 2016. Changes in horn size of Stone's sheep over four decades correlate with trophy hunting pressure. *Ecological Applications* 26:309–321.
- Erb KP. 2004. Consumptive wildlife utilization as a landuse form in Namibia. Master's Degree, Stellenbosch University.
- Festa-Bianchet M, Coltman DW, Turelli L, Jorgenson JT. 2004. Relative allocation to horn and body growth in bighorn rams varies with resource availability. *Behavioral Ecology* 15:305–312.
- Gallo T, Pejchar L. 2016. Improving habitat for game animals has mixed consequences for biodiversity conservation. *Biological Conservation* 197:47–52.
- Humavindu MN, Barnes JI. 2003. Trophy hunting in the Namibian economy: an assessment. South African Journal of Wildlife Research 33:65–70.

- Jones B, Weaver C. 2009. CBNRM in Namibia: growth, trends, lessons and constraints. In: *Evolution and innovation in wildlife conservation: parks and game ranches to transfrontier conservation areas*. Routledge, London. pp 223—242.
- Kasiringua E, Kopij G, Proches S. 2017. Daily activity patterns of ungulates at water holes during the dry season in the Waterberg National Park, Namibia. *Russian Journal of Theriology* 16:129–138.
- Katz BM, McSweeney M. 1980. A multivariate Kruskal-Wallis test with post hoc procedures. *Multivariate Behavioral Research* 15:281–297.
- Lindsey PA, Alexander R, Frank LG, Mathieson A, Romanach SS, 2006. Potential of trophy hunting to create incentives for wildlife conservation in Africa where alternative wildlife-based land uses may not be viable. *Animal Conservation* 9:283–291.
- Lindsey PA, Roulet PA, Romanach SS. 2007. Economic and conservation significance of the trophy hunting industry in sub-Saharan Africa. *Biological conservation* 134:455–469.
- Mendelsohn J, Jarvis AM, Roberts CS, Robertson T. 2002. Atlas of Namibia: A portrait of the land and its people. New Africa Books, Cape Town, South Africa.
- MET/NACSO. 2020. The state of community conservation in Namibia (Annual Report 2018). NACSO, Windhoek, Namibia.
- Munn IA, Hussain A, Spurlock S, Henderson JE. 2010. Economic impact of fishing, hunting, and wildlife-associated recreation expenditures on the southeast US regional economy: an input-output analysis. *Human Dimensions of Wildlife* 15:433–449.
- Naidoo R, Du Preez P, Stuart-Hill GC, Beytell P, Taylor R. 2014. Long-range migrations and dispersals of African buffalo (*Syncerus caffer*) in the Kavango–Zambezi Transfrontier Conservation area. *African Journal of Ecology* 52:581–584.
- Nel EJ. 2018. Potential risks and collateral damage that the shooting of intensively and selectively bred game, including captive-bred lions, may have on the contribution by the hunting sector to the biodiversity economy. Unpublished report: SA Hunters and Game Conservation Association. pp 1-46.
- Ngorima P, Mhlanga W. 2015. Analysis of trends on trophy quality of African elephant, lion, buffalo and stakeholders perceptions in Sengwa Wildlife Research Area, Zimbabwe from 2003 to 2013. Harare, Zimbabwe.
- PACEC. 2006. The economic and environmental impact of sporting shooting. Unpublished report: Public and Corporate Economic Consultants. pp. 1-28.
- Packer C, Brink H, Kissui BM, Maliti H, Kushnir H, Caro T. 2011. Effects of trophy hunting on lion and leopard populations in Tanzania. *Conservation Biology* 25:142–153.
- Patmore N, Wilson M, Clifford T. 2015. Analysis of trends on trophy quality of African elephant, lion, buffalo and stakeholders perceptions in Sengwa Wildlife Research Area, Zimbabwe from 2003 to 2013. Harare, Zimbabwe.
- Pigeon G, Festa-Bianchet M, Coltman DW, Pelletier F. 2016. Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications* 9:521–530
- van Rooyen N, van Rooyen J. 2016. Handling and measuring trophies. In *Game ranch management*, 6th edition. Van Schaik Publishers, Pretoria, South Africa. pp 719-753.

- van Schalkwyk DL, McMillin KW, Witthuhn RC, Hoffman LC. 2010. The contribution of wildlife to sustainable natural resource utilization in Namibia: a review. *Sustainability* 2:3479–3499.
- Schwabland J, Barnhart LI. 2016. Safari Club International: Official measurer's manual. Safari Club International, Tucson, AZ.
- Shapiro SS, Wilk MB, Chen HJ. 1968. A comparative study of various tests for normality. *Journal of the American statistical association* 63:1343–1372.
- Sheikh PA, Bermejo LF. 2019. *International trophy hunting*. Congressional Research Service, Washington, D.C.
- Skinner JD, Chimbimba CT. 2005. *The mammals of the southern African sub-region*. Cambridge University Press, London.
- Songorwa AN, du Toit M. 2007. Hunting in Tanzania: has science played its role? *Tanzania Journal of Agricultural Sciences* 8.
- StatSoft. 2011. Statistica 10 Features. Statistica 10. http://www.statsoft.fr (14 July 2020).
- du Toit JG, van Rooyen J, Bothma J du P. 2016. Trophy hunting. In *Game ranch management*, 6th edition. Van Schaik Publishers, Pretoria, South Africa. pp 671–673.

- Tekleghiorghis T, Moormann RJ, Weerdmeester K, Dekker A. 2016. Foot-and-mouth disease transmission in Africa: Implications for control, a review. *Transboundary and Emerging Diseases* 63:136–151.
- Tübbesing U. 2016. Rabies in kudus and eland: Implications to the game industry in Namibia. In: 9th International Wildlife Ranching Symposium. Colorado State University. Libraries.
- Tukey JW. 1949. Comparing individual means in the analysis of variance. *Biometrics*:99–114.
- Von Brandis R. 2004. *Trophy quality in monitoring ungulate population status in sub-Saharan Africa*. PhD, Tshwane University of Technology, Pretoria.
- Von Brandis RG, Reilly BK. 2007. A temporal analysis of trophy quality in South Africa: has trophy quality changed over time? *South African Journal of Wildlife Research* 37:153–158.
- Wilfred P. 2012. Trophy hunting and trophy size in Ugalla Game Reserve, western Tanzania. *Tanzania Journal of Science* 38:110–121.

Understanding community attitudes toward the Angolan giraffe (*Giraffa giraffa angolensis*) and its potential reintroduction into Iona National Park, Angola

J Hamutenya ^{1,2}, M Hauptfleisch¹, V De Cauwer¹, J Fennessy², S Fennessy², T Nzuma¹

URL: https://nje.org.na/index.php/nje/article/view/volume6-hamutenya Published online: 18th July 2022

Date received: 8th March 2022; Date accepted: 23rd June 2022.

ABSTRACT

Wildlife introductions are often preceded by habitat suitability studies, although to date the possible impact of human communities' attitudes towards reintroductions of species have seldom been assessed in any detail. Iona National Park (NP) in Angola is inhabited by people, predominantly on the eastern fringes, and as such any reintroduction would benefit from the buy-in of these communities. Therefore, understanding community attitudes is essential for successfully reintroducing the Angolan giraffe (*Giraffa giraffa angolensis*) in Iona NP where the species has been locally extinct since before the 1980s due to indiscriminate poaching during the Angolan civil war. We undertook structured interviews of individuals (n = 82) from the Iona community living inside the park to: a) investigate their attitudes toward an Angolan giraffe reintroduction, b) understand people's willingness to co-exist with giraffe, and c) assess the risk of poaching. Our analyses revealed that whilst most people in the study area had never seen a live giraffe, they remained positive towards reintroducing them into the park. Only the minority Mungambwe and Mucubal ethnic groups, who are traditional agro-pastoral farmers, showed a neutral or negative attitude towards the reintroduction and were concerned about possible poaching of giraffe. The observed support by the majority of local communities for the potential reintroduction will be an advantage for conservation planners and managers moving this valuable conservation initiative forward.

Keywords: Angola, Giraffa giraffa angolensis, giraffe, Iona National Park, poaching, public attitudes, reintroduction

INTRODUCTION

Over the last three and half decades, giraffe (Giraffa spp.) populations throughout the African continent have declined by approximately 30% (Brown et al. 2021). In contrast, those in southern Africa are bucking this trend with some giraffe populations flourishing (O'Connor et al. 2019; Brown et al. 2021). With these positive trends in giraffe numbers in several parts of southern Africa, there is now the opportunity to explore their reintroduction into areas where they have become locally extinct. The vast areas of historical giraffe range, including Iona National Park (NP) in Angola, have not been reestablished. Giraffe were known to have occurred in some areas of southern Angola until the 1980s (East 1999). Their local extinction was driven by anthropogenic factors, in particular indiscriminate poaching during the civil war that lasted more than four decades (Huntley & Russo 2019).

Following Angola's peaceful transition from the civil war in 2002, the country renewed its commitment to conservation (Mendelsohn & Mendelsohn 2018). With this renewed commitment, hunting is only allowed when permitted by the government. Also, a small number of extralimital South African giraffe

(G. giraffa giraffa) were translocated from South Africa into Kissama NP in 2017 (Marais et al. 2019). Whilst this was seen as a positive conservation effort by many, from a biodiversity perspective, it would have been more appropriate to reintroduce Angolan giraffe (G. g. angolensis) considering that this was their former natural range (Sarrazin & Barbault 1996). Efforts to re-establish demographically and genetically viable free-ranging populations of giraffe do not only benefit conservation (Muller et al. 2020; Lee et al. 2020), but also local communities through ecotourism. Since the local extirpation of Angolan giraffe from southern Angola, small-scale private conservation and tourism efforts have brought back giraffe (and other wildlife) to some private conservation areas but not to any state-run protected areas (Marais et al. 2019). There is concern that even if Iona NP's habitat was suitable, offering sufficient browse availability, the risk of poaching in the vast and under-resourced park might be a threat, especially as community perceptions toward giraffe were unknown. Historically, wildlife introductions have been preceded by habitat suitability assessments. However, the human dimensions of such introductions are often overlooked, inspite of the fact that most of the species were exterminated by humans or anthropogenic activities (Bencin et al.

Biodiversity Research Centre, Namibia University of Science and Technology, PO Box 13388, Windhoek, Namibia. jacksonshapumba@gmail.com

² Giraffe Conservation Foundation, PO Box 86099, Eros, Windhoek, Namibia

2016; Glikman *et al.* 2022; Kansky *et al.* 2016; König *et al.* 2020; Koziarski *et al.* 2016; Malviya *et al.* 2022; Nyhus 2016). Human dimension of wildlife (HDW) studies were identified to cover socioeconomic aspects of wildlife reintroduction (Bath 1989).

A review of existing literature revealed that HDW studies have been employed severally in assessing communities' attitudes and perceptions towards wildlife reintroductions (Bath 1989; Elizabeth et al. 2019; Miller 2009; Pate et al. 2016; Ruppert 2020; Glikman et al. 2022). Attitude surveys help to predict how people's attitudes could influence conservation policies and vice versa, allowing for more effective management and planning (Pamela & Lynn 1988). This approach has supported conservation managers in better understanding the local communities' opinions regarding the acceptance of conservation activities such as wildlife reintroductions. Importantly, HDW takes into account economic issues as well as attitudes and beliefs that can help wildlife managers to better understand the entire human component (Bath 1998). Understanding people's attitudes and perceptions prior to a specific proposal can help managers to predict where reintroductions may be supported by communities versus where they would be hindered (Elizabeth et al. 2019; Kansky et al. 2016).

general, implicit costs associated conservation, such as crop damage and livestock predation by wildlife, have negative effects on local attitudes, in comparison to the perceived and real benefits from tourism, employment, and other livelihood opportunities (Nyhus 2016). Negative attitudes toward wildlife often encourage people to kill wild animals (Mir et al. 2015; Mogomotsi et al. 2020; Pamela & Lynn 1988), which over time can take a toll on conservation efforts. Negative interactions between people and wildlife not only have adverse effects on rural livelihoods but can also to negative attitudes toward wildlife conservation and general aversion toward wildlife resources (Bencin et al. 2016; Glikman et al. 2022; Kansky & Knight 2014; Koziarski et al. 2016; Malviya et al. 2022; Nyhus 2016). Such negative attitudes can undermine local, national, regional, and international conservation initiatives, but can also be used to plan for awareness programmes and other related conservation interventions ensuring their long-term viability. Bath (1989) further stated that people are likely to oppose species that may endanger human lives and their properties and accept those that do not pose any threat. Based on experience from other giraffe populations throughout Africa, the interactions between humans, livestock and giraffe can potentially result in some level of conflict generally known as Human-Wildlife Conflict (HWC) including crop raiding, bi-direction transmission of pathogens, perceived forage competition and more (Fennessy *et al.* 2020). These scenarios are best assessed on a case-by-case basis before a reintroduction occurs to ensure long-term success.

Demographic characteristics of communities are also important predictors of attitudes toward species reintroductions (Deruiter & Donnelly 2002; Kansky et al. 2016). For example, race, sex, age, income, and educational level can influence people's attitudes toward wildlife. Mir et al. (2015) found that women, older people, people with a lower education level, people working in a natural-resource-dependent profession, or people living in a rural area within a carnivore distribution range tend to have more negative attitudes. Similarly in Kenya, the elderly were unhappy with African savanna elephants (Loxodonta africana) that raid their crops (Weinmann 2018). It is therefore important for wildlife managers to have information on each of these components and the interactions between humans, wildlife populations, and habitat to maximise a successful wildlife reintroduction (Elizabeth et al. 2019).

The recent increase of people in and around Iona NP highlights the importance of a HDW assessment to document and better understand the communities' attitudes and perceptions regarding a potential giraffe reintroduction. As such, the main objectives of the study were to analyse residents' willingness to coexist with giraffe, and to understand their attitudes towards reintroduction and the risk of giraffe poaching. These results will be used to inform any decisions regarding a potential reintroduction of giraffe into Iona NP in Angola.

METHODS

Study area

The study was conducted in Iona NP, located in the Namibe Province in the arid extreme south west of Angola (Mendelsohn & Mendelsohn 2018). The 15,150 km² park is bounded by the Curoca River to the north and the Cunene (Kunene) River to the south, which also forms the national border with Namibia. The Atlantic Ocean borders Iona NP to the west, whereas the Otchifengo Valley defines its boundary to the east. As some parts of the park are extremely inaccessible, Iona NP has not been completely de-mined especially in the far-east since the civil war (Landminesinafrica 2017). As such, the interviews were conducted along key access routes to the Iona village, which is located near a potential giraffe reintroduction site (Figure 1). There are several villages in the park, however, Iona is the largest and fastest growing settlement in the park, and the only village comprised of residents from many ethnic groups (Morais et al. 2019).

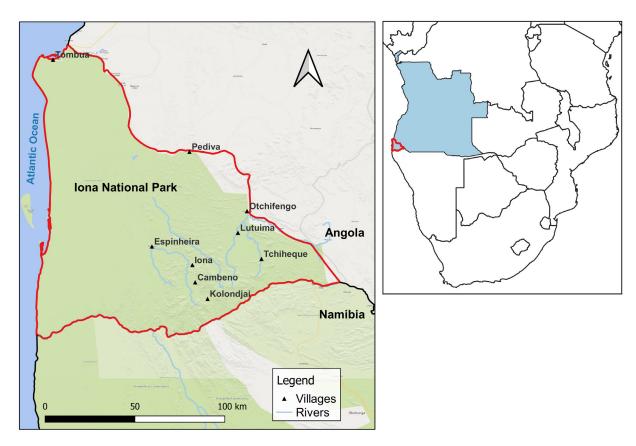


Figure 1: Map of Iona National Park and those communities within its boundaries, southwest Angola.

The study area is mainly inhabited by traditional pastoral or agro-pastoral communities that initially concentrated along the eastern and southeastern boundary (Curoca and Cunene Rivers) of the park. In the 1970s, 300 people were recorded living inside the park. This number increased to ~3,385 individuals in 2016, at which time 2,311 or 68% of the park's population had settled in Iona village (Mendelsohn & Mendelsohn 2018; Ministério do Ambiente 2015). Dairy products make up a major component of the population's diet, and the need for cattle enclosures close to dwellings has led to a relatively scattered settlement pattern.

Data collection

In October 2019, face-to-face closed-ended questionnaires (Table 1) were used to assess local community members' attitudes towards a proposed reintroduction of Angolan giraffe into Iona NP. For developing the interview questions, colleagues working in other parts of Africa on various aspects of HDW related to giraffe were consulted to ensure relevance and appropriateness. Access to the park and ethical clearance for the surveys were provided by the park authority through the EU funded transboundary SCIONA project (http://sciona.nust.na). The questionnaires were administered opportunistically to individuals with the only sampling criterion being those who were logistically

accessible and willing to answer. Each interview lasted about 25 to 30 minutes. Due to poor infrastructure in southern Angola, and a latent postwar threat of anti-personnel mines, it was not possible to access a wide geographical area or introduce a randomised survey design. Interviews were conducted in English and translated as appropriate into Portuguese and/or Otjiherero through local interpreters (two post-graduate students and a park ranger at different times).

Individuals were interviewed either at their house or a previously identified location in the village (e.g. at the waterholes). Before conducting the interviews, consent was obtained from all respondents and they were informed that all their responses will remain anonymous. A multiple Likert scale questionnaire was used to collect the data (Likert 1932). The Likert scale is broadly used as a rating scale that requires respondents to indicate their degree of agreement or disagreement (Kroonenberg & Greenacre 2004; Gyimah 2016). Question statements and measured variables are presented in Table 1.

The interview targeted adults, both men and women covering young adulthood (18-35 years; n = 45), middle age (36-55 years; n = 26), and older adulthood (56 years and older; n = 11). All responses were recorded on a Huawei tablet device using the survey software Epicollet5 App (Mathews & Flynn

Table 1: Question statement and variables measured during the HDW community surveys in Iona NP, Angola.

Demographics	Variables	MCP map variables
Gender	Male, Female	Gender
Age group	18-25, 26-35, 36-45, 46-55, 56-65, > 65	Age group
Ethnicity	Himba, Curoca, Mungambwe, Kimbari, Mucubal, Other	Ethnicity
Employment	Herder, Hunter-gatherer, Unemployed, Crop farmer, Livestock trader	Employment
Education	Pre-primary to 6, Grade 7-9, Grade 10-13, None	Education
Respondents' attitudes towards the presence of wildl	ife and benefits received from them	
Do you enjoy having wildlife in this area?	No, Yes	
Do you receive benefit from wildlife of any kind?	No, Yes	
Encounter or experience with giraffes		
Have you seen giraffe in your area before?	No, Yes	
Respondents' knowledge and views on the potential i	reintroduction of giraffe to the area	
Do you recommend the reintroduction of giraffe in this area?	No, Yes	Reintroduction (1)
It is possible to reintroduce giraffe in this area?	Not likely, Somewhat likely, Unsure, Likely, Very likely	Reintroduction (2)
It is possible for both people and giraffe to live together in this area	Not likely, Somewhat likely, Unsure, Likely, Very likely	Co-exist
Do you think that giraffe will have impact (s) on other wild animals or livestock?	No, Not sure, Yes	
Respondent's views on the potential poaching of rein	troduced giraffe in Iona National Park	
People would kill giraffe if they were in this area.	Strongly agree, Agree, Undecided, Disagree, Strongly disagree	Poaching (1)
How likely giraffe would be killed for bushmeat?	Not likely, Somewhat likely, Unsure, Likely, Very likely	Poaching (2)
How likely giraffe would be killed because of competition with livestock?	Not likely, Somewhat likely, Unsure, Likely, Very likely	Poaching (3)
How likely giraffe would be killed for (cultural) practices?	Not likely, Somewhat likely, Unsure, Likely, Very likely	Poaching (4)
Most people in this area would not be happy if someone killed a giraffe.	Strongly agree, Agree, Undecided, Disagree, Strongly disagree	Poaching (5)
Most people in this area would not be happy if someone killed a giraffe.	Strongly agree, Agree, Undecided, Disagree, Strongly disagree	Poaching (6)
Resident's views on legality and motivation for hunti	ng	
If someone is found hunting how likely would they be arrested?	Not likely, Somewhat likely, Unsure, Likely, Very likely	
If someone is found hunting how likely would they be fined?	Not likely, Somewhat likely, Unsure, Likely, Very likely	
If someone is found hunting how likely would they be beaten?	Not likely, Somewhat likely, Unsure, Likely, Very likely	

2018). The software allows the user to record a GPS point location, automatically records time, date and allows easy exporting of data into MS Excel for data processing and cleaning (Mathews & Flynn 2018). The direct data entry helps to limit additional human error from data transcription. To reduce potential external influences and biases in answers during the interviews, respondents were asked not to discuss anything from the interview with others who were yet to be interviewed (Sampson et al. 2019), or were asked to stay with the researchers until all other people were interviewed.

Data analysis

All quantitative data were analysed using descriptive statistics and performed in XLSTAT (www.xlstat.com). Multiple Correspondence Analysis (MCA) was used to assess the association between response categories and sociodemographic variables. A Chi-square test was used to assess the effect of all demographic variables.

RESULTS

Respondent demographics

Eighty-two individuals, 65 males (79%) and 17 females (21%), were interviewed in and around Iona village. The highest proportion of respondents were 26-35 year olds (37%), followed by 36-45 years (24%), 18-25 years (18%), 56-65 years (10%), 46-55 years (7%) and >65 years (4%). With respect to ethnicity/tribes. majority were the (Ovahimba) (n = 55; 67%), followed by Curoca (n = 22; 27%) and then low numbers of Mungambwe (n = 2; 2%), and Kimbari, Mucubal and Other (each n = 1; 1%, respectively). Sixty-three individuals (77%) identified as herders (cattle, goats, sheep and/or donkeys), nine (11%) as hunter-gatherers, five (6%) as unemployed, four (5%) as crop farmers and only one (1%) as a livestock trader. Most of the respondents had never attended school (n = 67; 82%), with only nine (11%) individuals holding preprimary to Grade 6 qualifications, and three (4%) each attending Grade 7-9 and Grade 10-13, respectively.

Respondents' attitudes towards the presence of wildlife and benefits received from them

Almost all respondents (n = 79; 96%) were happy to live with wildlife, with only a few exceptions (n = 3; 4%). The majority (n = 68; 83%) of respondents indicated that they do not receive any benefit of any kind from wildlife, whilst 14 (17%) individuals indicated they had have received minor benefits from tourists taking photographs with them. When the latter was tested against demographic variables, a significant difference was detected across age groups (χ 2 (12), df = 5, p < 0.015), whereby individuals aged 26-35 years mostly reported benefits.

Respondents' knowledge and views on the historical presence and potential reintroduction of giraffe to the area

Almost all interviewed respondents (n = 80, 98%) had never seen a giraffe; only 2 (2%) individuals had seen one in the area and both more than 30 years ago. When asked whether they support a future giraffe reintroduction, the majority (n = 80, 98%) said 'Yes' and only two (2%) responded 'No'. Ovahimba tribe showed a more positive attitude towards a potential giraffe reintroduction. The majority of respondents expressed a willingness to live with giraffe if introduced (n = 71; 86%), with nine (11%) being unsure, and two (2%) responded as somewhat likely. The results showed that there were significant differences across the ethnic groups (χ^2 (18.3), df = 10, p < 0.008) with Ovahimba people responding more positively to the prospect of living with giraffe. When asked whether they thought that giraffe would have any impact on livestock or other wildlife, almost two-thirds (n = 53, 65%) of the respondents were unsure, approximately a third (25, 31%) said 'No', and only four (5%) responded 'Yes', showing that only a few respondents thought that giraffe will impact other animals.

Respondents' views on the potential poaching of reintroduced giraffe

With respect to the poaching risk, more than twothirds (n = 57, 70%) indicated that giraffe would not be poached if they were in the area, whilst a fifth (n = 17; 20%) remained neutral or 'undecided', and only eight (10%) thought they will be poached.

The respondents' attitudes on how likely giraffe would be poached for bushmeat showed that a little more than half (n = 47, 57%) of the individuals feel it is unlikely. A total of 24 (29%) of respondents were unsure, nine (12%) individuals expressed it was somewhat likely and only two (2%) felt it was likely. Interestingly, 24 people were unsure, indicating that they didn't know whether giraffe meat was edible. The responses to this statement were significantly different across age groups (χ^2 (25), df = 15, p < 0.037). Individuals aged 26-45 years and those who never attended school were against killing giraffe for bushmeat. The majority (n = 68; 83%) of respondents felt that competition between livestock and giraffe would not be likely and thus not a reason for killing them, a small number (n = 13; 16%) was unsure and only one (1%) responded as likely. A highly significant difference between demographics was detected across ethnic groups (χ^2 (18.3), df = 10, p < 0.0001), and educational level (χ^2 (12.6), df = 6, p < 0.0001). The Ovahimba held more positive attitudes than others that it was unlikely giraffe would be killed as competitive herbivores to livestock, as well as a more positive attitude than respondents without school education.

The respondents were mostly optimistic that giraffe would not be killed for cultural practices – little more than half (n = 45, 55%) stated that it would not be likely, a third (n = 28; 34%) were unsure, and a low number (n = 9, 11%) responded somewhat likely. The majority of respondents (n = 70; 85%) agreed that people would not be happy if someone killed a giraffe, whilst six (7%) individuals were neutral (undecided), and six (7%) disagreed.

Residents' views on legality and motivation for hunting

This section aimed at understanding residents' knowledge towards law enforcement and their motives to hunt wildlife despite Angolan laws and regulations. Almost all respondents (n = 80; 98%) indicated that hunting wildlife was illegal.

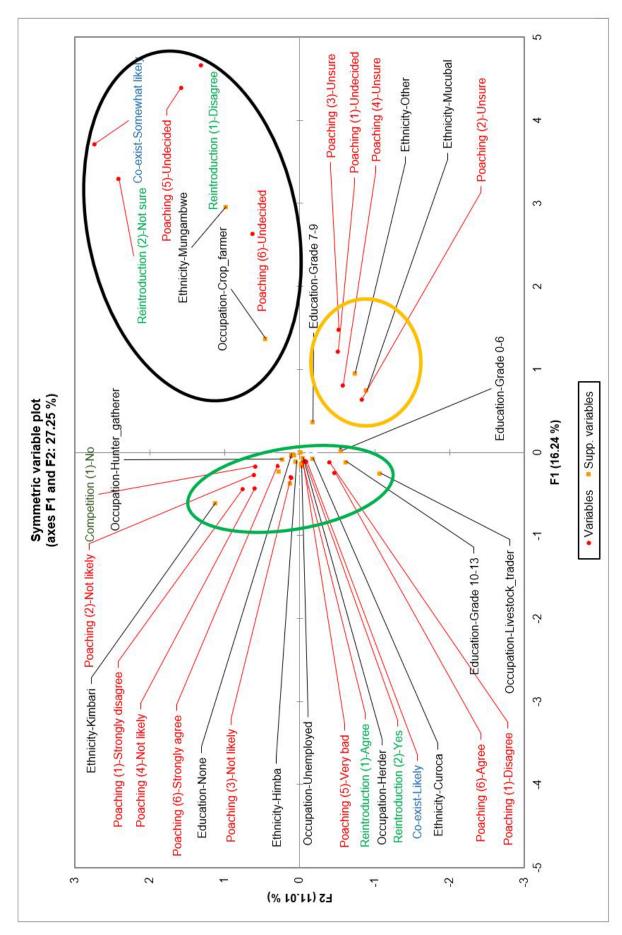


Figure 2: Multiple Correspondence Analysis of respondents towards response questions of giraffe reintroduction, co-existence and poaching risk in Iona National Park, Angola.

Respondents were asked if they were made aware that hunting of wildlife was prohibited, and how likely it was that would people still hunt. Almost half (n = 39; 48%) responded as somewhat likely, 29 (35%) individuals were unsure and a further 14 (17%) stated as not likely. Those that answered "somewhat likely" were further asked to briefly explain why people will still hunt regardless of regulations. Some responded that poaching would occur due to hunger, whilst others said that only carnivores are hunted simply because they prey on their livestock. A significant difference to this response was detected across occupations whereby herders (χ^2 (15.5), df = 8, p < 0.037) showed a negative attitude towards poaching.

Respondents were asked three questions about different law enforcement measures applied by conservation officials in Angola regarding poaching (illegal hunting):

1) If someone is found hunting how likely would they be arrested?

Almost all (n = 79; 97%) respondents believed that it is highly likely or likely, while three (3%) were unsure. The Ovahimba showed a more positive response which was statistically significant (χ^2 (25), df = 15, p < 0.0001) that poachers were very likely to be arrested.

2) If someone is found hunting how likely would they be fined?

Approximately two-thirds (n = 53; 64%) of respondents were unsure, with 22 (27%) mentioning that it is unlikely and seven (9%) responded as somewhat likely.

3) If someone is found hunting how likely is it that they would be beaten?

More than half (n = 49; 59%) of the respondents were unsure, whilst 31 (39%) indicated not likely, and only two (2%) considered the possibility as very likely.

Results of a holistic Multiple Correspondence Analysis

The graphical results of the MCA used to uncover the interrelationships between response categories of a set of questions and explanatory demographic variables in the survey is presented in Figure 2. Respondents who support reintroduction are located left (with positive views) on the upper and bottom (green circle). This group also contained those who opposed poaching and were willing to co-exist with giraffe. On the right upper side (black circle) are the individuals exhibiting negative attitudes towards giraffe reintroduction, have positive attitudes to

poaching and were not willing to co-exist with them. On the right lower quadrant (orange circle) lies respondents who were neutral towards a reintroduction, poaching and co-existing with giraffe.

All groups (Ovahimba, Curoca, herders, unemployed and those who did not attend school), with the exception of the Mungambwe and Mucubal ethnic groups, expressed positive attitudes towards a giraffe reintroduction and negative attitudes toward poaching (Figure 2).

DISCUSSION

The key findings from this study revealed a high level of support from the Iona communities towards a potential giraffe reintroduction into the park. Inspite of a majority of the respondents not knowing the giraffe physically nor having any knowledge regarding the impacts giraffe are likely to have on other wild animals or livestock, almost all interviewed (98%) reacted positively towards a potential reintroduction of the animal to the park. This was likely a result of their background knowledge that giraffe are not a carnivore and as such pose no livestock predation possibility. Similarly, there was a high willingness of the Iona community to co-exist with giraffe (96%), although only a few individuals (26-35 years old) indicated they had received minor monetary benefits from tourists who take their photographs but did not receive any such benefit from the presence of wildlife in the area.

A significant difference in attitude was detected between ethnic groups, with the dominant Ovahimba being most positive towards both the proposed reintroduction as well as willingness to co-exist with giraffe. The MCA revealed that individuals who never attended school as well as the herders, were all strongly supportive towards a giraffe reintroduction. With the legacy of the traditional Ovahimba pastoralist society, the most dominant tribe in the park, 82% of those interviewed never attended school but rather herd their livestock (Ministério do Ambiente, 2015). According to Malviya et al. (2022), education has been found to have a bearing on an individuals' acceptance to wildlife reintroduction and the success of conservation programs, with more educated people being more pro-conservation. However, in the case of this study, it can be assumed that people answered based on indigenous knowledge of the species being harmless. The limited few who indicated a negative attitude were from the traditional agro-pastoral Mungambwe tribe. It is likely they assumed that HWC would result from the introduced giraffe raiding their crops. However, giraffe rarely raid crops (Ruppert 2020), though in Niger they do seasonally feed on cowpeas and mangoes (Sogbohossou et al. 2013); none of which are grown in Iona NP. It is also unlikely that the low density of crops in Iona would attract giraffe unless extreme droughts are experienced. Importantly, community awareness, education and monitoring will be necessary pre-, during, and post- any proposed reintroduction to dispel such concerns, and manage any potential HWC results.

The positive views expressed towards living with wildlife in Iona NP, with herbivores preferred over carnivores, highlights the positive relationship the Ovahimba people have with their environment. This situational carnivore related conflict has been reported in other studies. For example, the loss of crops by megaherbivores, or loss of livestock as they became food for carnivores had affected the socioeconomic needs of the Maasai people (Bencin et al. 2016). It has been observed that if individuals' personal livelihoods are threatened by wildlife, they become less supportive of it, and more supportive when conflict is unlikely (Røskaft et al. 2007; Bath 1989; Ryo et al. 2014). Some residents of Yellowstone NP, USA opposed grey wolves (Canis lupus) on the basis that they depredate on their livestock (Bath 1989). In Japan, residents were unhappy to live with wild boar (Sus scrofa) and sika deer (Cervus nippon), because they caused frequent agricultural damage (Ryo et al. 2014). Similarly, in Kenya, the interviewed communities were unhappy with the African savanna elephant that raided their crops (Weinmann 2018).

Knowledge of wildlife regulations and their enforcement likely plays a valuable role in local-level conservation. Encouragingly, almost all interviewees (98%) were aware that hunting is prohibited. However, despite this knowledge, a minority still indicated that they might revert to poaching. It appears that the driving forces behind poaching in Iona were diverse, but they were mainly driven by poverty and hunger, especially after much of their livestock died during the recent drought. Some people resort to poaching because of negative human attitudes around wildlife (Kahler & Gore 2015). Some poach for avoidance of future HWC or to prevent economic loss (Williams et al. 2017). Provision of bushmeat for subsistence or commercial use can also be a driver (Ruppert 2020; Kahler & Gore 2015; Grey-ross et al. 2010; Bennett et al. 2017). However, due to food aid donated to Iona residents from the government and local businesses, coupled with the fear of law enforcement, the prevalence of bushmeat poaching in the park has declined markedly (Iona NP park rangers pers. comm.). Furthermore, there are legal measures in place to deal with poachers e.g. warrant of arrest, and in serious instances it was reported by park rangers that poachers were beaten if they refused to cooperate with law enforcement. Ruppert (2020) stated that increased law enforcement and prosecution in

northern Kenya deterred poaching and other harmful activities towards wildlife.

It is important to note that giraffe in Angola are fully protected and any attempt to kill them is illegal (Ministério do Ambiente 2015). According to a study by Dunn et al. (2021), giraffe are hunted both legally and illegally, country dependent, with the use of their body parts varying geographically. In southern Africa, giraffe were mostly killed legally for bushmeat and trophies, although some local subsistence poaching was reported (Dunn et al. 2021). Concerns around potential poaching of giraffe introduced to the study area appeared minimal, although the feelings expressed around their use for cultural practices would need targeted monitoring and education amongst the residents (Glikman et al. 2022). It was reported by the community members interviewed that giraffe tails were used historically as a whip for horse riders while their skins were used for clothing and shoes. However, such concerns were repressed by other Iona community members remarking that this would be unlikely in this era as animal skins previously used for clothes are being replaced by modern fabrics often donated to them by the government.

border in Namibia, important Across the consumptive and non-consumptive livelihood benefits for the last few decades have accrued to community members who live with and conserve wildlife in registered conservancies through the community based natural resources management (CBNRM) programme (NACSO 2016; Naidoo et al. 2011; NACSO 2019). The CBNRM programme in Namibia and Communal Areas Management Programme for Indigenous Resources (CAMPFIRE) programme in Zimbabwe are both mechanisms which have enabled local communities to manage and conserve their local wildlife resources, and in turn gain financially from sustainable nonconsumptive and/or consumptive use (Nuulimba & Taylor 2015). In areas of northern Kenya where communities receive benefits, residents tend to support conservation and are more likely to tolerate negative impacts wildlife such as livestock depredation (Ruppert 2020). However, within the Iona NP there are seemingly few or no community benefits from wildlife or associated tourism. It is thus in the best interest of the Angolan government as well as the community living in and around Iona NP, that programmes with benefit mechanisms like the above cited are assessed and implemented to engage these communities in the long-term.

CONCLUSION

We demonstrated that the majority of interviewed community residents in Iona NP are in favour of giraffe being reintroduced. As local communities experience the direct cost of living alongside wildlife, it is critical that they are involved in their management and benefit from wildlife and forestry products through local CBNRM programmes. A basic understanding and general positive attitude towards conservation was observed in Iona NP. By assessing and better understanding the HWD with regards to giraffe management in Iona, and more generally throughout the continent, the long-term viability of giraffe (and other wildlife) conservation efforts can be assessed better. Due to the low level of formal education in the area, we recommend increasing awareness conservation among the local communities. These conservation education programs should take advantage of traditional beliefs and highlight the ecological, economic and social benefits of wildlife. This study provides valuable insights into further decision-making regarding a potential reintroduction of Angolan giraffe into Iona NP. It is important to note that an ecological feasibility assessment is critical to inform the process. This should involve all stakeholders, including representatives government, NGOs, academia and relevant communities, to make appropriate decisions on the feasibility of reintroducing giraffe. We believe that this study provides a valuable initial contribution towards the potential reintroduction of giraffe and other species currently locally extinct in Iona NP in Angola.

ACKNOWLEDGEMENTS

The authors would like to thank the staff of Iona NP, in particular Sango De Sa, Park Manager, and Cassute Maximino, Park Ranger. We thank Mitchitalele Tchundiro and Tchafeleni Albano for assisting in the field. Additionally, our thanks go to Dr. Monica Bond and Dr. Christian Kiffner for their constructive comments which greatly improved the manuscript. We also thank Giraffe Conservation Foundation (GCF) for their time and support during the writing up this paper. Lastly, we thank all the local community members who voluntarily took part in the focus groups and interviews. This project was funded by the European Union (EU) under the Skeleton Coast-Iona Transfrontier Conservation Area (SCIONA TFCA) project, grant agreement FED/2017/394-802 and the Namibian Chamber of Environment (NCE).

REFERENCES

- Bath AJ (1989) The public and wolf reintroduction in Yellowstone National Park. *Society & Natural Resources* 2(1): 297–306.
- Bath AJ (1998) The role of human dimensions in wildlife resource research in wildlife management. *Ursus* 10: 349–355.
- Bencin H, Kioko J, Kiffner C (2016) Local people's perceptions of wildlife species in two distinct landscapes of Northern Tanzania. *Journal for Nature Conservation* 34: 82–92.
- Bennett NJ, Roth R, Klain SC, Chan K, Christie P, Clark DA *et al.* (2017) Conservation social science:

- Understanding and integrating human dimensions to improve conservation. *Biological Conservation* 205: 93–108.
- Brown MB, Kulkarni T, Ferguson S, Fennessy S, Muneza A, Stabach JA, Fennessy J (2021) Conservation Status of Giraffe: Evaluating Contemporary Distribution and Abundance with Evolving Taxonomic Perspectives. *Imperiled: The Encyclopedia of Conservation* 1–17.
- Deruiter DS, Donnelly MP (2002) A qualitative approach to measuring determinants of wildlife value orientations. *Human Dimensions of Wildlife* 7: 251–271.
- Dunn ME, Connor DO, Veríssimo D, Ruppert K, Glikman JA, Fennessy S, Fennessy J (2021) Investigating the international and pan-African trade in giraffe parts and derivatives. *Conservation Science and Practice* 1–18.
- East R (1999) African Antelope Database 1998. IUCN/SSC Antelope Specialist Group. In *IUCN/SSC Antelope Specialist Group*. IUCN, Gland, Switzerland and Cambridge, UK. x +434pp.
- Elizabeth HT, Miljanich CP, Anderson SE, Hiroyasu EHT, Miljanich CP, Anderson SE (2019) Drivers of support: The case of species reintroductions with an ill-informed public. *Human Dimensions of Wildlife* 24(5): 401-417.
- Glikman JA, Frank B, Bogardus M, Meysohn S, Sandström C, Zimmermann A, Madden F (2022) Evolving Our Understanding and Practice in Addressing Social Conflict and Stakeholder Engagement Around Conservation Translocations. Frontiers in Conservation Science 3: 1–6.
- Grey-ross R, Downs CT, Kirkman K (2010) An assessment of illegal hunting on farmland in KwaZulu-Natal, South Africa: Implication for oribi (*Ourebia ourebi*) conservation. *African Journal of Wildlife Research* 40(1): 43–52.
- Gyimah I (2016) Understanding the attitudes and perceptions of South African residents towards antirhino poaching initiatives. Masters degree, Universty of South Africa.
- Huntley BJ, Russo V (2019) Biodiversity of Angola. In: Huntley BJ, Lages VRF, Ferrand NB (Eds.) *Biodiversity* of Angola Science and Conservation: A Modern Synthesis. pp. 1-11. Springer Nature, Switzerland AG.
- Kahler JS, Gore ML (2015) Local perceptions of risk associated with poaching of wildlife implicated in human-wildlife conflicts in Namibia Local perceptions of risk associated with poaching of wildlife implicated in human-wildlife conflicts in Namibia. *Biological Conservation* 1–9.
- Kansky R, Kidd M, Knight AT (2016) A wildlife tolerance model and case study for understanding human wildlife conflicts. *Biological Conservation* 201: 137–145.
- Kansky R, Knight AT (2014) Key factors driving attitudes towards large mammals in conflict with humans. *Biological Conservation* 179: 93–105.
- König HJ, Kiffner C, Kramer-Schadt S, Fürst C, Keuling O, Ford AT (2020) Human-wildlife coexistence in a changing world. *Conservation Biology* 34(4): 786–794.
- Koziarski A, Kissui B, Kiffner C (2016) Patterns and correlates of perceived conflict between humans and large carnivores in Northern Tanzania. *Biological Conservation* 199: 41–50.
- Kroonenberg PM, Greenacre MJ (2004) Correspondence Analysis. In *Encyclopedia of Statistical Sciences*.
- Landminesinafrica (2017) The Month in Mines, August 2017. Retrieved from Landmines in Africa website: https://landminesinafrica.wordpress.com/tag/namibia/on 18 August 2020.

- Lee DE, Fienieg E, Van Oosterhout C, Muller Z et al. (2020) Giraffe translocation population viability analysis. *Endangered Species Research* 41: 245-252.
- Likert R (1932) A technique for measurement of attitudes. *Archives of Psychology* 140: 5-55.
- Malviya M, Kalyanasundaram S, Krishnamurthy R (2022) Paradox of Success-Mediated Conflicts: Analysing Attitudes of Local Communities Towards Successfully Reintroduced Tigers in India. *Frontiers in Conservation Science* 2: 1–16.
- Marais A, Fennessy J, Fennessy S, Brand R, Carter K (2020) Giraffa camelopardalis *ssp.* angolensis *(amended version of 2018 assessment)*. The IUCN Red List of Threatened Species 2020: e.T88420726A176393590. https://dx.doi.org/10.2305/IUCN.UK.2020-
 - 3.RLTS.T88420726A176393590.en. Accessed on 23 February 2022.
- Marais AJ, Fennessy S, Ferguson S, Fennessy J (2019) Country Profile: Republic of Angola - Giraffe Conservation Status Report February 2019. Windhoek, Namibia: Giraffe Conservation Foundation.
- Mathews AJ, Flynn KC (2018) Supporting Experiential Learning With No-Cost Digital Tools: A Comprehensive GPS Lesson. *The Geography Teacher* 15(3): 117–128.
- Mendelsohn J, Mendelsohn S (2018) SUDOESTE DE ANGOLA. Retrieved from http://id.loc.gov/authorities/names/no2007149181 on 18 August 2020.
- Miller KK (2009) Human dimensions of wildlife population management in Australasia history, approaches and directions. *Wildlife Research* 36: 48–56.
- Ministério do Ambiente (2015) Estudo das comunidades do Parque Nacional do Iona: Relatório de Perfis das Comunidades. Retrieved from https://www.quadrante-engenharia.pt/pt/projetos/ambiente/estudo-das-comunidades-no-parque-nacional-do-iona/ on 18 August
- Mir ZR, Noor A, Habib B, Veeraswami GG (2015) Attitudes of local people toward wildlife conservation: A case study from the Kashmir Valley. *JSTOR* 35(4): 392–400
- Mogomotsi PK, Mogomotsi GEJ, Dipogiso K, Phonchi-Tshekiso N. D, Stone LS, Badimo D (2020) An Analysis of Communities' Attitudes Toward Wildlife and Implications for Wildlife Sustainability. *Tropical Conservation Science* 13.
- Morais J, Castanho RA, Loures L, Pinto-Gomes C, Santos P (2019) Villagers' Perceptions of Tourism Activities in Iona National Park: Locality as a Key Factor in Planning for Sustainability. *Sustainability* 11(4448): 1–18.
- NACSO (2016) The state of community conservation in Namibia a review of communal conservancies, community forests and other CBNRM initiatives. Retrieved from http://www.met.gov.na/files/files/State of the Parks Report.pdf on 19 August 2020.
- NACSO (2019) Keep Namibia's wilfdlife on the Land! Retrieved from http://www.nacso.org.na/sites/default/

- files/2019_Wildlife-on-the-land_rgb_F_201207s.pdf on 19 August 2020.
- Naidoo R, Weaver LC, De Longcamp M, Du Plessis P (2011) Namibia's community-based natural resource management programme: An unrecognized payments for ecosystem services scheme. *Environmental Conservation* 38(4): 445–453.
- Nuulimba K, Taylor JJ (2015) 25 years of CBNRM in Namibia: A retrospective on accomplishments, contestation and contemporary challenges. *Journal of Namibian Studies: History Politics Culture* 18: 89–110.
- Nyhus PJ (2016) Human-Wildlife Conflict and Coexistence. In *Annual Review of Environment and Resources* 41.
- O'Connor D, Stacy-Dawes J, Muneza A, Fennessy J, Gobush K, Chase MJ *et al.* (2019) Updated geographic range maps for giraffe, *Giraffa* spp., throughout sub-Saharan Africa, and implications of changing distributions for conservation. *Mammal Review* 49(4): 1–15
- Pamela MH, Lynn RK (1988) A structural equation test of the value-attitude-behavior hierarchy. *Journal of Personality and Social Psychology* 54(4): 638–646.
- Pate J, Manfredo MJ, Bright AD, Tischbein G, Pate J, Manfredo MJ *et al.* (1996) Coloradans' attitudes toward reintroducing the gray wolf into Colorado. *Wildlife Society Bulletin* 421–428.
- Røskaft E, Ha B, Bjerke T, Kaltenborn BP (2007) Human attitudes towards large carnivores in Norway. *Wildlife Biology* 12: 172–185.
- Ruppert K (2020) Human-Giraffe Interactions: Characterizing Poaching and Use of Parts as a Threat to Giraffe in Northern Kenya. PhD thesis, University of Maine.
- Ryo S, Susan K, Ueda G (2014) Public Perceptions of Significant Wildlife in Hyogo, Japan. *Human Dimensions of Wildlife* 19(1): 88–95.
- Sampson C, Leimgruber P, Rodriguez S, McEvoy J, Sotherden E, Tonkyn D (2019) Perception of Human–Elephant Conflict and Conservation Attitudes of Affected Communities in Myanmar. *Tropical Conservation Science* 12(1): 1–17.
- Sarrazin F, Barbault R (1996) Reintroduction: challenges and lessons for basic ecology. *Trends in Ecology & Evolution* 11(11): 474-478.
- Sogbohossou E, Kassa B, Aboibacar Z, Mahamane A (2013) Human-Giraffe conflicts in the central Range of the giraffe (*Giraffa camelopardalis peralta* Linnaeus 1758) in Niger. *Annals of Agronomic Sciences* 17(2).
- Weinmann S (2018) Impacts of Elephant Crop-Raiding on Subsistence Farmers and Approaches to Reduce Human-Elephant Farming Conflict in Sagalla, Kenya. Masters degree, University of Montana, USA.
- Williams VL, Loveridge AJ, Newton DJ, Macdonald DW (2017) Questionnaire survey of the pan-African trade in lion body parts. *PLoS one* 12(10): 1-35.

Media coverage of climate change in Namibia and South Africa: A comparative study of newspaper reports from October 2018 to April 2019

MN Shimhanda¹, B Vivian²

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-shimhanda Published online: 20th July 2022

- Department of Computing, Environment and Engineering, Coventry University, United Kingdom; Okavango Research Institute, University of Botswana. 202108016@ub.ac.bw
- ² Department of Computing, Environment and Engineering, Coventry University, United Kingdom

Date received: 8th March 2022; Date accepted: 5th June 2022.

ABSTRACT

Climate change is among the global issues that have permeated the media agenda, yet studies on climate crises have mostly focused on Western media. Less in-depth analysis has been conducted in developing countries that are extremely subject to climate change and where awareness and adaptation will be more pressing than reducing emissions. This study presents a comparative content analysis of newspaper coverage of climate change in southern Africa from October 2018 to April 2019; a critical period when significant events conjoined to raise the need to tackle climate breakdown globally. The analysis included 108 newspaper articles published in English by news media in Namibia and South Africa that have a significant influence on policymakers and present global and local coverage of climate change. The assessment included news articles from The Namibian, Windhoek Observer, Cape Argus, and Sunday Times. Data were collected and analysed using content discourse analysis. The study found that articles are frequently sourced from foreign news agencies. Significant international and local events like Cyclone Idai and the United Nations Climate Change Conferences (COP24 - Katowice) strongly influenced the reporting of climate change in southern Africa, and dominant climate change thematic frames and linguistic repertoires were used to discuss the climate crises. The discussions of global warming were framed around public opinion (civil/protest) while small actions and alarmist were mostly used as linguistic repertoires in reporting climate change. The causes and effects of climate change are discussed with alarm, while mitigations and measures are reported as small actions. Reporters frequently used adjectives such as no tomorrow, extinction, and heatwaves to warm the public about the severity of climate change. The study strongly suggests a need for reporters to widen local report sourcing and to strike a balance in framing climate change news while not undermining the seriousness of global warming. It is important to balance warning journalists about alarmist reporting and not underestimating the severity of climate change. Journalists and editors who are trained in environmental journalism may better report on climate change.

Keywords: climate change; coverage; linguistic repertoires; Namibia; newspapers; South Africa; thematic frames

INTRODUCTION

Exceeding the 1.5 °C warming threshold would impact the planet, according to the 2018 special report by the Intergovernmental Panel on Climate Change (IPCC). The projection of global warming at 1.5 °C, and 2 °C or higher shows that vulnerable countries in southern Africa are likely to get hotter, drier and more water-stressed (IPCC et al. 2018). Developing countries and the industrialised world seek to tackle climate change to avoid future adverse effects. Creating awareness of environmental issues to influence policymakers and the public to combat climate change is becoming crucial in this climate change era (Tagbo 2010, Boykoff & Luedecke 2016, Chand 2017). According to Barkemeyer et al. (2017), existing effective measures to mitigate climate change are only growing with public awareness across the world. There has been a massive increase in media attention to tackle climate change worldwide recently (Shanahan 2013). Furthermore, a study by Tagbo (2010) stressed the necessity for better communication with policymakers about climate change. Influencing to create suitable legislation and adaptation strategies through media coverage is important.

Even though the climate crisis is a worldwide phenomenon that affects societies around the world, studies have mostly focused on climate change media discourse for developed countries as argued by Boykoff (2007, 2008, Boykoff & Luedecke 2016). Consequently, few in-depth analyses on climate change discourse have been done in the countries that are currently impacted by global warming and where awareness and adaptation are more pressing than reducing emissions (Tagbo 2010, Shanahan 2013, Barkemeyer *et al.* 2017). Many studies represent loosely the concept of framing and explicitly define their theoretical approach and analytic method of examining the framing of climate change (Boyd 2015, Schäfer & O'Neill 2017). Consequently, far

too many news media in Africa depend on foreign media sources placing a huge constraint on the opportunities for participation in combating the local impact of climate change in Africa (Boykoff 2007, Tagbo 2010, Batta et al. 2013). Sourcing information from across southern African regions would provide opportunities for the public to relate their climate change experiences. Newspapers will be able to document what individuals and groups need to do to deal with climate change at a local and regional level. This study addressed these gaps by providing a comparative content analysis of media coverage in South Africa and Namibia from October 2018 to April 2019 and argued the effort to improve climate change journalism. The study further explored how climate change is being communicated and discussed in newspaper articles, the origin of news sources of information on climate change published in southern Africa newspaper articles, climate change trends, dominant thematic frames, and linguistic repertoires. The study found that climate change was poorly reported in southern Africa's newspapers despite awareness and adaptation being crucial as the effect of climate change was projected to be more severe in the region. Half of the newspaper articles were based on stories that were originally produced and circulated by other foreign news agencies with neither a local nor regional context.

METHODS

Sources

Newspapers from South Africa and Namibia were studied because these countries have a comparable degree of vulnerability to the consequences of climate change (United Nations Environment Programme 2018). The two southern African countries have been faced with water scarcity due to prolonged droughts, providing a good case for a comparative study (Ruppel & Ruppel-Schlichting 2016, United Nations Environment Programme 2018). Namibia and South Africa have similar newspaper ownership. The print media system in both countries varies significantly, for instance, South Africa's newspaper ownership is more corporate with media controlled by big firms, while Namibia has independent journalist trusts and stateowned companies. Two newspapers were chosen from each country, including one daily and one weekly newspaper to represent the diversity of newspaper types. Newspapers were selected based on their circulation, quality of reporting, and global and local coverage of climate change. For Namibia The Namibian (daily) and Windhoek Observer (weekly) newspapers were selected. The Namibian has been the country's largest-selling and most influential independent national English newspaper since 1985 that covers national and international news (The Namibian 2019). Windhoek Observer is the oldest and largest circulating weekly newspaper in Namibia. For South Africa Cape Argus (daily) and Sunday Times (weekly) newspapers were chosen. Sunday Times is the most prominent weekly South Africa Sunday newspaper. Sunday Times distributes newspapers all over South Africa, including bordering countries like Lesotho, Botswana, and Swaziland (Sunday Times 2019). On the other hand, Cape Argus is a local newspaper in Cape Town (Brand South Africa 2013). Although it is a local paper, it also covers national news including environmental problems (Whitfield 2019), creating a basis for how local newspapers cover local news related to climate change, making it a perfect choice for this study.

Data collection

The study included all newspaper articles concerning the climate crisis from 1st October 2018 to 30th April (7 months). The timeframe was considered significant as events conjoined to raise the visibility of climate change issues and the need for solutions. Special events range from the release of the Intergovernmental Panel on Climate Change (IPCC) special report in 2018 and the United Nations Climate Change Conferences (COP24 – Katowice) to cyclone Idai and the then 16-year-old Swedish activist Greta Thunberg, who inspired the climate emergency strikes. In addition, the prolonged drought in southern Africa gave cause for concern.

Newspaper articles were accessed online from newspaper archives and newspapers' website search engines (for those newspapers without archives). Keywords searches were conducted using the newspapers' online search engines. Recommended keywords from a study undertaken by Boykoff (2007 p. 1194), and Schmidt et al. (2013) were adapted as search terms. The keywords included climate change or disaster, warm, heat, cool, greenhouse effect, global/earth/world warming, and temperature rise/decrease. The research added additional key terms such as IPPC, drought, and cyclone while key terms synonyms such as climate breakdown, climate change and/or global warming were used between October 2018 (IPCC report publication noted) to December 2018 (COP24 noted) and from January 2019 (its first date of publication) to April (last date of publication) for all newspaper outlets. IPPC report and UNFCCC COP24 and their full name were also used as keywords. This created a broad search string which enhanced the search, providing better coverage of the targeted sample size than other studies.

A reference to climate change is present when: a) the keyword climate is connected with words such as change, emergency, crisis, breakdown, development, warming, cooling; b) synonyms such as greenhouse effect, global warming and global heating or c) when

Table 1: Southern African newspapers used as sources of newspaper articles used in the study.

Newspaper	Newspaper website URL	Publication frequency	Number of articles
Windhoek Observer	https://www.observer.com.na	Weekly	10
The Namibian	https://www.namibian.com.na	Daily	34
Cape Argus	https://www.iol.co.za/capeargus	Daily	30
Sunday Times	https://www.timeslive.co.za/sunday-times	Weekly	34

extreme events or temperature change were discussed (Schmidt *et al.* 2013). A pilot study was done to validate the method through selected newspapers from each country and conducted key terms search created by Schmidt *et al.* (2013).

The articles were downloaded and sorted according to relevance (climate change) and publication date (October 2018-April 2019). A total of 108 articles referring to climate change were sourced, as shown in Table 1. The newspaper article links were copied to a Microsoft word document on OneDrive for further review as well as to check for duplicates. The articles were downloaded and noted for further review. Articles were also printed to make it easier to read, analyse and double-check for duplicates. As per Coventry University research ethics requirements, this study was approved before data collection.

Data analysis

The first assessment examined the trend of climate discourse from October 2018 to April 2019. This assessment compared the monthly trends in climate change coverage for the four newspapers. The study adopted an approach used by Boykoff (2008) and Chand (2017) to determine the total proportion of climate change articles published per month:

No of articles published per month with reference to climate change Total proportion of all articles published in a specific month

x 100 = Coverage per month.

A line graph was plotted in Microsoft Excel to compare climate change coverage trends for each month. The most challenging part was counting articles manually from the website search engines for newspapers with online archives. The newspaper information centres were contacted by mobile to provide newspaper articles archives, but they had no track of the total number of articles published monthly. Therefore, for newspapers without archives, the research counted one by one to attain the total proportion of articles published per month. The research counted more than two times for validation.

Moreover, two content-coding strategies were used, focusing on thematic frames and linguistic repertoires. Initially, newspaper articles were downloaded using NVivo capture and coded in NVivo software to understand qualitative content such as linguistic reporters and thematic frames. Then, qualitative data were coded in Microsoft Excel from NVivo for analysis using pivot charts and tables to produce quantitative data in charts and graphs.

Thematic frames analysis

According to Erlickyte (2014), the way the climate crisis is framed in media influences the opinion and attitudes of readers. Assessing thematic framing is crucial. In this study, climate change thematic frames were analysed using a content-oriented frame (manual deductive framing approach) because it is suitable for medium to extensive studies (Boyd 2015, Schäfer & O'Neill 2017).

A list of questions suggested by Semetko and Valkenburg (2000 p. 100) as cited by Erlickyte (2014), were used to identify thematic frames in each newspaper article. Furthermore, five thematic framesets well-known in literature were adapted as a guide. The thematic frameset consists of conflict, human interest, responsibility, morality and economic consequences, as illustrated by (Trumbo 1996, Takahashi 2011, O'Neill *et al.* 2015, Brüggemann & Engesser 2017, Schäfer & O'Neill 2017). Since the preceding studies failed to demonstrate assessment of articles with different structures, the research adopted a process from (Stoddart *et al.* 2016 p. 222) with editions tailored to this study.

- 1. Ecological/Wildlife focus on the natural environment and how climate crisis impacts wildlife or the ecological system.
- 2. Policymaking includes government policies, laws, strategies, and projects to mitigate climate breakdown.
- 3. Economic/Agriculture entails financial costs of climate breakdown impacts and responses as well as climate change impacts on agriculture.
- 4. Culture/fashion/lifestyle focus on the impact of people's lifestyles on climate change, or popular culture (celebrities, fashion, or artists) in relation to the climate crisis. Also emphasises actions for tackling global

- warring through lifestyle changes like vegan diets and recycling in the fashion industry.
- 5. Extreme events focus on extreme events and their impact on the people and their livelihood, for example droughts or cyclones.
- Civil society and conflict entail public opinions or public debate about the cause, effect, and mitigations of climate change. Climate change campaigns, protests, or activities by activists, non-governmental organisations, and experts.
- 7. Social focus on climate crisis social impacts and health impacts.
- 8. Water emphasis on the impact of climate change on water-related issues or water-climate change nexus.
- 9. Technology looked at the development and application of new and smart technology to mitigate climate change, for example electric cars.

Each article was assigned to a thematic frame that best represented the climate change discussion in the article, in order of importance. Where an article contained more than two themes, the most dominant setting was assigned. This was determined by reviewing the entire article.

Climate change linguistic repertoire analysis

Ereaut and Segnit defined climate change linguistic repertoires are styles and registers of reporting that represent various versions of what might be viewed as "common sense" or "different ways of making sense of the world" (Ereaut & Segnit 2006 p. 12). Climate repertoires can also be used as a framework for interpretation and decision-making (Ereaut & Segnit 2006). As a result, an assessment framework from (Ereaut & Segnit 2006, and Erlickyte 2014) was used to analyse how linguistically the media portrays climate change. The most common adjectives, phrases, and metaphors were considered to get a better picture of how the climate crisis is described linguistically in the media. The climate repertoires listed below were used:

- 1. Alarmist Distinguished by using extreme and inflated words to portray climate change impacts such as "it's too late" and or "it is the end of the world".
- Settlers Denies climate change exitance by rejecting and mocking the discourse of alarmists.
- 3. Comic nihilism Denial of climate change seems less aggressive than that of the settlers. It is a British trait of self-mocking and contrary, dealing with adversity and threat by use of humour. It can be referred to as British Comic nihilism.
- 4. Rhetorical Scepticism Portrays the green movement as illogical and supports "free market protection".

- Small actions These can be personal or corporate actions to tackle climate change. It includes things like "10 things you need to do to save the planet" and is commonly placed alongside alarmism
- 6. Expert denials Scientists slow down the debate on climate change on their terms, with concepts such as "warming is good", backing it up with scientific data and statistics. Portrays climate change as inevitable and having potential benefits.
- 7. David and Goliath Imply that even a small number of people can mitigate climate change.

The legitimacy of newspaper articles

The authors of the published climate change news articles were scrutinised for credibility and authentication. The credibility of the report was determined by looking at how many articles were published by qualified and experienced climate change reporters. The author's name and profile, as well as the source of the information cited by the author of the articles, were the primary focus of the investigation. Articles published by unknown authors were referred to as unnamed authors, while articles copied from other news outlets or news agencies were referred to as imported authors. There is no specific method for assessing news media credibility in the literature, but Tagbo (2010) takes a similar approach.

RESULTS

Newspaper coverage of climate change in southern Africa

Overall, newspapers covered climate change differently, but there were some similarities. From March to April 2019, all newspapers reported an increase in coverage of the impact of global warming, which shaped local news. Weekly newspapers (Windhoek Observer and Sunday Times) had narrow coverage, while daily newspapers (The Namibian and Cape Argus) had wider coverage, as shown in Figure 1. These trends were expected, given the differences in the size of daily and weekly newspaper publications. As illustrated by Figure 1, the trends in climate change reporting stood at a low percentage with 5.4% (Windhoek Observer), 2.4% Sunday times, 1.7% Cape Argus and 0.3% (The Namibian). Windhoek Observer showed the highest climate crisis coverage compared to other newspapers with 14.28%, peaking in 2018. On the other hand, Sunday Times had an interesting trend as coverage gradually rose from October 2018 to January 2019 and saw a drastic fall in March and a rise in April (see Figure 1). The Namibian had the lowest peak not exceeding 2% having a similar trend to Cape Argus.

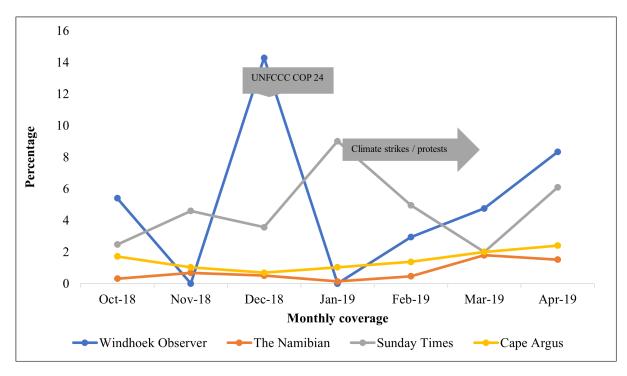


Figure 1: Monthly climate change newspaper reporting trends between October 2018 to April 2019 in Namibia and South Africa's newspapers outlet.

Climate change thematic frames discourse

The assessment included a total of 108 articles, with sixty-four (64) from South Africa and forty-four (44) from Namibian news outlets as illustrated in Table 1. Ten (10) articles are from Windhoek Observer, 34 articles are from the The Namibian, 30 articles are from the Cape Argus, and thirty-four articles are from the Sunday Times website (see Table 1).

The climate crisis in Namibia is mostly framed based on the civil/protest thematic frame, dominant in both The Namibian and Windhoek Observer, found in (14/44 articles), as illustrated in Table 2. The second most prevalent thematic frames employed in The Namibian were economic & agriculture seen in 8/44 articles and policymaking framed in 7/44 articles. Even though the impact of climate change on the environment is prevalent in Namibia, none of the articles in the country's newspapers used the ecological/wildlife thematic frame. This could be

because the most prominent themes in the articles, such as civil, economic, or agricultural, overshadow most thematic frames. For example, Namibia experienced a prolonged drought from February 2019 to the present, affecting water availability; as a result, some water themes are framed in terms of agriculture, with a focus on how water scarcity affects agricultural activities. Portraying agriculture is the dominant theme in the articles like the 08 March article in The Namibian newspaper (see Figure 2).

On the other hand, the most prevalent thematic frame in South African newspapers (Cape Argus and Sunday Times) was civil/protest with (11 out of 64 articles), which is also a similar high thematic trend in Namibia. The next prominent themes used were water (9/64 articles) and ecological/wildlife (9/64 articles) with stories oriented toward the effect of climate change on water sources and ecologic systems or wildlife. In Cape Argus, a hashtag (#) was created to report a series of water challenges due to

 Table 2: Dominant thematic frames employed by newspaper outlets in southern Africa.

	Namibian	newspapers	South Africa			
Dominant frame	Windhoek Observer	The Namibian	Sunday Times	Cape Argus	Number of articles	
Civil/protest	4	10	8	3	25	
Culture/lifestyle	0	0	7	0	7	
Ecological/wildlife	0	0	4	5	9	
Economic/agriculture	1	7	5	1	14	
Extreme events	0	2	1	2	5	

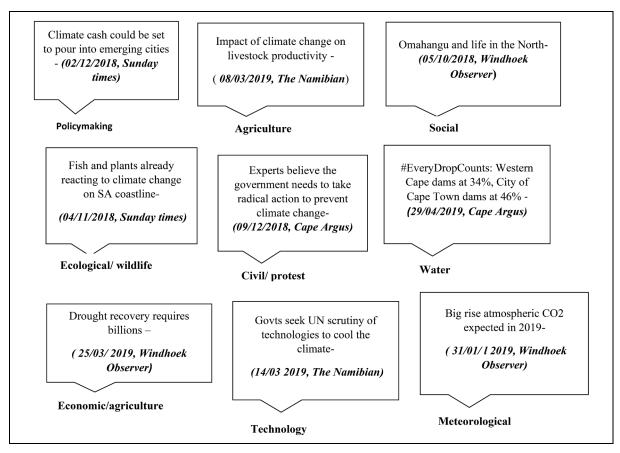


Figure 2: Thematic frames evident in the South African media outlets (Sunday Times and Cape Argus).

climate change (see example in Figure 2). Examples of articles characterised by the water theme include: "every drop counts" (Cape Argus). By illustration, an interesting article was also found in Sunday Times (see Figure 2). Interestingly, all thematic themes are employed in South African newspapers unlike in Namibia.

Climate linguistic repertoires discourse

The outcomes are based on linguistic repertoires adapted from (Ereaut and Segnit 2006 p. 12; Erlickyte 2014). This section provides an overview of the most important keywords, metaphors, adjectives, and other linguistic features found in the articles. As illustrated in Figure 3, three climate repertoires were practised in Namibia namely small actions, alarmist, and techno-optimism. Small actions was the most prominent employed in 44% of the articles in The Namibian newspaper while in Windhoek Observer it was 60% of the articles. The next most common repertoire is alarmist found in 38% of the articles in The Namibian newspaper and 40% in Windhoek Observer (Figure 3). The Namibian newspaper also practised techno-optimist; which was evident in 18% of the articles.

Examples of linguistic repertoires used are illustrated in Figure 4. Words like biggest rise, huge, and severe are common in alarmist articles, describing the magnitude of global warming's impacts. Extreme events, such as drought, were frequently described as persistent. While the articles with small actions have one thing in common, it is that they show how cooperates and organisations provide funds or aid for climate change programs (see Figure 4). Adjectives such as green bond and sustainable projects were used to describe the funds and the programs and projects funded. The small number of articles published by Windhoek Observer (weekly) newspapers may have contributed to the lack of diversity in the newspapers' climate lexicon, as only ten articles were linked to climate change between October 2018 and April 2019.

When it comes to South African newspapers, three climate repertoires are dominant. As shown in Figure 4, The most frequent one is alarmist which is quite different from what is frequently practised in Namibia. Cape Argus fairly employed three climate repertoires with each repertoire covering a quarter or more of the pie chart (see Figure 4). This is interesting as none of the newspapers in Namibia practised it. On the other hand, Sunday Times news outlets are more diversified compared to Cape Argus, The Namibian, and Windhoek Observer. Sunday Times employed alarmist (47%), small actions (32%), techno-optimism (18%) and expert denial (3%) respectively. Expert denial, despite being the

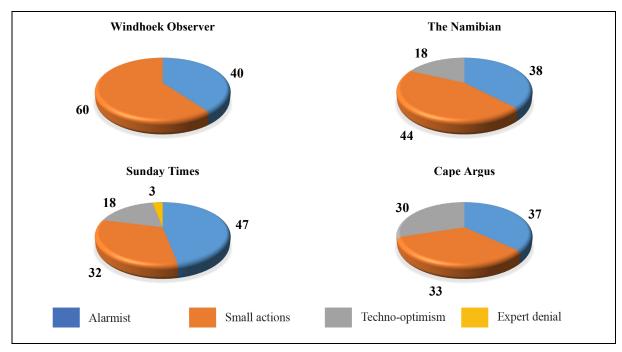


Figure 3. Linguistic repertoires employed in articles about climate change by selected newspapers from Namibia and South Africa. Values are percentages.

only different climate repertoire used in four newspaper outlets (see Figure 4), showed how experts blame the impact of the flood on a governments failure of proper planning. Experts claimed that climate change should not be used as a "cop-out" for poor planning or inadequate governance. They further backed their argument with scientists stating that the calculations of the rainfall and assessment of the most recent global climate models showed that it was too early to attribute the floods to climate change. Examples of climate repertoires discussed in Cape Argus and Sunday Times are shown in Figure 4.

What are the sources and authors of climaterelated articles in southern Africa?

This section focused on the source of the information reported and the author's ability to relate it to climate change at the local, regional, and local levels. The author's profile was reviewed to determine whether the authors have the necessary qualifications or experience to report on climate change. The references cited by the authors in the articles were checked for plagiarism.

In the analysed articles from two Namibian newspapers, only six per cent of the articles were written by authors with their names indicated. The remaining were either written by an unknown or unnamed author or the third-party source of information indicated as the author, raising a question of the ability and confidence of the local authors to report comprehensive climate crisis news. Absalom Shiwedha, the solely identified journalist for wildlife

and environment at The Namibian newspaper, accounted for 6% of the climate change-related articles. It was confirmed through a telephone call that he had no university qualification on the topic, and he has subsequently left the company. Consequently, half of the articles (50%) published by The Namibian newspaper and 40% by Windhoek Observer were copied and pasted from secondary sources and reported without relating it to a local or regional context. These articles were frequently sourced from Namibia Press Agency which published articles reported by BBC News, Reuters, Apo Group, Agency France-Presse (AFP), Thomson Reuters Foundation, and Xinhua news.

When it comes to South Africa, authors who report on climate change were quite different from Namibia. Named authors from Cape Argus and Sunday times are responsible for 36.5% and 26.5% of global warming coverage, respectively. However, none of the authors specialised in reporting environmental or climate change reporting by qualification. On the other hand, 27% of climate change coverage in Sunday Times was imported from other news media. Just moderately different to the neighbouring country Namibia, sources such as AFP-Relax news and AFP were referenced. However, the style of taking materials from other news agencies is similar.

DISCUSSION

Climate change coverage trends

The climate change trend analysis allowed a closer look at coverage of climate newspaper discourse in

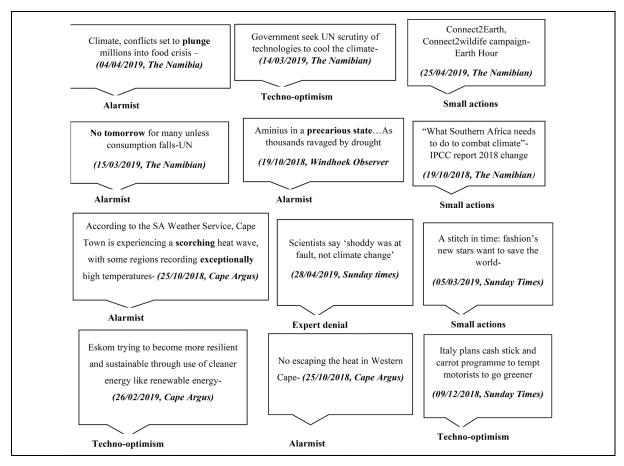


Figure 4: Examples of climate repertoires practised used in Namibian and South African news outlets.

Namibia and South Africa from October 2018-April 2019. Climate change coverage fluctuations were driven by different events with different attention levels such as IPPC reports, UNFCC COP24 or local extreme events such as drought. Climate change coverage was narrower and steeper in weekly newspapers such as Windhoek Observer and Sunday Times than in daily newspapers (The Namibian and Cape Argus). However, claiming that weekly newspapers have better climate change trends is naive, as other factors such as the total number of articles published per month may come into play. According to trends and the evidence from the analysed news outlet, the impacts of climate breakdown drive and influence the newspapers' coverage. Climate change coverage trends fluctuated and reached a peak during specific events that occurred. According to Schmidt et al. (2013), fluctuating newspaper coverage is "typical." Peaks were observed in this case during the month (December 2018) when the UNFCC COP24 was held, as well as when activists or protesters worldwide went on strike in response to the climate crisis. Following such events, there is likely to be a lot of media debate about the outcomes, which increases climate change discourse. The study's findings are consistent with trends discovered by other researchers (Chand 2017). These trends can be seen in all newspapers, particularly since March

2019, when coverage of all newspapers gradually increased. For example, since February 2019, the effects of drought and water scarcity have been covered in both countries following their impacts on agriculture. Consequently, the newspapers' coverage trends on climate change portrayed how the impact of the climate crisis was felt in southern Africa, as predicted in the 2018 IPPC report. These include predictions of the water crisis and its effect on agriculture and wildlife. Because the effects of water scarcity are rapidly increasing, they may have influenced climate coverage trends in the next six months. Similar trends can be seen in climate-affected countries such as India, Mexico, and China, according to Schmidt *et al.* (2013).

Climate change thematic frames

According to the research of Chand (2017), the way news is framed, as well as the "strength and repetition of the frame, the competitive environment, and individual motivations", all have an impact on individual thinking. As a result, what the media leaves out or emphasises in their articles, whether intentionally or unintentionally, influences how readers perceive climate change., In this study, all newspaper outlets emphasised primarily the public opinion (civil/protest) thematic frame. The climate crisis news was frequently framed based on

organisations, experts, and activists' ideas on the impacts and measures to compact global heating. The theme was seen in The Namibian and Sunday Times. For example, Sunday Times published an article about experts claiming that flooding of houses in KwaZulu-Natal and the Eastern Cape was caused by poor planning rather than climate change. Although the articles did not explicitly state that climate change does not exist, the framing of such articles may lead readers to believe that extreme events are caused by government planning failures rather than climate change, encouraging readers to shift blame to government planning and policies. This is not either/or, it could be both climate change and government planning. In a different case, articles published by The Namibian on water scarcity mostly emphasised agricultural activities. Consequently, this portrays to the reader that water availability has mostly impacted the agriculture sector in Namibia. Overall, South African newspapers practised more diversified thematic frames compared to newspapers in Namibia. This might be because reporters in Namibia lack the skills to employ thematic frames.

Climate change linguistic repertoires

The most dominant climate repertoire in Namibia is small actions, followed by alarmists, whereas South Africa was dominated by alarmists, followed by small actions, especially when discussing the effects of global warming on water scarcity, economics, and agriculture. According to Ereaut & Segnit (2006 p. 12), the small actions and alarmists repertoires are direct contrapositions that are commonly placed alongside each other. The consequences of climate change have been described using adjectives like no tomorrow, extinction, and heatwaves. Adjectives like changing diet, emission reductions, and green bond, on the other hand, were frequently used to describe climate change small actions. Even though alarmist reporting is a way to warm the public and decisionmakers on the impacts of global warming, alarmist repertoire may instil in readers a sense of doom, causing them to freeze rather than act. Overall, the causes and effects of climate change are discussed alarmingly while reporting mitigations and measures as small actions to encourage people's actions toward compacting and adapting to climate change. The current effect of climate change in the two countries may explain the popularity of small actions and alarmist actions in southern Africa. However, bearing in mind that the two countries are in the same geographic area one might have expected to see significant similarities. More differences might emerge if the sample area was diversified to include other countries with different geographic and media systems such as other sub-Saharan countries.

Overview of climate change news sources and authors

Most of the climate change articles are imported from other media agencies without further interpretation, showing an image that authors do not have the skills nor the confidence to develop their climate change reports. This also indicates that the agendas set by the newspapers were focused on the external concern of climate change outside the region. The overdependence on foreign news on climate change may limit the opportunities for participation in combating climate change at a local level. The case is popular in newspapers in Namibia. According to Tagbo (2010), African newspapers tend to use foreign reports, without developing their own story on the issue. As a result, most African countries rely on international reports to keep climate change coverage alive. Furthermore, Batta et al. (2013) stated that African news media frequently report on climate change without an African context because most of the news is foreign-sourced. A concern of unqualified climate change is raised, and climate change is still poorly reported by the newsprint media. If international climate news in African newspapers is not accompanied by local context, especially when the news is relevant to local climate impacts, the role of newspapers in combating global warming is ineffective. National or regional news may entice the reader's interest. Moerdyk (2019) stated that readers are likely to opt for newspapers that report local news by local authors rather than international news from authors or experts they do not know.

CONCLUSION AND RECOMMENDATIONS

This study's findings sparked further research into what barriers impede the progress of climate change reporting in southern Africa. More research can be done to investigate how people use thematic frames and climate linguistic repertoires in informal settings like group discussions or interviews. Coverage and the communication of climate change issues in southern Africa can be improved if journalists change their reporting styles. A balance must be struck between cautioning journalists against alarmist reporting and not diminishing the seriousness of climate change as a global crisis. Small actions encourage people to act, so a balance can be achieved by using fewer alarmist adjectives accompanied by pragmatic adjectives. Moreover, environmental journalism training for journalists and editors, as well as increased collaboration with climate change organisations, could help achieve good climate change reporting. Furthermore, newspapers should broaden their local report sourcing to include a local context, which they can do by working with experts, farmers, and non-governmental organisations. News media in southern Africa should follow the advice from The Guardian newspaper article by its environmental editor Carrington (2019) on keywords changes when reporting climate change. This ranges from interchanging keywords such as climate change to climate crisis or global warming to global heating. The lack of newspaper archives proved to be an issue in achieving better analysis in this study. Therefore, newspaper companies, particularly the Cape Argus and Sunday Times, should create news outlet archives that can be used in future studies.

ACKNOWLEDGEMENTS

This paper would not have been possible if not for financial support from the Commonwealth Scholarship Commission. The Sigma Centre's statistical assistance, as well as that of everyone associated with Coventry University, is appreciated. Gratitude to Bernadine Jones for your contribution as an expert in southern Africa's media discourse. John Mendelsohn and Peter Sullivan, the reviewers, deserve special thanks. Appreciations go to Toini Kauluma for changing figures into high resolution.

REFERENCES

- Barkemeyer R, Figge F, Hoepner A, Holt D, Kraak JM, Yu PS (2017) Media coverage of climate change: An international comparison. *Environment and Planning C: Politics and Space* 35(6): 1029–1054. https://doi.org/10.1177/0263774X16680818.
- Batta HE, Ashong AC, Bashir AS (2013) Press Coverage of Climate Change Issues in Nigeria and Implications for Public Participation Opportunities. *Journal of Sustainable Development* 6(2). https://doi.org/10.5539/jsd.v6n2p56.
- Boyd E (2015) *Resilience*. Oxford University Press. https://doi.org/10.1093/acrefore/9780190228620.
- Boykoff MT (2007) a dead norm? Newspaper coverage of Flogging climate change in the United States anthropogenic and the United Kingdom from 2003 to 2006. Royal Geographical Society 39(2): 1–11.
- Boykoff MT (2008) The cultural politics of climate change discourse in UK tabloids. *Political Geography* 27: 549–569. https://doi.org/10.1016/j.polgeo.2008.05.002.
- Boykoff MT, Luedecke G (2016) Elite News Coverage of Climate Change. Oxford Research Encyclopedia of Climate Science:: 1–27. https://doi.org/10.1093/acrefore/9780190228620.013.357.
- Brand South Africa (2013) A guide to South African newspapers. *Brand South Africa*. https://www.brandsouthafrca.com/south-africa-fast-facts/media-facts/a-guide-to-south-african-newspapers#daily.
- Brüggemann M, Engesser S (2017) Beyond false balance: How interpretive journalism shapes media coverage of climate change. *Global Environmental Change* 42: 58–67. https://doi.org/10.1016/j.gloenvcha.2016.11.004.
- Carrington D (2019) Why the Guardian is changing the language it uses about the environment. *The Guardian*. https://www.theguardian.com/environment/2019/may/17/why-the-guardian-is-changing-the-language-it-uses-about-the-environment.
- Chand S (2017) 2. Newspaper coverage of climate change in Fiji: A content analysis. *Pacific Journalism Review* 23(1): 169–185.

- Ereaut G, Segnit N (2006) *Warm Words How are we telling* the climate story and can we tell it better? Unpublished report: Unknown company or institution, London. pp. 32–32. www.ippr.org.
- Erlickyte V (2014) Communicating Climate Change: Content analysis of British and Russian website coverage of climate change. Unpublished report: Unknown company or institution, Gothenburg. pp. 4–44. https://gupea.ub.gu.se/bitstream/2077/36333/1/gupea_2 077 36333 1.pdf.
- IPCC, Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J *et al.* (2018) Global warming of 1.5°C-IPCC.: 32–32
- Moerdyk C (2019) Confessions of a newspaper junkie. *The Media Online*: 1–1.
- O'Neill S, Williams HTP, Kurz T, Wiersma B, Boykoff M (2015) Dominant frames in legacy and social media coverage of the IPCC Fifth Assessment Report. *Nature Climate Change* 5(4): 380–385. https://doi.org/10.1038/nclimate2535.
- Ruppel OC, Ruppel-Schlichting K (2016) *Environmental Law and Policy in Namibia*, Third Edit. Hanns Seidel Foundation, Windhoek. http://www.jstor.org/stable/43240892.
- Schäfer MS, O'Neill S (2017) Frame Analysis in Climate Change Communication. Oxford University Press. https://doi.org/10.1093/acrefore/9780190228620.013.48
- Schmidt A, Ivanova A, Schäfer MS (2013) Media attention for climate change around the world: A comparative analysis of newspaper coverage in 27 countries. *Global Environmental Change* 23(5): 1233–1248. https://doi.org/10.1016/j.gloenvcha.2013.07.020.
- Shanahan M (2013) Climate change and the media. *Choice Reviews Online* 47(06): 145–157. https://doi.org/10.5860/choice.47-2990.
- Stoddart MCJ, Haluza-DeLay R, Tindall DB (2016) Canadian News Media Coverage of Climate Change: Historical Trajectories, Dominant Frames, and International Comparisons. *Society & Natural Resources* 29(2): 218–232. https://doi.org/10.1080/08941920.2015. 1054569.
- Sunday Times (2019) About TimesLIVE, Times Select and the Sunday Times. *Tiso Blackstar group*. https://www.timeslive.co.za/about-us/.
- Tagbo E (2010) Media coverage of climate change in Africa: a case study of Nigeria and South Africa. *Reuters Institute Fellowship Paper*: 1–39. https://doi.org/10.1016/j.cpr.2008.05.001.
- Takahashi B (2011) Framing and sources: A study of mass media coverage of climate change in Peru during the V ALCUE. *Public Understanding of Science* 20(4): 543–557. https://doi.org/10.1177/0963662509356502.
- Trumbo C (1996) Constructing climate change: Claims and frames in US news coverage of an environmental issue. *Public Understanding of Science* 5(3): 269–283. https://doi.org/10.1088/0963-6625/5/3/006.
- United Nations Environment Programme (2018) *Understanding the IPCC Special Report on 1.5°C.* Unpublished report: Unknown company or institution, Geneva 2. pp. 12–12. https://library.wmo.int/doc num.php?explnum_id=5188.
- Whitfield C (2019) Cape Argus About Us. *Cape Argus*. https://www.iol.co.za/capeargus/about-us.

Spatio-temporal functional diversity of large herbivores in Mudumu National Park, northeastern Namibia

SL Mbeha¹, LP Rutina^{1,2}

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-mbeha Published online: 26th August 2022

- Department of Wildlife Management and Tourism Studies, University of Namibia, Private Bag 1096, Katima Mulilo, Namibia.
- ² Ecosystem Conservation Foundation, Private Bag 20227, Maun, Botswana. prutina@unam.na

Date received: 31st December 2021; Date accepted: 14th July 2022.

ABSTRACT

Functional diversity is a component of biodiversity that includes the range of roles that organisms perform in communities and can explain and predict the impact of organisms on ecosystems. Mudumu National Park is an important ecosystem that acts as a wildlife corridor for migratory fauna moving between Botswana, Namibia, Angola and Zambia. Thus, a thorough understanding of the functional diversity of large herbivores would assist with the management of the park. The present study examined large herbivore species contribution to total large herbivore biomass; dominant species' functional similarities; and whether or not functional diversity is affected by increasing distance from the Kwando River. A total of twenty-two roads were selected that provided good coverage of the park and were surveyed using the line transect distance sampling method. All large herbivores seen on either side of the transects were identified to species level and recorded. The hierarchical cluster analysis in SPSS was used to classify the herbivores into functional groups. Only a small number of species were found to be dominant in both numbers and biomass. Furthermore, dominant species were found to be functionally distinct, and functional dominance changed with respect to season and distance from the river.

Keywords: dominant species; functional diversity; functional similarity; functional traits; large herbivores; Mudumu National Park; Namibia

INTRODUCTION

Large herbivores are a crucial component of biodiversity in the world's ecosystems. They provide important ecological services such as the regulation of vegetation dynamics, seed dispersal and pollination, as well as nutrient cycling among others (Duffus & Dearden 1990, Jefferies *et al.* 1994, Wilson & Reeder 2005, Lapeyre & Laurans 2017). Large herbivores are at the centre of wildlife tourism, making up three of Africa's famed Big Five – tourists' most sought-after animals on the continent (Owen-Smith 1982). Their products, skins and horns, have cultural importance in rural African societies where they are used as utensils and decorations, particularly on ceremonial occasions.

Large herbivores are among the most widespread animals on the continent where they actively affect the structure and processes of the African savanna (Owen-Smith 1982). According to Owen-Smith (1982) the African continent is home to about 44 large herbivore species. The term large herbivore here refers exclusively to ungulates (artiodactyls and perissodactyls), as well as elephants from the order Proboscidea. Other large herbivores like the ostrich (*Struthio camelus*) and primates were not considered.

Due to the undeveloped nature of the field of functional ecology, there still is no consensus on the one true definition of functional diversity. However, a widely accepted definition is "the value and the range of those species and organismal traits that influence ecosystem functioning" (Tilman 2001). Unlike classical measures of biodiversity such as species richness which assume that all species and individuals are equal despite size differences, functional diversity is a trait-based measure of diversity (Petchey et al. 2004, Petchey & Gaston 2006, Mouchet et al. 2010, Laureto et al. 2015, Zhu et al. 2017, Ahmed et al. 2019). A functional trait is any measurable feature of an individual that potentially impacts fitness of the organism and can be physical, biochemical, behavioural, and temporal or phenological. Traits can determine how organisms utilise resources and how they react to environmental pressure, and consequently determine the varying contributions of species to ecosystem function and processes (Mokany et al. 2008, Lavorel et al. 2011). In its true essence, functional diversity represents trait diversity but is usually taken to represent the diversity of niches or functions in an ecosystem (Petchey et al. 2004, Petchey & Gaston 2006, McGill et al. 2006, Villéger et al. 2008). Moreover, functional diversity has been successfully used to understand how classical measures of species richness and diversity relate to ecosystem function (Petchey et al. 2004, Cadotte et al. 2009, Flynn et al. 2011) and how organisms respond to environmental disturbance (Norberg et al. 2001, Suding et al. 2008). Although there is a plethora of research on functional diversity of ecosystems around the world, there is a paucity of information on trait ecology in all parts of Namibia. A number of studies have been carried out on species diversity and abundance (e.g. Griffin 1998, Robertson et al. 1998, Naidoo et al. 2011), however studies on the functional diversity of wildlife have not yet been carried out.

Namibia has a vast diversity of mammals, including large herbivores (Griffin 1998), and the present study area sits at the heart of one of the world's most important biodiversity hotspots: the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA). Mudumu National Park (hereafter the park) is surrounded by a mosaic of communal areas that are partitioned into different land uses, such as residential, agricultural land, community forestry and community wildlife managed areas under the Community-Based Natural Resources Management (CBNRM) model. The park serves as a source of wildlife resources to the surrounding community conservation areas. Furthermore, the park also forms part of the Kwando corridor, a wildlife dispersal area that links northern Botswana through Namibia to western Zambia and Eastern Angola. However, it is also a source of human-wildlife conflict to adjacent communities. Thus, understanding the dynamics of biodiversity in the park can aid in the management of the park, as well as that of conservancies and forestry areas at a landscape level.

We tested the hypotheses that:

- The abundance and biomass of the large herbivore community in Mudumu National Park are dominated by a few species,
- 2) Dominant species are functionally distinct because they occupy different ecological niches (hence perform different functions), and
- A decline in dominant large herbivore species, for example away from the Kwando River in the dry season, resulted in an increase in abundance of functionally similar minor species.

METHODS

Study Area

Mudumu National Park is found in the south-central part of Namibia's Zambezi Region (Figure 1). The park was established in 1990 and covers an area of 737 square kilometres. Its borders, apart from its western border on the Kwando River, are entirely

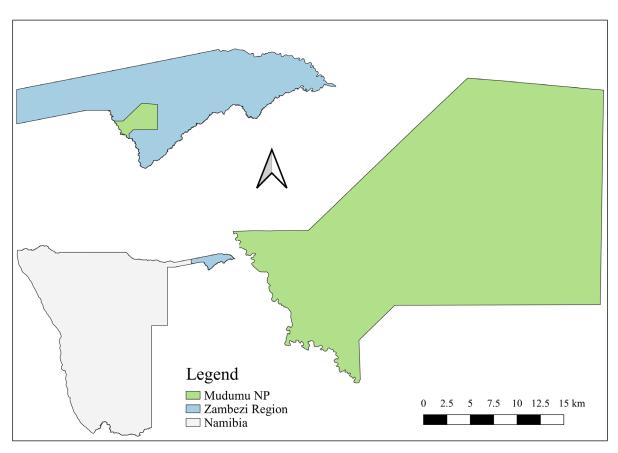


Figure 1: Mudumu National Park and its location in the Zambezi Region of Namibia.

surrounded by various communal area conservancies and community forests. It is located in the centre of the KAZA TFCA and provides a corridor for wildlife movement from Botswana through Namibia and into Angola and Zambia of many important large herbivores such as elephant, buffalo, roan and sable antelope. The area is easily accessible by road and is about 1 173 km from the capital city of Windhoek, and 461 km and 116 km from the two regional towns of Rundu and Katima Mulilo respectively.

Sampling design

The line transect method was used to effectively survey the species diversity and abundance of large herbivores. All routes were pre-established as part of an annual long-term game count system used by park staff to monitor wildlife. Transect routes were of varying lengths and only about half of each transect was surveyed. The entire study area was stratified into two sections, (i) near to the river - up to about 9 km, and (ii) away from the river - from about 13 km on a line created by the C49 road passing through the park and connecting the villages of Kongola and Sangwali.

Field Survey

The study was conducted in the dry season (June 2019) and in the wet season (December 2019), and each transect route was only visited once per season. A total of 22 transect routes of varying lengths were surveyed. The routes provided good coverage of the park. Six routes are situated near the river (west of the C49 road) and 16 are found away from the river (east of the C49 road).

Large herbivores were counted from a vehicle at a constant speed of ~ 15 km/h during the morning and late afternoon when they are most active, and within a transect width of ~ 100 meters on either side of the track. A hand-held GPS was used to record the coordinates of each sighting.

Species were assigned to functional groups using traits that are known to influence ecosystem functions and processes such as: body mass, feeding guild, feeding habitat, activity time, social behaviour, metabolic rate, fecundity, digestive physiology, home range size, water requirements, gestation period, foraging behaviour, gape width, lifespan, and breeding among others. Information on these attributes was acquired from southern African wildlife literature (e.g. Skinner & Chimimba 2005, Bothma & du Toit 2016). Following Walker *et al.* (1999) and McCarthy *et al.* (1998) the attributes were standardised on a scale of 1 to 5 for comparisons.

Data Analysis

On each transect route, species abundances were ranked and their relative proportion to total abundance was determined. The number of animals of each species was used to calculate each species' biomass and their respective contribution to total large herbivore biomass. For a well sampled community, the proportion of individuals found in a species (P_i) is estimated as:

$$P_i = \frac{ni}{N}$$

where n_i is the number/biomass of individuals in species i and N is the total number/biomass of individuals in the community. P_i ranges from 0 to 1.

Species with a collective relative abundance $\geq 80\%$ on each transect were considered to be dominant. Ecological distances for all species on each transect were determined and summed up for each distance category. Ecological distance here refers to the chasm between two species in attribute space, and is used as a measure of functional diversity and functional redundancy (Walker *et al.* 1999).

A Fisher's exact test for homogeneity (Fisher 1935) was performed to test frequencies by spatio-temporal categories between dominant species and all species in the park. Correspondingly, another test was performed to test functional similarities by spatio-temporal categories of dominant species between population numbers and biomass.

The hierarchical classification in SPSS was performed in order to classify species into functional groups. Subsequently, a k-classification was performed on the clusters obtained from the hierarchical classification, as well as the Euclidean Distance (ED) to estimate ecological differences among species. The simplified version of ED has the formula:

$$ED_{jk} \equiv \sum{(A_{ij} - A_{ik})^2}$$

where ED_{jk} is the ecological distance between species j and k, and A_{ij} and A_{ik} are values of species j and k for trait i.

Following (Walker et al., 1999), the expression:

dry season abundance near the river
wet season abundance far from the river

was used to examine differences in abundances for each functional group between season and distance from the Kwando River, in order to predict the spatio-temporal increase or decrease in functional abundance. Values < -1 or > 1 denote a significant increase or decrease in abundance, respectively.

RESULTS

Proportional Contribution

Overall, 17 large herbivore species were recorded in the park (see Table 1 for the list and scientific names). In general, it was found that large mammal herbivores were dominated by only a few species (Figure 2). In terms of numbers, the dominant species were buffalo, impala, zebra, elephant, blue wildebeest and roan antelope with a collective population contribution of 0.84. The other 11 species shared the remaining 0.16 with duiker and bushbuck

having the lowest numbers. In terms of biomass, the dominant species were elephant, buffalo, zebra and blue wildebeest with a collective biomass contribution of 0.86. The other 13 species shared the remaining 0.14 with duiker and bushbuck having the lowest biomass contribution.

In the dry season, 16 species were recorded, with 16 found near the river (Figure 3) and four found away from the river (Figure 4). In terms of numbers near the river (Figure 3a), the dominant species were impala, elephant, kudu, buffalo, zebra and blue wildebeest with a collective population contribution

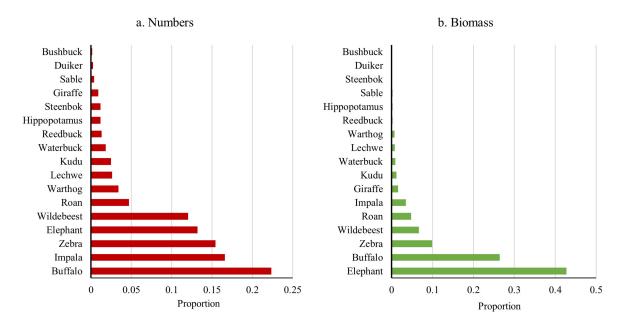


Figure 2: Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park.

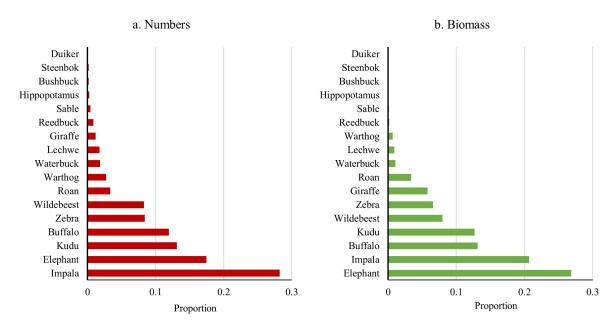


Figure 3: Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the dry season, near to the river.

of 0.86. In terms of biomass near the river (Figure 3b), the dominant species were elephant, impala, buffalo, kudu and blue wildebeest with a collective biomass contribution of 0.82. Away from the river, the most dominant species in both numbers and biomass were steenbok and zebra with a collective contribution of 0.84 in terms of numbers and 0.94 in terms of biomass.

In the wet season, 13 species were recorded, with only one species, impala, found near the river (Figure 5) and 13 species away from the river (Figure 6). Away from the river, the dominant species in terms

of numbers were kudu, buffalo, roan antelope, steenbok, zebra and blue wildebeest with a collective population contribution of 0.84 (Figure 6a). In terms of biomass, the most dominant species were kudu, buffalo, roan antelope, giraffe and blue wildebeest with a collective biomass contribution of 0.82 (Figure 6b).

There was no significant difference between the whole park and the spatio-temporal scales within the park for both the abundance (number) and biomass (Fisher Exact Test, p > 0.05 for all tests). However, the composition of dominant species at different

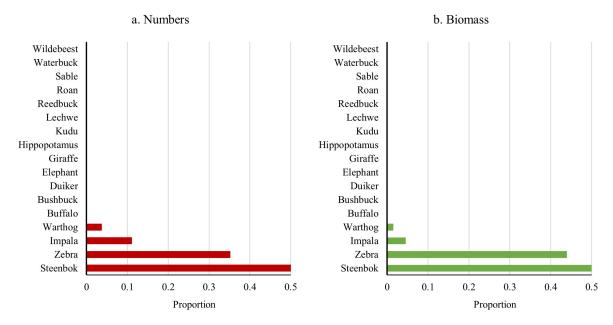


Figure 4: Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the dry season, away from the river.

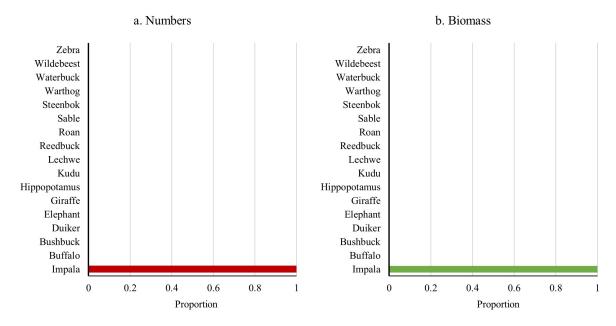


Figure 5: Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the wet season, near to the river.

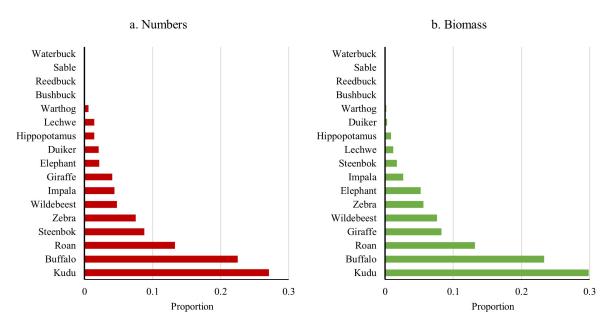


Figure 6: Proportion of each large mammal herbivore species to total a) numbers and b) biomass of large mammal herbivores in Mudumu National Park in the wet season, away from the river.

spatio-temporal categories differs from the overall dominant species of the park. For dry season and near to the river, species composition of dominant species was similar to those of the entire park for both abundance and biomass (Morisita similarity index (Cm) = 0.85 for abundance and 0.80 for biomass). For dry season and away from the river, species composition of dominant species was different to those of the entire park for both abundance and biomass (Cm = 0.30 for abundance and 0.13 for biomass). For wet season and away from the river, species composition of dominant species was approximately 50% of those of the entire park for both abundance and biomass (Cm = 0.62 for abundance and 0.47 for biomass).

Functional Dissimilarity

To determine the functional dissimilarity of the dominant species in the park, pairwise comparisons were performed. Out of the 15 pairwise comparisons produced by matching the six dominant species in population numbers, it was found that 27% (4) of the pairs were similar, 33% (5) were intermediate, and 40% (6) were dissimilar (Figure 7). In terms of biomass contribution, the four dominant species compared generated six pairwise comparisons out of which 33%, (2) were similar; none were intermediate; and 67%, (4) were dissimilar (Figure 7).

In the dry season near the river, in terms of numbers, the six dominant species generated 15 pairwise comparisons, out of which 27% were similar, 33% were intermediate and 40% were dissimilar (Figure 8). In terms of biomass, the five dominant species

generated 10 pairwise comparisons, out of which 30% were similar, 40% were intermediate and 30% were dissimilar. Far from the river, the dominant species in both numbers and biomass contribution were steenbok and zebra only. The two dominant species allowed only one pairwise comparison, resulting in only a single intermediate relationship.

In the wet season near the river, only one species was recorded, allowing no pairwise comparisons for numbers and biomass. Away from the river, the six dominant species in terms of numbers provided 15 pairwise comparisons, of which 40% were similar, 33% were intermediate and 27% were dissimilar (Figure 8). In terms of biomass, the five dominant species provided 10 pairwise comparisons, of which all were similar.

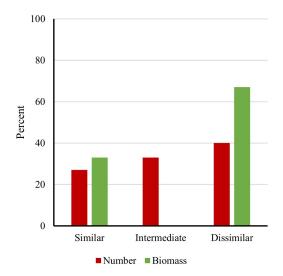


Figure 7: Functional dissimilarity among dominant large herbivore species in Mudumu National Park.

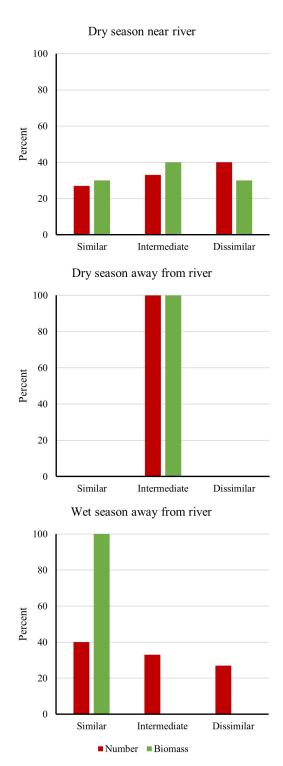


Figure 8: Functional dissimilarity of dominant large herbivore species in different spatio-temporal categories.

A hierarchical cluster analysis was also used to classify the herbivores into functional groups and substantiate the functional dissimilarity results yielded by the pairwise comparison method. All 17 species were divided into three functional groups according to their trait similarities and differences (Table 1). Dominant species are evenly represented in all three functional groups, suggesting good functional diversity.

Table 1: Functional group membership of large herbivores in Mudumu National Park. Dominant species (numbers # and biomass *) are evenly distributed among the three functional groups. Distance refers to the gap between an observation or the collective attributes of a particular species and the centroid of that group. The average distance from a species to the group centroid is a measure of the functional variability of the species within each group. A group that has a larger average distance is more diverse.

Group	Species	Distance
	Elephant # * Loxodonta africana	0.94
1	Burchell's Zebra # * Equus burchellii	1.37
	Hippopotamus amphibius	1.60
	Common warthog Phacochoerus africanus	1.75
	Red lechwe Kobus leche	0.96
	Southern reedbuck Redunca arundinum	1.75
2	Common impala # Aepyceros melampus	0.45
	Grey duiker Sylvicapra grimmia	0.45
	Steenbok Raphicerus campestris	0.45
	Bushbuck Tragelaphus sylvaticus	0.96
	Giraffe Giraffa camelopardalis	1.25
	Greater kudu Tragelaphus strepsiceros	1.00
	Roan antelope # Hippotragus equinus	0.54
3	Sable antelope Hippotragus niger	0.54
	Waterbuck Kobus ellipsiprymnus	0.54
	Blue wildebeest # * Connochaetes taurinus	0.54
	African savanna buffalo # * Syncerus caffer	1.51

Spatial Functional Variation

In terms of numbers, five large mammal herbivore species belonging to all three functional groups (elephant and zebra – group 1, impala – group 2, and buffalo and wildebeest – group 3) were dominant near the river (Table 2). Away from the river, three species (elephant, impala and zebra) declined in numbers. Of the declining species, only elephant lost its dominance. It was replaced by a functionally similar species, the hippopotamus, which was not dominant near the river. Kudu (group 3) also became

Table 2: Change in the contribution of numbers and biomass of large herbivore species in Mudumu National Park from the river inland.

		Numbers	Biomass			
Group	Decreased	Increased	Decreased	Increased		
1	Elephant Zebra	Hippopotamus	Elephant	Hippopotamus Zebra		
2	Bushbuck Impala Reedbuck Warthog	Duiker Lechwe Steenbok	Bushbuck Reedbuck	Duiker Impala Lechwe Steenbok Warthog		
3	Roan Sable Waterbuck	Buffalo Giraffe Kudu Wildebeest	Roan Sable Waterbuck	Buffalo Giraffe Kudu Wildebeest		

dominant away from the river. This changed the contribution of functional groups from 40%, 20% and 40% to 33%, 17% and 50% for group 1, 2 and 3 respectively, away from the river.

In terms of biomass, three large mammal herbivore species belonging to two functional groups (elephant and zebra – group 1, and buffalo – group 3) were dominant near the river (Table 2). Away from the river, only the elephant declined in dominance. Despite the decline, the elephant remained dominant away from the river, along with zebra and buffalo. Two more species, kudu and wildebeest in group 3 joined these. This changed the contribution of functional groups from 67%, 0% and 33% to 40%, 0% and 60% for group 1, 2 and 3, respectively, away from the river.

DISCUSSION

Proportional Contribution

This study shows that only a few species make up most of the large herbivore numbers and biomass in the park. Other studies (Walker *et al.* 1999, Rutina & Moe 2014) also found that ecosystems comprise a few dominant species that are functionally more effective and a multitude of minor species. This dominant-minor species relationship occurs when, despite performing similar functions, a single species or a relatively small group of species exert more pressure on their environment in comparison to all other species in the area. These minor species have relatively trivial functional influence but may help keep the system stable in case of an extinction event (Walker 1992, 1995, Duffy *et al.* 2001, Philpott *et al.* 2012, Kang *et al.* 2015, Biggs *et al.* 2020).

The study also revealed that high population numbers do not always guarantee high biomass contribution, as is the case with impala and roan antelope that were dominant in numbers but not in biomass. Another noteworthy case is the elephant which had lower population numbers in relation to some other species but still contributed the most in terms of biomass. This suggests that besides species richness, biomass contribution and ecological function are highly affected by ecological traits, such as the size or behaviour of an animal. Body size is one of the most fundamental traits of an organism (White *et al.* 2007). It is related to lifespan, home range size and other aspects of life history and ecology, and is one of the primary determinants of metabolism and therefore, resource use (Brown *et al.* 2004). The overwhelming influence of this trait is apparent in the role that the elephant plays in the savanna ecosystem.

Furthermore, zebra, which was dominant in numbers during the dry season near the river lost its dominance in terms of biomass contribution; and steenbok and zebra that were dominant in numbers during the wet season away from the river were not dominant in biomass contribution. Giraffe, which was not dominant in numbers, was one of the dominant species in terms of biomass. This further demonstrates the restricted association between how much a particular species affects its environment and how many individuals of that species are present.

Functional Dissimilarity

The study revealed that dominant species are dissimilar in terms of both population numbers and biomass contribution in the entire national park. This is in line with (Walker *et al.* 1999) who also found that the dominant species among their sampled vegetation were diverse. The findings also confirm the resilience hypothesis, first defined by (Holling 1973), as the amount of disturbance that an ecosystem can withstand without changing selforganised processes and structures. Resilience here means the persistence of function, or the capacity for function to be restored after a major change, rather than just the rate of return following a minor

disturbance (Ludwig et al. 1997, Walker et al. 1999). The functional dissimilarity of the dominant species shows that the area has diverse large herbivore driver traits affecting ecological processes and that, should a disturbance of some kind destabilise the ecosystem, there would be enough large herbivore trait variation to restore the system back to equilibrium.

When seasonal and spatial variation were considered, the pattern was different from that of the whole park. In the dry season, there was average functional dissimilarity between dominant species, peaking near the river, most likely due to the movement of large herbivores to the river when water becomes scarce elsewhere. However, during the wet season there was less large herbivore functional dissimilarity, especially near the river, most likely due to the animals dispersing back into the park in response to water availability in waterholes and lush pastures.

The hierarchical cluster analysis revealed that the area had three large herbivore functional groups. The first group comprised ecosystem engineers such as elephant (Mosepele *et al.* 2009, Sidle & Ziegler 2010) and hippopotamus (McCarthy *et al.* 1998, Deocampo 2002, McCauley *et al.* 2015). The third group comprised megaherbivores such as giraffe and buffalo, while the middle group contained small herbivores such as duiker and impala.

Spatial Functional Variation

Large herbivore functional diversity changed with an increase in distance from the Kwando River. This change resulted from a change in dominant species. Dominant species that were absent or lost their dominance either near or away from the river were replaced by functionally similar minor species. These results are consistent with other studies that show that environmental and spatial variation has an effect on the species richness of organisms (Fierer & Jackson 2006, Chen *et al.* 2017). Stevens *et al.* (2003) also observed an abrupt increase in functional diversity of bats towards the equator when travelling from the tropics and concluded that increase in species richness alone could not account for that change.

CONCLUSIONS AND RECOMMENDATIONS

The effective management of protected areas is greatly improved by precise knowledge of the functional diversity of species contained within. This study confirmed that only a small number of large herbivore species contribute the most in terms of numbers and biomass within the park, and that species with large population numbers did not always have the most functional influence due to constraints in communal body mass and related ecological traits. Moreover, the park was found to have three diverse functional clades and that season and distance from

the river greatly influenced the distribution of functions across space and time. Lastly, there is need to further investigate and understand the functional ecology of the park to help facilitate management efforts.

ACKNOWLEDGEMENTS

We are grateful to Christopher Brown and the editor for their constructive comments and suggestions. We are also thankful to the Ministry of Environment, Forestry and Tourism (MEFT), and the British Ecological Society for financial support. We further appreciate the assistance of Justin Moya, Tuwilika Angula, Martha Alfious, and Shampondili Shihwandu in the field. This study was conducted as part of the Mudumu National Park Biodiversity Monitoring Framework.

REFERENCES

- Ahmed DA, van Bodegom PM, Tukker A (2019) Evaluation and selection of functional diversity metrics with recommendations for their use in life cycle assessments. *The International Journal of Life Cycle Assessment* 24(3): 485–500. https://doi.org/10.1007/s11367-018-1470-8.
- Biggs CR, Yeager LA, Bolser DG, Bonsell C, Dichiera AM, Hou Z *et al.* (2020) Does functional redundancy affect ecological stability and resilience? A review and meta-analysis. *Ecosphere* 11(7): e03184. https://doi.org/10.1002/ecs2.3184.
- Bothma J du P, du Toit JG (2016) Game Ranch Management. Van Schaik Publishers.
- Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a Metabolic Theory of Ecology. *Ecology* 85(7): 1771–1789. https://doi.org/10.1890/03-9000.
- Cadotte MW, Cavender-Bares J, Tilman D, Oakley TH (2009) Using Phylogenetic, Functional and Trait Diversity to Understand Patterns of Plant Community Productivity. *PLOS ONE* 4(5): e5695. https://doi.org/10.1371/journal.pone.0005695.
- Chen Y, Kuang J, Jia P, Cadotte MW, Huang L, Li J, Liao B, Wang P, Shu W (2017) Effect of Environmental Variation on Estimating the Bacterial Species Richness. *Frontiers in Microbiology* 8: 690. https://doi.org/10.3389/fmicb.2017.00690.
- Deocampo DM (2002) Sedimentary Structures Generated by *Hippopotamus amphibius* in a Lake-Margin Wetland, Ngorongoro Crater, Tanzania. *PALAIOS* 17(2): 212–217.
- Duffus DA, Dearden P (1990) Non-consumptive wildlifeoriented recreation: A conceptual framework. *Biological Conservation* 53(3): 213–231. https://doi.org/10.1016/ 0006-3207(90)90087-6.
- Duffy J, Macdonald KS, Rhode JM, Parker JD (2001) Grazer diversity, functional redundancy, and productivity in seagrass beds: An experimental test. *Ecology* 82(9): 2417–2434.
- Fierer N, Jackson RB (2006) The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences* 103(3): 626–631. https://doi.org/10.1073/pnas.0507535103.
- Flynn DFB, Mirotchnick N, Jain M, Palmer MI, Naeem S (2011) Functional and phylogenetic diversity as predictors of biodiversity-ecosystem-function relationships. *Ecology* 92(8): 1573–1581. https://doi.org/10.1890/10-1245.1.

- Griffin M (1998) The species diversity, distribution and conservation of Namibian mammals. *Biodiversity & Conservation* 7(4): 483–494. https://doi.org/10.1023/A:1008875511827.
- Holling CS (1973) Resilience and Stability of Ecological Systems. *Annual Review of Ecology and Systematics* 4(1): 1–23. https://doi.org/10.1146/annurev.es.04. 110173.000245.
- Jefferies RL, Klein DR, Shaver GR (1994) Vertebrate Herbivores and Northern Plant Communities: Reciprocal Influences and Responses. *Oikos* 71(2): 193–206. https://doi.org/10.2307/3546267.
- Kang S, Ma W, Li FY, Zhang Q, Niu J, Ding Y, Han F, Sun X (2015) Functional Redundancy Instead of Species Redundancy Determines Community Stability in a Typical Steppe of Inner Mongolia. *PLOS ONE* 10(12): e0145605.
 - https://doi.org/10.1371/journal.pone.0145605.
- Lapeyre R, Laurans Y (2017) Contractual arrangements for financing and managing African protected areas: insights from three case studies. *PARKS* 23(1): 75–88. https://doi.org/10.2305/IUCN.CH.2017.PARKS-23-1RL.en.
- Laureto LMO, Cianciaruso MV, Samia DSM (2015) Functional diversity: an overview of its history and applicability. *Perspectives in Ecology and Conservation* 13(2): 112–116. https://doi.org/10.1016/j.ncon.2015.11. 001.
- Lavorel S, Grigulis K, Lamarque P, Colace M-P, Garden D, Girel J, Pellet G, Douzet R (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology* 99(1): 135–147. https://doi.org/10.1111/j.1365-2745. 2010.01753.x.
- Ludwig D, Walker B, Holling CS (1997) Sustainability, Stability, and Resilience. *Conservation Ecology* 1(1). https://doi.org/10.5751/ES-00012-010107.
- McCarthy TS, Ellery WN, Bloem A (1998) Some observations on the geomorphological impact of hippopotamus (*Hippopotamus amphibius* L.) in the Okavango Delta, Botswana. *African Journal of Ecology* 36(1): 44–56. https://doi.org/10.1046/j.1365-2028.1998. 89-89089.x.
- McCauley DJ, Dawson TE, Power ME, Finlay JC, Ogada M, Gower DB *et al.* (2015) Carbon stable isotopes suggest that hippopotamus-vectored nutrients subsidize aquatic consumers in an East African river. *Ecosphere* 6(4): 1–11. https://doi.org/10.1890/ES14-00514.1.
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21(4): 178–185. https://doi.org/10.1016/j.tree.2006.02.002.
- Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96(5): 884–893. https://doi.org/10.1111/j.1365-2745.2008.01395.x.
- Mosepele K, Moyle P, Merron G, Purkey D, Mosepele B (2009) Fish, Floods, and Ecosystem Engineers: Aquatic Conservation in the Okavango Delta, Botswana. *BioScience* 59(1): 53–64. https://doi.org/10.1525/bio. 2009.59.1.9.
- Mouchet MA, Villéger S, Mason NW, Mouillot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology* 24(4): 867–876.

- Naidoo R, Stuart-Hill G, Weaver LC, Tagg J, Davis A, Davidson A (2011) Effect of Diversity of Large Wildlife Species on Financial Benefits to Local Communities in Northwest Namibia. *Environmental and Resource Economics* 48(2): 321–335. https://doi.org/10.1007/s10640-010-9412-3.
- Norberg J, Swaney DP, Dushoff J, Lin J, Casagrandi R, Levin SA (2001) Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proceedings of the National Academy of Sciences of the United States of America* 98(20): 11376–11381. https://doi.org/10.1073/pnas.171315998.
- Owen-Smith N (1982) Factors Influencing the Consumption of Plant Products by Large Herbivores. In: Huntley, B.J., Walker, B.H. (eds) *Ecology of Tropical Savannas*. Ecological Studies, vol 42. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-68786-0 17.
- Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. *Ecology Letters* 9(6): 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x.
- Petchey OL, Hector A, Gaston KJ (2004) How Do Different Measures of Functional Diversity Perform? *Ecology* 85(3): 847–857.
- Philpott SM, Pardee GL, Gonthier DJ (2012) Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity. *Ecology* 93(5): 992–1001. https://doi.org/10.1890/11-1431.1.
- Robertson A, Jarvis AM, Brown CJ, Simmons RE (1998) Avian diversity and endemism in Namibia: patterns from the Southern African Bird Atlas Project. *Biodiversity & Conservation* 7(4): 495–511. https://doi.org/10.1023/A: 1008827628666.
- Rutina LP, Moe SR (2014) Elephant (*Loxodonta africana*) Disturbance to Riparian Woodland: Effects on Tree-Species Richness, Diversity and Functional Redundancy. *Ecosystems* 17(8): 1384–1396. https://doi.org/10.1007/s10021-014-9801-5.
- Sidle RC, Ziegler AD (2010) Elephant trail runoff and sediment dynamics in northern Thailand. *Scopus*. https://scholarbank.nus.edu.sg/handle/10635/19718.
- Skinner JD, Chimimba CT (2005) *The Mammals of the Southern African Sub-region*. Cambridge University Press. Place?
- Stevens RD, Cox SB, Strauss RE, Willig MR (2003) Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. *Ecology Letters* 6(12): 1099–1108. https://doi.org/10.1046/j.1461-0248.2003. 00541.x.
- Suding KN, Lavorel S, Chapin FS, Cornelissen JHC, Diaz S, Garnier E *et al.* (2008) Scaling environmental change through the community level: a trait-based response-and-effect framework for plants. *Global Change Biology.* 14: 1125–1140.
- Tilman D (2001) Functional diversity. *Encyclopedia of biodiversity* 3(1): 109–120.
- Villéger S, Mason NW, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89(8): 2290–2301.
- Walker BH (1992) Biodiversity and ecological redundancy. *Conservation biology* 6(1): 18–23.
- Walker B (1995) Conserving biological diversity through ecosystem resilience. *Conservation biology* 9(4): 747–752.

- Walker B, Kinzig A, Langridge J (1999) Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2(2): 95–113.
- White EP, Ernest SM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. *Trends in ecology & evolution* 22(6): 323–330.
- Wilson DE, Reeder DM (2005) Mammal Species of the World. Johns Hopkins University Press. *Baltimore and London*.
- Zhu L, Fu B, Zhu H, Wang C, Jiao L, Zhou J (2017) Trait choice profoundly affected the ecological conclusions drawn from functional diversity measures. *Scientific reports* 7(1): 1–13.

At home or passing through? Leopard population and spatial ecology on a private game reserve

S Périquet¹, S Crawford², S Naholo¹, S Stratford¹ and K Stratford¹

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-periquet Published online: 8th September 2022

¹ Ongava Research Centre, Private Bag 12041, Ausspannplatz, Windhoek, Namibia. stephanie.periquet@gmail.com

Date received: 23rd February 2022; Date accepted: 28th August 2022.

ABSTRACT

Estimating large carnivore population size and understanding how individuals share space is crucial for their conservation, even more so now they are increasingly restricted to small, fenced game reserves where active management is often required. Combining data from GPS collars and camera traps, we estimated population size for leopards (*Panthera pardus*) on Ongava Game Reserve, northern Namibia, and investigated their spatio-temporal use of waterholes. Over three years of camera trapping, we identified a total of 29 individuals (including 12 adult or sub-adult females and 15 adult or sub-adult males). Based on the time interval over which they were observed, we defined 10 of these individuals as resident (four adult or sub-adult males and six adult or sub-adult females). The remaining 19 individuals (66%) were classified as transient. During the same period, we deployed two GPS collars, one on a resident adult male, the other on a resident adult female. Home range sizes from GPS data were estimated at 193 km² for the male and 122 km² for the female. Based on home range overlap found in the literature, we estimated Ongava's resident population to be composed of 2-4 males and 3-6 females. We found no evidence of exclusive use of waterholes by individuals, suggesting an absence of spatial avoidance. Our work highlights the importance of taking social status (resident vs transient) into account and of using multiple methods when estimating population size of leopards.

Keywords: camera trap, GPS collar, home range, leopard, Namibia, overlap, Panthera pardus, spatial ecology

INTRODUCTION

Estimating and monitoring the population sizes of carnivores is increasingly important in the current context of their global decline and even more so in small fenced game reserves where intensive management of predator populations is often required (Miller et al. 2013). Large carnivores are notoriously difficult to census due to their wide-ranging behaviour, elusive and nocturnal activities and their low density (Balme et al. 2009). However, as most large carnivore species are territorial at least to some extent, it is possible to use home size and overlap of a few individuals to produce an estimate of population size and/or density in a given area (e.g. Devens et al. 2018). In addition, for species in which individuals can be identified based on natural markings (e.g. stripes or spots), camera trapping has been used extensively to estimate carnivore population size (e.g. tigers, Panthera tigris, Karanth et al. 2004, cheetahs, Acinonyx jubatus, Broekhuis & Gopalaswamy 2016). The leopard (Panthera pardus) is a highly secretive and adaptable species, capable of living in landscapes with high anthropogenic disturbance levels, including near large towns such as Mumbai, India (Odden et al. 2014) and Johannesburg, South Africa (Kuhn 2014). However, leopard populations are decreasing throughout their range (Jacobson et al. 2016), for example by more than 30% in Southern Africa in the past 22 years (Stein et al. 2016). Due to their climbing abilities, leopards are not easily constrained by fences (Balme et al. 2007, du Preez et al. 2015) and thus cannot be effectively restricted within protected areas. These protected areas are often seen as sources for large predator populations, from which sub-adults disperse across neighbouring lands (sometimes across very long distances, such as the ~200 km reported by Fattebert et al. 2015a) in search of free space to establish their own territory.

In this study, we focus on estimating population size and density of leopard on the Ongava Game Reserve bordering Etosha National Park in northern Namibia. Given that we might expect leopard populations to be composed of resident individuals (with established territories) and transients (either sub-adults looking to establish a territory or sub-dominant adults displaced from their territory), we also assess resident versus transient status. The reserve is dedicated to non-consumptive tourism, but despite intensive use for game-viewing tourism (as many as 15 safari vehicles driving through the reserve on a daily basis), leopards are rarely seen. However, Ongava represents a prime habitat for leopards, being mostly covered by rocky hills providing numerous caves and

² Ongava Game Reserve, PO Box 58, Okaukuejo, Namibia.

refuges from competitors (namely lions, *Panthera leo*) and harbouring a high density of leopards' preferred prey (Hayward *et al.* 2006). We used camera traps deployed at waterholes over a 3-year study period and identified individual leopards based on their coat patterns to produce estimates of population size. In addition, we investigated the potential for intraspecific competition which might be manifested in spatio-temporal avoidance in the use of waterholes.

METHODS

Study area

Ongava Game Reserve (Ongava hereafter) borders the south of Etosha National Park (Figure 1), covering an area of approximately 300 km². At the time of the study, the boundary with Etosha was a low non-electrified cattle fence permeable to carnivores, but not to medium and large-sized herbivores, whereas all other fences were electrified high game fences. The habitat is termed Karstveld, with vegetation primarily (up to 70%) Colophospermum mopane shrub and woodland, with some savanna-like areas (about 30%). Ongava's relief is mostly dolomite hills, with an open plain area in the southeast corner (~11 km²) and a well-defined ridge and small mountain covering about 6 km² in the northern part of the reserve. The weather zone for the reserve is typical for semi-arid northern Namibia,

with an average annual rainfall of 380 mm (see Stratford & Stratford 2011 for further details). There are several natural dams on the reserve, although most of these only contain water during the rainy season (January - March). Water is accessible all year at 12 waterholes spread across the reserve. We defined the wet season as the period from January to April during which water was still available in natural dams and ephemeral pans and the dry season as the period from May to December when water was only available at artificial waterholes where herbivores congregate.

Ongava supports a range of mammalian herbivores that are candidate prey species for leopards such as common duiker (*Sylvicapra grimmia*), black-faced impala (*Aepyceros melampus petersi*), springbok (*Antidorcas marsupialis*) and rock hyrax (*Procavia capensis*; Hayward *et al.* 2006) with an overall herbivore density of about 10.4 animals per km² (Stratford and Stratford 2011).

Data collection

We used two methods to estimate the number of leopards on Ongava. First, we computed home range (HR) size from GPS data of two collared individuals (one adult male and one adult female) and used HR overlap metrics from the literature to calculate how many resident males and females would be predicted to have permanent HRs on Ongava. Second, we used

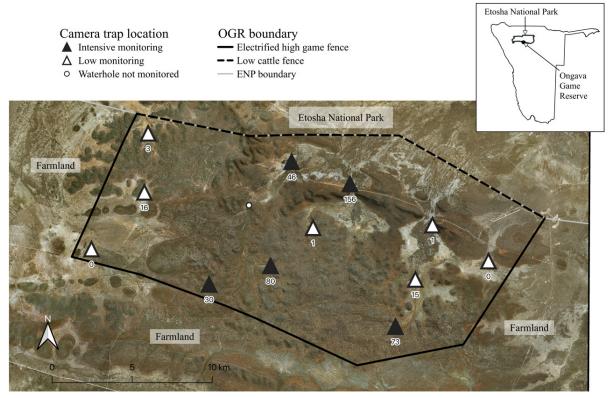


Figure 1: Location of camera traps deployed at 10 waterholes in Ongava Game Reserve, northern Namibia showing intensive (black triangles) and low (white triangles) monitoring locations. Figures indicate the number of leopard records at each location, including unidentified individuals.

camera traps deployed at waterholes across the reserve to identify individual leopards and estimate their number. Based on individual capture histories, we classified each individual as resident or transient and characterised their spatio-temporal overlap in waterholes usage.

Leopard collaring

We captured leopards in 2013 (February for the female, October for the male) in steel box traps deployed close to waterholes on suspected leopard trails. We baited traps with remains of carcasses and the trap door release was triggered by a conventional pressure plate. We monitored each trap using camera traps and implemented a remote alert system with a signal being triggered when the door was released allowing for a rapid response to minimise the time that animals were captive. Leopards immobilised in the trap by a professional team using a CO₂ dart gun (Dan Inject, www.dan-inject.com) with an induction dose of 350 mg of Zoletil (Vibrac RSA, Halfway House, RSA). Once sedated, we removed the animals from the trap to take measurements and fit a collar. Each individual received a 50 mg Zoletil IM top-up at some point in the procedure to keep the immobilisation stable. We then transferred the animals to a padded and ventilated recovery crate (1 x 1 x 2 m) close to the capture site and kept them enclosed until fully recovered from the anaesthetic, upon which they were released.

We fitted each leopard with a GPS radio-collar (Vectronic, Berlin) of weight adjusted to fit an adult male and adult female; 550 g and 280 g respectively. Both collars were equipped with VHF beacons, as well as automatic drop-offs (programmed to activate 12 months after deployment) to ensure collar recovery after the study period. Due to battery size difference (smaller for the female) to provide a full year of monitoring, we programmed the collars to record GPS locations every 3 h for the male and every 6 h for the female.

Camera trap survey

We deployed camera traps (Reconyx RC-55 and HC-500) at 12 waterholes spread across the reserve (Figure 1) from January 2012 to December 2014 (see Appendix 1 for operation table of camera traps). Some waterholes (n = 5, see Figure 1) were part of an intensive monitoring programme, while the rest were monitored during shorter periods across the three years. To provide the best coverage of the waterhole area, we deployed multiple (2-5) camera traps simultaneously at a given waterhole, and pooled their data together, resulting in a single set of images defined as a single observation. We mounted each camera inside a stainless-steel protection case that had been bolted to a tree and additionally secured using a locking steel cable. We set the cameras to

record a sequence of 10 images separated by one second with a delay of 15 seconds between successive triggers. For some remote waterholes, we used a 30 second delay between sequences to extend the interval between trap servicing.

We identified individual leopards based on their unique coat patterns. Pattern comparisons were manually performed over several areas of the body, as small changes in posture, light, and picture quality images complicate between the Identification was helped by the fact that images recorded at night using infrared flash provide an enhanced contrast between dark spots and light coat. We developed a reference database for individual leopards, with a minimum of one picture for each side available for each individual. When possible, we determined the sex of each individual based on based on body size, size of dewlap, and the presence of external genitalia (Balme et al. 2012). From the camera trap images, it was not possible to accurately age individuals, and animals of adult size were therefore classified as adults or sub-adults.

GPS data analysis

Home range size and overlap

To allow for comparison with other studies, we defined HR and core for each leopard as 95% and 50% location based kernel respectively (Worton 1989). We used a fixed kernel density estimator using the reference smoothing factor *href* as recommended by Hemson *et al.* (2005). We calculated HR and core sizes using the whole dataset for each individual.

We computed HR and core overlap between the two individuals using percentage overlap to allow comparison with other studies. We also provided a measure of three-dimensional utilisation distribution overlap index (UDOI, Fieberg & Kochanny 2005). UDOI values range from 0 (no overlap) to 1 when uniformly distributed utilisation distributions (UDs) overlap completely.

Prediction of the number of leopards present Similarly to Devens et al. (2018), we estimated the resident leopard population size using HR size and overlap obtained from the literature (Table 1) to predict the number of possible HRs, N, for both sexes separately on Ongava using the following formula:

$$N = \frac{Ongava \ area}{HR \ size - (overlap \times HR \ size)}$$

where *Ongava area* = 300 km², *HR size* is the size of the 95% kernel computed in this study and *overlap* is the value of percentage overlap taken from the literature. For each sex, we used the minimum and maximum overlap values taken from the literature to produce a resident leopard population size range for

Ongava. Density was calculated as the number of resident leopards per 100 km².

Camera trap data

Resident versus transient individuals

We estimated the number of resident and transient leopards based on each individual's capture history from camera trapping. Residents were defined as individuals having a stable HR on Ongava that would lead to consistent captures over time, while transients were individuals with no defined HR and are thus passing though, spending an unpredictable amount of time on Ongava. Based on capture histories, we therefore defined residents as individuals captured at least twice per year for at least two consecutive years.

Spatio-temporal overlap in waterhole use

For each waterhole, we computed the number of identified leopards seen during each dry season for each sex separately. We restricted our analyses to the dry season as this was when most of the observations occurred (see Results).

For each identified individual observation, we computed the time elapsed since the last visit of another identified individual. If the previous individual was not identified, we discarded the observation. We calculated the time since the last visit for the overall dataset of identified leopards (i.e. time since the last visit by any other known individual irrespective of its sex) and each sex (i.e. time since last visit by a known male and a known female) separately.

Table 1: Leopard home range size and overlap as reported in published scientific literature. Numbers in brackets give the range of estimates and n is the number of individuals used in each case.

		ange size in km² er of animals)	Home range	% Overla	D.4		
Study area	Adult male	Adult Female	estimation method	Between males	Between females	Reference	
Waterberg farmland, Namibia	229 (125-312, n = 3)	179 (52-394, n = 4)	95% MCP	24	22	Marker & Dickman (2005)	
Khaudum Game Reserve, Namibia	451 (210-1164, n = 6)	188 (183-194, n = 3)	95% MCP	46 (18-59)	35 (28-51)	Stander <i>et al</i> . (1997)	
Hobatere Concession, Namibia	94.9 (n = 1)	171.1 (84.5-285.4, n = 5)	95% Kernel		27.8	Stander (2001)	
Waterberg farmland, Namibia	109 (n = 1)	50 (46-53, n = 2)	95% Kernel		Existent but not quantified; no core overlap	Stein (2008), Stein <i>et al</i> . (2011)	
Okonjima Nature Reserve, Namibia	100.2 (71.4-221.5, n = 6)	72 (70.8-73.2, n = 2)	95% Kernel	26 Males overlap females by 31%	4 Females overlap males by 38%	Stander & Hanssen (2000)	
Okonjima Nature Reserve, Namibia	21.7 ± 10.1 $(n = 14)$ 15.6 ± 13.4 $(n = 9)$	8.9 ± 4.3 (n = 14) 7.8 ± 1.3 (n = 9)	100% MCP From camera trap data	Extensive overlap with dispersing sub- adult males. All male HRs overlapped with at least one female home range	Limited overlap	Noack (2016)	
Phinda Game Reserve, South Africa	74 (n = 11)	30 (n = 10)	95% Kernel	23	18	Fatteberg <i>et al</i> . (2016)	
Cederberg, South Africa	51 (40-69, n = 3)		95% MCP	10-57		Norton & Henley (1987)	
Eastern and Western Cape, South Africa	179.5 (71.7-690, n = 12)	72.5 (34.8-150, n = 9)	95% Kernel	15 (n = 4)	0 (n = 2)	Devens <i>et al</i> . (2018)	

We used R software (R Core Team 2022) to extract and analyse data using the packages *adehabitatHR* (Calenge 2006) and *oSCR* (Sutherland *et al.* 2019). Means are given \pm their standard error (SE) unless mentioned otherwise.

RESULTS

Spatial ecology from GPS data

GPS data were collected for 365 days (November 2013 to October 2014, 2 790 locations) for the male and 314 days (March to December 2013, 1 125 locations) for the female. Both individuals established spatially and temporally stable HRs and we thus classified them as resident. While the male was never recorded outside the reserve, 5.6% (n = 63)

of the female GPS locations were outside the reserve fence. The male had both a larger HR (192.8 km² versus 121.8 km²) and a larger core than the female (51.7 km² versus 22.1 km², Figure 2). From the male's perspective, 40% of its HR and 18% of its core was overlapped by the female HR and core respectively. From the female's perspective, 64% of its HR and 41% of its core was overlapped by the male HR and core respectively (Figure 2). UDOI was 0.39 for HR and 0.05 for cores, showing different space use of the area shared by the two individuals.

Camera trapping

Camera traps were deployed for the three-year study period (from January 2012 to November 2014) with trapping effort varying across waterholes from four

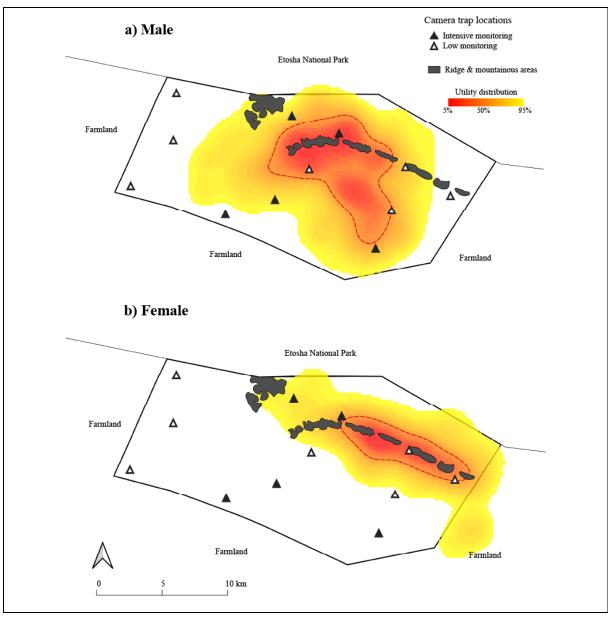


Figure 2: a) Male and b) female leopard home ranges (HRs) computed using location-based fixed kernels showing utility distribution. Core areas (50% kernel isopleth) are shown as red dashed lines. Dark grey polygons represent ridges and mountainous areas.

days to 915 days (Figure 1, Appendix 1). Across all waterholes, traps were operational for a total of 5 283 days.

We collected 407 independent observations of leopards across 10 of the 12 waterholes surveyed (Appendix 2, Figure 1). Trapping rate, defined as the percentage of active trap nights on which leopards were observed, was low and averaged $6.2 \pm 4.8\%$ (range: 0.3-13.1). Most of the observations (96.3%) occurred during the dry seasons, with only 15

observations during the wet seasons across the three years (Figures 3 and 4).

Leopards were observed alone on 396 occasions, and in pairs on 11 occasions. We identified 29 individuals (12 adult or sub-adult females, 15 adult or sub-adult males and two juveniles of unknown sex) from 245 observations (i.e. individual identification was possible for 60% of the sightings across the whole study period). Among the 11 pairs observed, four were of a male and a female, three involved at least

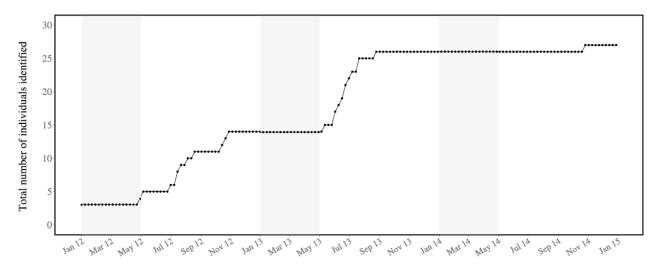


Figure 3: Acquisition rate of new individuals during the study period (three years) of camera trapping on Ongava Game Reserve. Shaded areas represent wet seasons.

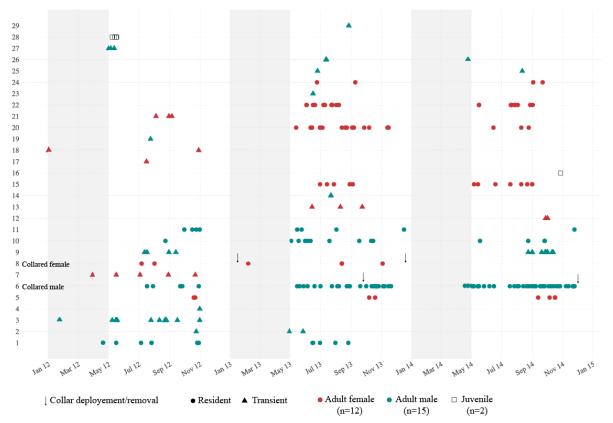


Figure 4: Individual leopard capture histories and status. Transient individuals are represented by triangles and resident individuals by circles. Collar deployment and removal are shown with vertical arrows. Shaded areas represent wet seasons.

one female with an unknown individual, three involved at least one male and in the last case we could not identify either of the individuals.

Known individuals were observed between one and 75 times during the three-year study period with eight individuals seen more than 10 times and 16 seen five times or fewer (Figure 4 and Appendix 2). We classified four males and six females as resident, resulting in 66% of the population being composed of transients.

Population size predictions

In the literature, within-sex HR overlaps for resident individuals range from 20% to 60 % (Table 1) with

no core overlap. Therefore, we would predict 2-4 resident males (HR size estimated at 193 km²) and 3-6 resident females (HR size estimated at 121 km²) on the 300 km² of Ongava Game Reserve. This would result in a density of 1.7-3.3 leopards/100 km².

Spatio-temporal overlap in waterhole use

Based on the 12 individuals (six males and six females) observed more than five times during the study period, leopards used on average 2.7 ± 1.9 waterholes (range: 1-8). Males tend to use a higher number of waterholes $(3.0 \pm 2.5, 1-8)$ compared to females $(2.0 \pm 0.6, 1-3)$. A maximum of eight individuals were observed using the same waterhole within a given dry season (Figure 5a).

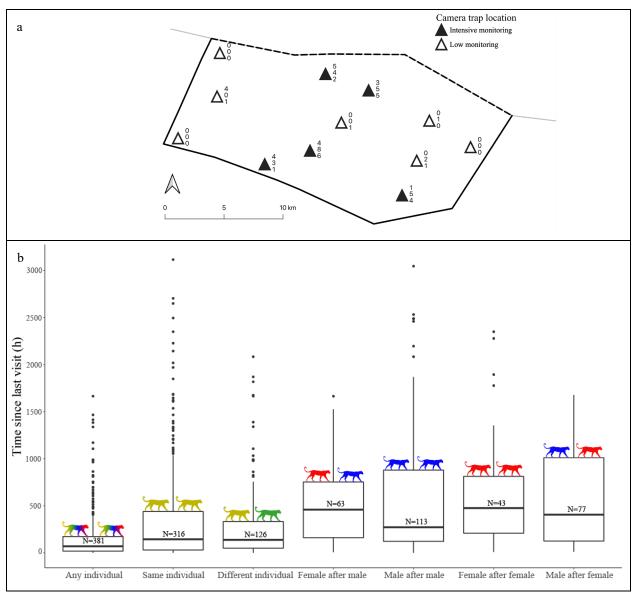


Figure 5: Spatio-temporal overlap in waterhole visitation by individual leopards. a) Number of identified leopards at each camera trap location for each year (top to bottom 2012, 2013 and 2014) of trapping. Black triangles show intensely monitored waterholes while white triangles represent waterholes monitored less intensively. b) Time (in hours) since the last visit of a given waterhole by another identified leopard for resident and transient females and resident and transient males. Error bars represent standard errors, N gives the sample size over which the mean was computed.

On most of the nights (94.4%, n = 204) during which leopards could be seen and identified, only one individual was observed at any given waterhole. On 4.6% (n = 10) and 1% (n = 2) of nights, two and three leopards were observed at the same waterhole respectively.

Time elapsed between the visit of any leopard at a given waterhole (same individual or not) averaged 6.5 days \pm 12.8 hours (12 minutes to 69 days, Figure 5b). A given individual would revisit the same waterhole with an average interval of 14.9 days \pm 1.2 hours (12 minutes to 129.9 days) while visits between different individuals were separated by 13.1 ± 3.2 days on average (51 min to 18.3 days). Females visited a waterhole on average 25.5 ± 3.6 days after another female and 25.0 ± 2.6 days after a male (Figure 5b). Males visited a waterhole on average 25.2 ± 2.8 days after another male and 22.1 ± 2.2 days after a female (Figure 5b).

DISCUSSION

Resident leopard space use

We found that leopard HR sizes on Ongava were well within the known range for the species and that the male had a larger HR than the female, as reported elsewhere (e.g. Snider et al. 2021, Rodríguez-Recio et al. 2022, and see Table 1). The female had a HR size larger than the average reported for Africa overall but confirms that leopards in Namibia have larger HRs than in other African countries (Snider et al. 2021, Rodríguez-Recio et al. 2022). Leopards on Ongava were not significantly constrained by fences (as the female repeatedly crossed the eastern boundary fence, even though it was an electrified high game fence), which has been observed in other areas such as Phinda Game Reserve, South Africa (Fattebert et al. 2015b). HR overlap between the male and the female was high. This has been reported in other areas (e.g. Odden & Wegge 2005, du Preez 2014, Fattebert et al. 2016) and is typical in species with a polygynous mating system, where females defend exclusive territories and male HRs overlap with several females, therefore accessing more mating opportunities (e.g. cougar, Puma concolor, Elbroch et al. 2016). The UDOI was low, especially for cores, which suggests some extent of resource partitioning between the male and female. This might be due to difference in diet as female leopards have been shown to have a wider and more opportunistic diet (Voigt et al. 2018). This could also result from females trying to avoid males to avoid infanticide which is common in this species, with up to 40% of cub mortality caused by males (Balme et al. 2012, Balme & Hunter 2013). HR cores were mainly located over the northern ridge, which highlights the importance of this habitat for leopards. In South Africa, leopards have also been shown to select for habitat of intermediate ruggedness and make use of steep slope areas (Fattebert et al. 2015b, Mann et al. 2020). Ridges most probably provide ideal habitat for hunting and resting (dense vegetation and rocky outcrops) and are rich in leopards' preferred prey such as rock hyrax and small antelopes (e.g. common duiker or Kirk's dik-dik, Madoqua kirkii, Hayward et al. 2006). Ridges could also provide refuges from competitors like lions and spotted hyaenas (Crocuta crocuta). Leopards have also been shown to react less strongly to lions in closed habitats such as are found on Ongava's ridges (du Preez 2014). However, since ridges only cover a small proportion of Ongava, the availability of this optimal habitat could restrict the number of leopards that could establish stable HRs in Ongava, despite the abundance of prey.

Leopard population on Ongava

There was an apparent discrepancy between the number of individuals that we predicted might reside in Ongava based on HR overlap and camera trap data. While HR overlap has been used elsewhere to estimate leopard density (Devens et al. 2018), it can only be applied to estimate the resident population size, and therefore might underestimate the total number of individuals that can be present on the reserve at any given time. On the other hand, not examining capture histories from camera trap surveys in detail (e.g. number of observation and temporal distribution of these observations) would lead to an overestimation of population size (i.e. a total of 29 adults or sub-adults in the population, while only a subset of these were actually residing on the reserve). HR overlap predicts 5-10 resident leopards on Ongava, and this is in agreement with the number of residents that were identified from the capture history (a maximum of four resident males and six resident females). The resulting density of 1.7-3.3 leopards/100 km2 falls within the range of density estimates across their range (Allen et al. 2020) and in Namibia (Richmond-Coggan 2019; see Figure 6). Leopard density on Ongava is far lower than that estimated for Okonjima Nature Reserve in Namibia (estimated at 14.5 leopards per 100 km², Noack et al. 2019), where the surrounding 2.4 m high electrified fences do appear to effectively constrain leopard movement.

Transients might be young adults or sub-adults dispersing across the landscape in search of a territory. These individuals might find it difficult to displace mature resident animals. That our collared male was still recorded with very good body condition in 2019 (pers. obs.), some six years after he was collared, suggests that resident leopards on Ongava may have long tenures.

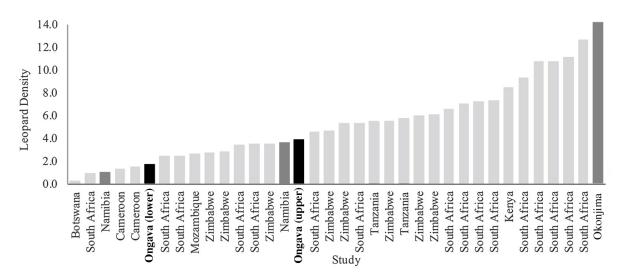


Figure 6: A comparison of leopard densities adapted from Allen et al. (2020) showing Ongava's lower and upper estimates (black) and an estimate for Okonjima Game Reserve, central Namibia (dark grey).

Relationships between individuals

We did not find any evidence of spatial partitioning in the use of waterholes since several individuals made use of the same waterhole within a few hours of each other. This suggests that there is little competition for access to water and that multiple residents can use common waterholes in overlapping zones of their HRs. Social large carnivores such as lions and spotted hyaenas usually have exclusive use of waterholes within their territories (e.g. Valeix et al. 2011, Périquet 2014), which represent prey hotspots and prime hunting grounds. However, permanent waterholes might not be as important for leopards who can find their preferred prey elsewhere and meet their water requirements from other water sources. Leopards on Ongava were rarely seen together, which is characteristic of this solitary species (Bailey 1993) but does not necessarily result from temporal partitioning in activity patterns. Several studies (e.g. Havmøller et al. 2020, Rouse et al. 2021) have shown leopards to be mainly nocturnal and not to display significant differences in activity between males and females, despite some fine scale differences in time of activity peaks. Nevertheless, the very low number of simultaneous observations of multiple individuals, but the short time span between visits from different individuals suggests that subordinate individuals might wait for dominant ones to leave the waterhole before coming to drink. Such a fine-scale spatio-temporal avoidance has also been suggested for leopards in Iran (Rouse et al. 2021).

Limitations and way forward

It is clear from the GPS data that fences did not constrain leopard movement within the reserve boundaries, and we did not account for individuals having only part of their HR on the reserve. Therefore, our prediction of the resident population size may be an underestimate. We also had a very small sample size for collared individuals, and it would be beneficial to equip leopards with GPS collars in other parts of the reserve to better understand their spatial ecology.

We found that many camera trap images failed to yield positive identification of animals and that capture rate was low, especially during the wet season. The camera traps were not deployed specifically to capture leopards but to survey waterholes in a more general way. Additionally, since leopards were observed drinking at other water sources (e.g. leaks in pipes, sewage overflows) during the study, our reported trapping frequency did not reflect drinking frequency. We would therefore recommend that future studies use camera trapping to concentrate efforts in the dry season (when capture rate will be the highest) and employ the traps in ways that maximise the potential for individual identification. Placing two camera traps facing each other has successfully been used for tigers and leopards along trails (e.g. Karanth et al. 2004, Chapman & Balme 2010), although this might be difficult to implement at waterholes.

We found that identifying resident and transient individuals from their capture histories can be misleading. For instance, while the female's GPS data clearly showed that she was resident, she was only captured on camera trap three times during the entire tracking period (Figure 4), and would have therefore been naively classified as transient. This also suggests once more that leopard drink from sources other than waterholes. Baiting camera trap stations has also been found to significantly increase capture rates (e.g. du Preez et al. 2014, Tarugara et al. 2019).

This study raises many questions about the transient part of the leopard population, which on a yearly basis can represent 20-70% of the population. Despite having a sizable lion population, Ongava provides an optimal environment for leopard with high habitat suitability and high prey availability. Due to its location between private farmlands where leopards might be trophy hunted and/or persecuted over livestock losses, and the sub-optimal habitat in the neighbouring area of Etosha, we argue that Ongava is highly attractive to leopards, hence the high number of individuals observed on camera traps. At this stage, we do not know where transients come from or go to once leaving Ongava, and we encourage further work to investigate these questions, most probably via tracking devices.

Our work highlights the importance of taking into account the social status of individuals when estimating and presenting population size estimate. This has already been demonstrated in cheetahs (Edwards *et al.* 2018) and failure to do this might yield highly biased estimates. We also call attention to the value of using multiple methods to approach population estimates for species as elusive as leopard.

ACKNOWLEDGEMENTS

We would like to thank Ongava's Anti-Poaching Teams and Abigail Guerier for assistance with the servicing of camera traps. GPS collars and camera traps were sponsored by the Directors of Ongava Game Reserve and West Midland Safari Park (via the Namibian Wildlife Conservation Trust, UK). Additional camera traps were also sponsored by Premier Tours, Philadelphia, USA. Veterinary costs were sponsored by The Zoological Society of Philadelphia, USA. This research was authorised by MET research permits 1748/2012, 1843/2013 and 1962/2014 (GPS collars), and 1685/2012 and 1797/2013 (camera traps).

We thank two anonymous reviewers and Miha Krofel for their constructive comments on previous versions of this manuscript.

REFERENCES

- Allen ML, Wang S, Olson LO, Li Q, Krofel M (2020) Counting cats for conservation: seasonal estimates of leopard density and drivers of distribution in the Serengeti. *Biodiversity and Conservation* 29(13): 3591–3608. https://doi.org/10.1007/s10531-020-02039-w.
- Bailey T (1993) *The African Leopard: Ecology and Behavior of a Solitary Felid.* Columbia University Press, New York, USA.
- Balme GA, Batchelor A, Britz N de W, Seymour G, Grover M, Hes L, Macdonald DW, Hunter LTB (2012) Reproductive success of female leopards *Panthera pardus*: the importance of top-down processes. *Mammal Review* 43(3): 221–237. https://doi.org/10.1111/j.1365-2907.2012.00219.x.
- Balme GA, Hunter LTB (2013) Why leopards commit infanticide. *Animal Behaviour* 86(4): 791–799.

- https://doi.org/10.1016/j.anbehav.2013.07.019.
- Balme GA, Hunter LTB, Slotow R (2007) Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behaviour* 74(3): 589–598.
- Balme GA, Hunter LTB, Slotow R (2009) Evaluating methods for counting cryptic carnivores. *Journal of Wildlife Management* 73(3): 433–441. https://doi.org/10.2193/2007-368.
- Broekhuis F, Gopalaswamy AM (2016) Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLoS ONE* 11(5): e0153875. https://doi.org/10.1371/journal.pone.0153875.
- Calenge C (2006) The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197(3–4): 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017.
- Chapman S, Balme GA (2010) An estimate of leopard population density in a private reserve in KwaZulu-Natal, South Africa, using camera-traps and capture-recapture models. *South African Journal of Wildlife Research* 40(2): 114–120. https://doi.org/10.3957/056.040.0202.
- Devens C, Tshabalala T, McManus J, Smuts B (2018) Counting the spots: The use of a spatially explicit capture-recapture technique and GPS data to estimate leopard (*Panthera pardus*) density in the Eastern and Western Cape, South Africa. *African Journal of Ecology* 56(4): 850-859. https://doi.org/10.1111/aje.12512.
- Edwards S, Fischer M, Wachter B, Melzheimer J (2018) Coping with intrasexual behavioral differences: Capturerecapture abundance estimation of male cheetah. *Ecology* and *Evolution* 8: 9171–9180. https://doi.org/10.1002/ ecc3.4410.
- Elbroch LM, Lendrum PE, Quigley H, Caragiulo A (2016) Spatial overlap in a solitary carnivore: support for the land tenure, kinship or resource dispersion hypotheses? *Journal of Applied Ecology* 85(2): 487–496. https://doi.org/10.1111/1365-2656.12447.
- Fattebert J, Balme GA, Dickerson T, Slotow R, Hunter LTB (2015a) Density-Dependent natal dispersal patterns in a leopard population recovering from over-harvest. PLoS ONE 10(4): e0122355. https://doi.org/10.1371/journal.pone.0122355.s001.
- Fattebert J, Balme GA, Robinson HS, Dickerson T, Slotow R, Hunter LTB (2016) Population recovery highlights spatial organization dynamics in adult leopards. *Journal of Zoology* 299(3): 153–162. https://doi.org/10.1111/jzo.12344.
- Fattebert J, Robinson HS, Balme GA, Slotow R, Hunter LTB (2015b) Structural habitat predicts functional dispersal habitat of a large carnivore: how leopards change spots. *Ecological Applications* 25(7): 1911–1921. https://doi.org/10.1890/14-1631.1.sm.
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management* 69(4): 1346–1359. https://doi.org/10.2193/0022-541X.
- Havmøller RW, Jacobsen NS, Scharff N, Rovero F, Zimmermann F (2020) Assessing the activity pattern overlap among leopards (*Panthera pardus*), potential prey and competitors in a complex landscape in Tanzania. *Journal of Zoology* 311: 175–182. https://doi.org/10.1111/jzo.12774.
- Hayward MW, Henschel P, O'Brien J (2006) Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270: 298–313.

- Hemson G, Johnson P, South A, Kenward RE, Ripley R, Macdonald DW (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* 74(3): 455–463. https://doi.org/10.1111/j.1365-2656. 2005.00944.x.
- Jacobson AP, Gerngross P, Lemeris Jr JR, Schoonover RF, Anco C, Breitenmoser-Würsten C *et al.* (2016) Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4(1): e1974-28. https://doi.org/10.7717/peerj.1974.
- Karanth KU, Chundawat RS, Nichols JD, Kumar NS (2004) Estimation of tiger densities in the tropical dry forests of Panna, Central India, using photographic capture–recapture sampling. *Animal Conservation* 7(3): 285–290. https://doi.org/10.1017/S1367943004001477.
- Kuhn BF (2014) A preliminary assessment of the carnivore community outside Johannesburg, South Africa. *South African Journal of Wildlife Research* 44(1): 95–98. https://doi.org/10.3957/056.044.0106.
- Mann GKH, O'Riain MJ, Parker DM (2020) A leopard's favourite spots: Habitat preference and population density of leopards in a semi-arid biodiversity hotspot. *Journal of Arid Environments* 181: 104218. https://doi.org/10.1016/j.jaridenv.2020.104218.
- Marker LL, Dickman AJ (2005) Factors affecting leopard (*Panthera pardus*) spatial ecology, with particular reference to Namibian farmlands. *South African Journal of Wildlife Research* 35(2): 105–115. https://journals.co.za/content/wild/35/2/EJC117223.
- Miller SM, Bissett C, Burger A, Courtenay B, Dickerson T, Druce DJ *et al.* (2013) Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research* 43(2): 138–154. http://www.bioone.org/doi/abs/10.3957/056.043.0202.
- Noack J (2016) The assessment of leopard (Panthera pardus) density and population size via a capture recapture framework in an island bound conservation area in Namibia. Unpublished report: AfriCat Namibia. https://africat.org/wp-content/uploads/2018/10/africat_foundationprogress_report_leopard_density_stu dv 1.pdf.
- Noack J, Heyns L, Rodenwoldt D, Edwards S (2019) Leopard density estimation within an enclosed reserve, Namibia using spatially explicit capture- recapture models. *Animals* 9(10): 724. https://doi.org/10.3390/ani9100724.
- Norton PM, Henley SR (1987) Home range and movements of male leopards in the Cedarberg Wilderness Area, Cape Province. *South African Journal of Wildlife Research* 17(2): 41–48. https://journals.co.za/content/wild/17/2/AJA03794369 3497.
- Odden M, Athreya V, Rattan S, Linnell JD (2014) Adaptable neighbours: Movement patterns of GPS-collared leopards in human dominated landscapes in India. *PLoS ONE* 9(11): e112044-9. https://doi.org/10.1371/journal.pone.0112044.
- Odden M, Wegge P (2005) Spacing and activity patterns of leopards *Panthera pardus* in the Royal Bardia National Park, Nepal. *BioOne* 11(2): 145–152. https://doi.org/10.2981/0909-6396.
- Périquet S (2014) Sharing the top: How do spotted hyaenas cope with lions? Apex predator coexistence in a wooded savanna. PhD, Université Claude Bernard, Lyon 1, Lyon, France.

- du Preez BD (2014) The impact of intraguild competition with lion Panthera leo on leopard Panthera pardus behavioural ecology. PhD, University of Oxford, Oxford, UK
- du Preez B, Hart T, Loveridge AJ, Macdonald DW (2015) Impact of risk on animal behaviour and habitat transition probabilities. *Animal Behaviour* 100(C): 22–37. https://doi.org/10.1016/j.anbehav.2014.10.025.
- du Preez BD, Loveridge AJ, Macdonald DW (2014) To bait or not to bait: A comparison of camera-trapping methods for estimating leopard *Panthera pardus* density. *Biological Conservation* 176(C): 153–161. https://doi.org/10.1016/j.biocon.2014.05.021.
- R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Richmond-Coggan L (2019) National Leopard Census Project. Unpublished report.
- Rodríguez-Recio M, Burgos T, Krofel M, Lozano J, Moleón M, Virgós E (2022) Estimating global determinants of leopard home range size in a changing world. *Animal Conservation*. https://doi.org/10.1111/acv.12777.
- Rouse S, Behnoud P, Hobeali K, Moghadas P, Salahshour Z, Eslahi H *et al.* (2021) Intraspecific interactions in a high-density leopard population. *Ecology and Evolution* 11(23): 16572–16584. https://doi.org/10.1002/ece3.8227.
- Snider MH, Athreya VR, Balme GA, Bidner LR, Farhadinia MS, Fattebert J *et al.* (2021) Home range variation in leopards living across the human density gradient. *Journal of Mammalogy* 102(4): 1138–1148. https://doi.org/10.1093/jmammal/gyab068.
- Stander PE (2001) Predator Research Programme Research Progress Report May 2001. pp. 1–18.
- Stander PE, Haden PJ, Kaqece, Ghau (1997) The ecology of asociality in Namibian leopards. *Journal of Zoology* 242: 343–364.
- Stander PE, Hanssen L (2000) Predator Research Programme Research Progress Report October 2000. Unpublished report: pp. 19.
- Stein AB (2008) Ecology and conservation of the leopard (Panthera pardus linnaeus 1758) in northcentral Namibia. PhD, University of Massachusetts Amherst.
- Stein AB, Athreya V, Gerngross P, Balme GA, Henschel P, Karanth U *et al.* (2016) *Panthera pardus*. http://www.iucnredlist.org/details/15954/0.
- Stein AB, Fuller TK, DeStefano S, Marker LL (2011) Leopard population and home range estimates in north-central Namibia. *African Journal of Ecology* 49(3): 383–387. https://doi.org/10.1111/j.1365-2028.2011.01267.x.
- Stratford KJ, Stratford SMC (2011) Fine-scale movements and use of space by spotted hyaena (*Crocuta crocuta*) on Ongava Game Reserve, Namibia. *African Journal of Ecology* 49(3): 343–352. https://doi.org/10.1111/j.1365-2028.2011.01270.x.
- Sutherland C, Royle JA, Linden DW (2019) oSCR: A spatial capture-recapture R Package for inference about spatial ecological processes. *Ecography*: 42(9): 1459-1469. ecog.04551-17. https://doi.org/10.1111/ecog.04551.
- Tarugara A, Clegg BW, Gandiwa E, Muposhi VK (2019) Cost-benefit analysis of increasing sampling effort in a baited-camera trap survey of an African leopard (*Panthera pardus*) population. *Global Ecology and Conservation* 18: e00627. https://doi.org/10.1016/j.gecco.2019.e00627.

- Valeix M, Chamaillé-Jammes S, Loveridge AJ, Davidson Z, Hunt JE, Madzikanda H, Macdonald DW (2011) Understanding patch departure rules for large carnivores: lion movements support a patch disturbance hypothesis. *The American Naturalist* 178(2): 269–275. https://doi.org/10.1086/660824.
- Voigt CC, Krofel M, Menges V, Wachter B, Melzheimer J (2018) Sex-specific dietary specialization in a terrestrial
- apex predator, the leopard, revealed by stable isotope analysis. *Journal of Zoology* 306(1): 1–7. https://doi.org/10.1111/jzo.12566.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70(1): 164–168. http://www.esajournals.org/doi/abs/10.2307/1938423.

Appendix 1: Trapping effort at each waterhole. Grey shading indicates intensively monitored waterholes.

Waterhole	Session	Start	Stop	Trapp	oing Days
Andersson's	1	17/09/2013	28/09/2013	11	27
AND	2	01/10/2014	17/10/2014	16	27
Bobbejaan's Pos BOB	1	02/10/2014	18/10/2014	16	16
	1	22/10/2012	01/11/2012	10	
Lodge	2	11/05/2013	17/06/2013	37	60
LOD	3	05/09/2014	11/09/2014	6	69
	4	01/10/2014	17/10/2014	16	
Margo	1	10/01/2012	05/11/2012	300	015
MAR	2	24/04/2013	30/12/2014	615	915
	1	17/07/2012	01/11/2012	107	
Onduri OND	2	27/04/2013	28/09/2013	154	566
OND	3	05/03/2014	04/01/2015	305	
	1	27/09/2012	01/10/2012	4	
Ongarangombe ONG	2	07/05/2013	28/09/2013	144	359
ONG	3	20/03/2014	17/10/2014	211	
	1	01/01/2012	01/10/2012	274	
OTC	2	17/09/2013	25/09/2013	8	405
OTC	3	15/06/2014	19/06/2014	4	405
	4	21/08/2014	18/12/2014	119	
	1	10/01/2012	02/11/2012	297	
	2	14/05/2013	22/05/2013	8	
Rainer's Pos RAI	3	17/09/2013	27/09/2013	10	405
TO II	4	31/07/2014	18/10/2014	79	
	5	06/12/2014	17/12/2014	11	
Roland's Pos	1	05/01/2012	03/11/2012	303	914
ROL	2	04/05/2013	05/01/2015	611	914
	1	27/09/2012	02/11/2012	36	
Sonop	2	08/05/2013	22/05/2013	14	124
SON	3	17/09/2013	27/09/2013	10	134
	4	05/08/2014	18/10/2014	74	
	1	01/01/2012	02/11/2012	306	
Suiderkruis SUI	2	30/04/2013	24/09/2013	147	675
	3	10/03/2014	18/10/2014	222	
Tiervlei	1	30/04/2012	31/10/2012	184	700
TIE	2	24/04/2013	29/12/2014	614	798
Total					5 283

Appendix 2: Capture histories of individual leopards by waterhole. Grey shading indicates intensively monitored waterholes. Two waterholes (SON and AND) did not yield any leopard pictures. Waterholes are represented by the first three letters of their name; see Figure 1 for their location.

Individual	Sex	BOB	LOD	MAR	OND	ONG	OTC	ROL	RAI	SUI	TIE	Total
L1	Male	-	-	6	-	-	-	2	2	3	-	13
L2	Male	-	-	2	-	-	-	1	-	-	-	3
L3	Male	-	-	-	-	-	-	-	-	-	14	14
L4	Male	-	-	-	-	-	-	-	-	-	1	1
L5	Female	-	-	-	-	-	-	6	-	-	2	8
L6 (collared)	Male	-	1	34	17	4	1	-	6	6	6	75
L8 (collared)	Female	-	-	4	-	-	-	-	-	1	-	5
L10	Female	-	-	4	-	-	-	-	-	2	-	6
L11	Male	-	-	13	-	-	-	-	1	-	-	14
L12	Male	-	-	11	2	-	-	-	-	1	-	14
L13	Male	-	-	4	-	-	-	-	-	-	5	9
L14	Female	-	-	2	-	-	-	-	-	-	-	2
L15	Female	-	-	-	3	-	-	-	-	-	-	3
L16	Male	-	-	-	2	-	-	-	-	-	-	2
L17	Female	-	-	-	11	3	-	-	-	-	-	14
L18	Juvenile	-	-	-	1	-	-	-	-	-	-	1
L19	Female	-	-	-	-	-	-	1	-	-	-	1
L20	Female	-	-	-	-	-	-	-	3	-	-	3
L21	Male	-	-	-	-	-	-	-	1	-	-	1
L22	Female	-	-	-	-	-	-	-	13	12	1	26
L23	Female	-	-	-	-	-	-	-	-	3	-	3
L24	Female	-	-	-	-	-	-	-	-	20	-	20
L25	Male	-	-	-	-	-	-	-	-	1	-	1
L26	Female	-	-	-	-	-	-	-	-	4	-	4
L27	Male	-	-	-	-	-	-	-	-	2	-	2
L28	Male	-	-	-	-	-	-	-	-	3	-	3
L29	Male	-	-	-	-	-	-	-	-	-	3	3
L30	Juvenile	-	-	-	-	-	-	-	-	-	4	4
L31	Male	-	-	-	-	-	-	-	-	-	1	1
Unknown	NA	3	-	72	37	8	-	6	4	23	9	162
TOTAL		3	1	152	73	15	1	16	30	81	46	418

Analysis of records from community game guards of human-elephant conflict in Orupupa Conservancy, northwest Namibia

MJ Wenborn^{1*}, V Nijman¹, D Kangombe², R Katira Zaako², U Tjimuine², A Kavita², J Hinu², R Huwe², VJ Ngarukue², KJ Kapringi², MS Svensson¹

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-wenborn Published online: 21st November 2022

- ¹ Faculty of Humanities and Social Sciences, Oxford Brookes University, Gipsy Lane, Oxford OX3 0BP, UK.
- ² Orupupa Conservancy, Orundu, Kunene Region, Namibia.
- * 16040486@brookes.ac.uk

Date received: 4th May 2022; Date accepted: 4th November 2022.

ARSTRACT

Competition between local people and elephants (Loxodonta africana) for water and vegetation is an increasing concern in many conservancies in northwest Namibia. Many livestock were lost during droughts in 2018-2019, and there are risks of more severe droughts in the future because of climate change. Little research has been published on elephants in the Northern Highlands, although the community game guards have been collecting data for many years in Event Books, as part of their role within conservancies. These include records of human-elephant conflict incidents. The objective of this study was to assess in detail the data on human-elephant conflict in Event Books for Orupupa Conservancy. In addition to analysis of Event Book data, consultations were carried out with community game guards in 2021 and 2022. Incidents involving elephants tend not to be frequent, but damage at water points can have a major impact on a local community because of the time taken and expenses of repairing the infrastructure. In 2019 and 2020 there was a changing dynamic in which some local communities set up vegetable gardens near water points or springs. The number of incidents of elephant damage at vegetable gardens greatly increased in 2020. Our study demonstrates that detailed analysis of Event Book data for additional conservancies would be useful. Combined with local ecological knowledge, the Event Book data can be used to inform the planning of local actions to reduce human-elephant conflict, including conservation of elephants and their habitats, in line with the actions in Namibia's National Elephant Conservation and Management Plan. The study also confirmed the substantial knowledge of community game guards and their important work in keeping records in Event Books. The expansion of their monitoring role to identify specific elephant herds would provide benefits in terms of improving knowledge on the elephant population and movements, and the potential for early warning between villages about the more problematic herds.

Keywords: community conservancies, game guards, human-wildlife conflict, Kunene, local ecological knowledge, Namibia

INTRODUCTION

National Elephant Conservation Management Plan in Namibia, adopted in 2021, stated that conflict between local communities and elephants (Loxodonta africana) is increasing, including on communal lands as well as commercial farms (MEFT 2021). Over 80% of the elephant population in Namibia is located in the Zambezi and Khaudom-Kavango Regions in the northeast of the country, with a significant population also in Etosha National Park (Thouless et al. 2016). There is a small elephant population in Kunene Region in northwest Namibia (Figure 1a), across parts of former Kaokoveld and Damaraland, and this population is impacting local communities.

Located between the Skeleton Coast National Park and Etosha National Park, the Northern Highlands is a mountainous and remote area of about 12,000 km² (Figure 2). Some people refer to its population of elephants as "Highland elephants". These elephants live alongside the communities in the Highlands,

where the human population density is very low (about 1 person/km², NACSO 2020). The rural communities in Kunene Region are some of the poorest in Namibia (GRN 2015; Heydinger et al. 2019). Northwest Namibia is an extremely dry area and the communities have been greatly affected by droughts between 2013 and 2020, with poverty levels increasing because of the loss of livestock due to the lack of vegetation during the droughts (Inman et al. 2020). The economic impact of the Covid-19 pandemic has added to the challenges for local communities. The drought years have resulted in increasing pressures in terms of competition between wildlife and communities for local resources (Heydinger 2021). It has been reported that humanelephant conflict at community water points in northwest Namibia is a particular problem that is adding to challenges for the communities (Hunninck et al. 2017; MEFT/NACSO 2021; MEFT 2021).

The desert-adapted elephants in areas such as the lower Hoanib River have been researched in detail (Viljoen & Botha 1990; Leggett *et al.* 2003; Leggett

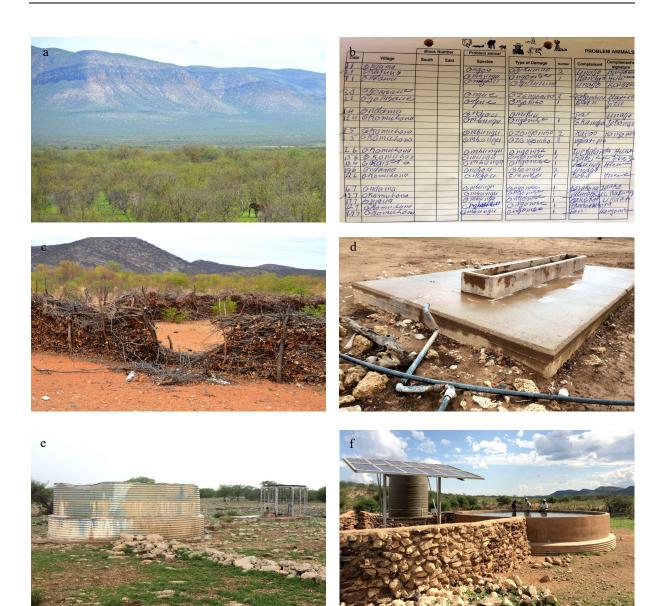


Figure 1: a) Highland elephant, Orupupa Conservancy; b) Table in the Event Book that relates to "problem animals", used to record incidents of human-elephant conflict; c) Damage by elephants at a vegetable garden in Otjitoko village, in Otuzemba Conservancy; d) Damage by elephants at a water point in Okazorongua village, Orupupa Conservancy; e) The water point at Otjamusirika cattle post has no protection infrastructure and was damaged by elephants in 2021; f) Upgraded water point with solar power and walls to protect the infrastructure from elephants, at Oupako cattle post in Orupupa Conservancy.

et al. 2011; Ramey & Brown 2019), and their profile has been raised through wildlife documentaries (BBC 2008; BBC 2019; Sky Nature 2020). In addition, the elephant populations in Etosha National Park have been monitored for many years; one of the reasons is that Etosha generates significant tourism revenue (MEFT 2021). However, there has been minimal published research on the elephants in the Northern Highlands.

In the 2021 assessment of the IUCN Red List of Threatened Species, the African savanna elephant was classified as Endangered (Gobush *et al.* 2021). The previous classification for the species, in 2008, had been Vulnerable (Blanc 2008). The change in Red List status reflects the increasingly serious risk

to the population of the species. The National Elephant Conservation and Management Plan includes strategic objectives to plan local interventions to protect the elephants and their habitats in northwest Namibia, and in particular to reduce the incidents of human-elephant conflict (MEFT 2021).

Although there has been very limited published research on the Highland elephants, there is much knowledge in the local communities, in particular with the community game guards, about the elephants and their movements. There are also records of incidents of elephant damage in Event Books filled in by the game guards (Figure 1b). The records include date and location of the incident, type

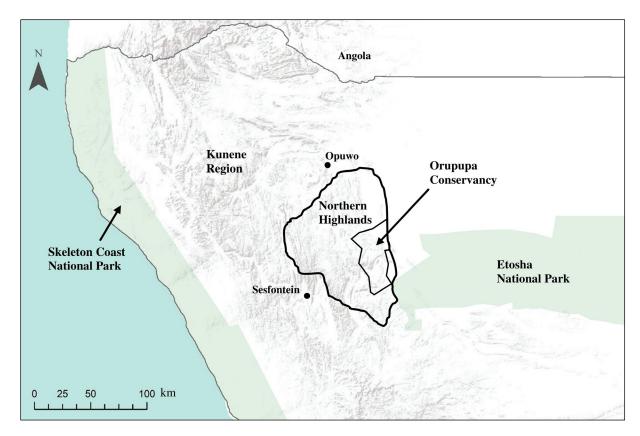


Figure 2: The Northern Highlands, showing Orupupa Conservancy in northwest Namibia.

of damage and complainant, and the number of elephants if known. The Event Books have provided a tool for consistent monitoring and many conservancies in Namibia have records going back over 10 years. The Event Book system was set up by the Ministry of Environment, Forestry and Tourism (MEFT) and Namibian NGOs, and extensive training has been provided to game guards. It is evident from discussions with the game guards that the training and support from MEFT and the NGOs has resulted in strong commitment to the monitoring system by the conservancies, as had been the intention at an early stage in the monitoring system (Stuart-Hill *et al.* 2005).

The objective of this study is to assess in detail the data on human-elephant conflict incidents in Event Books for one conservancy. The analysis of incidents can potentially provide useful information for detailed planning of local interventions for conservation of elephants and to address community priorities.

METHODS

Orupupa Conservancy was gazetted in 2011 and has an area of 1,234 km² (NACSO 2020). This excludes the area east of the C35 main road, which is under review in terms of becoming gazetted as part of the conservancy. The conservancy has been monitoring

wildlife and recording in Event Books since 2012, including the area to the east of the main road.

Orupupa is located in the eastern part of the Northern Highlands. According to community game guards, it is potentially part of a corridor on a historical migratory route for elephants from western Etosha National Park in the rainy season to find their preferred vegetation, and back to the park in the dry season. The main villages in the conservancy are near the roads or springs in the northern part. Since it was set up in 2011, Orupupa Conservancy has had no investment in tourism and received minimal revenues. According to the Conservancy Management Team, the communities have growing concerns about incidents of human-elephant conflict.

We consulted with the Conservancy Chairperson and the six community game guards that work in the conservancy in April 2021 and March 2022 about trends in types of human-elephant conflict and reasons for changes. We also conducted site visits with game guards through much of the conservancy to villages, natural springs and community water points. The Conservancy Chairperson gave approval for analysis of the Event Book data. Copies were taken, with co-operation from the game guards, of relevant sections of the Event Books for the 10 years from 2012 to 2021 inclusive.

RESULTS

The six community game guards recorded a total of 148 pages of incidents of human-wildlife conflict between 2012 and 2021. The total number of reported incidents involving elephants was 310. Thus over the 10 years, an average of 31 incidents involving elephants were reported each year, with the highest number being in 2020 when 70 incidents were reported (Figure 3).

Of all reported incidents in Orupupa Conservancy involving elephants, 53% occurred at vegetable gardens (Figures 3 and 1c). There was a large increase in incidents at vegetable gardens in 2020. Incidents at water points (e.g. pipes, tanks) accounted for 21% of the total reported incidents over the 10 years (Figure 1d). The "other" category of incidents in Figure 3 mainly refers to damage to structures, such as fence enclosures for livestock, but there were also a few reports of livestock loss because of elephants.

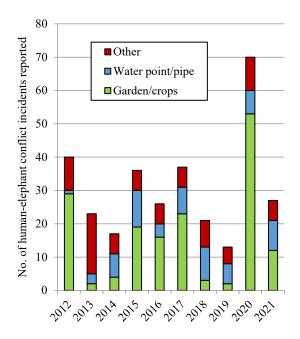


Figure 3: Trends in total human-elephant incidents recorded by game guards in Orupupa Conservancy.

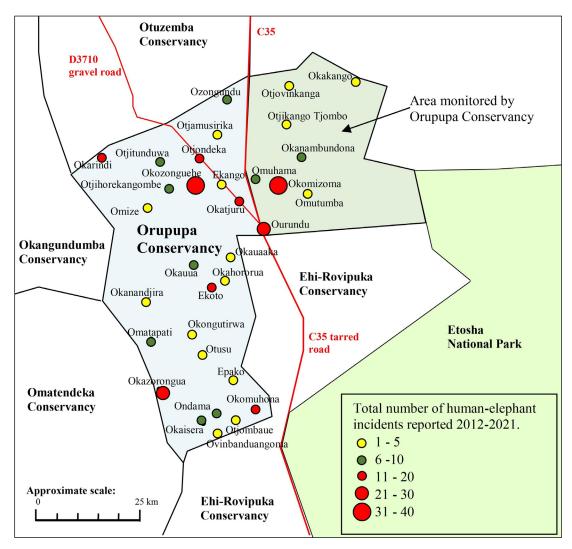


Figure 4: Location of human-elephant incidents recorded by game guards in Orupupa Conservancy between 2012 and 2021.

Of all incidents involving elephants over the 10 years, 65% were reported in the northern part of Orupupa Conservancy, including the area to the east of the C35 road that is not yet formally part of the conservancy but is monitored by its game guards (Figure 4).

Different types of incidents were recorded in different parts of the conservancy (Figure 5). In southern parts 39% of the human-elephant conflict incidents involved damage to water points and 30% to vegetable gardens. In the north, more vegetable gardens have been set up, and 65% of the incidents reported there involved damage to vegetable gardens, and 12% involved damage to water points. There

were increases in the number of incidents in 2020 in the villages of Otjondeka, Okozonguehe, Ourundu and Otjihorekangumbe in the north, and Okazorongua and Ekoto in the south, and many of those increases were at vegetable gardens. In 2021, the number of recorded incidents involving elephants at vegetable gardens decreased to the typical levels reported for 2012 to 2019. If analysed on the basis of incidents per square kilometre during the 10 years, there were over double the number of incidents (0.21 per km²) in the mountainous areas of the conservancy to the west of the main C35 tar road than in the flat, sandy area to the east of the main road (0.09 incidents per km²).

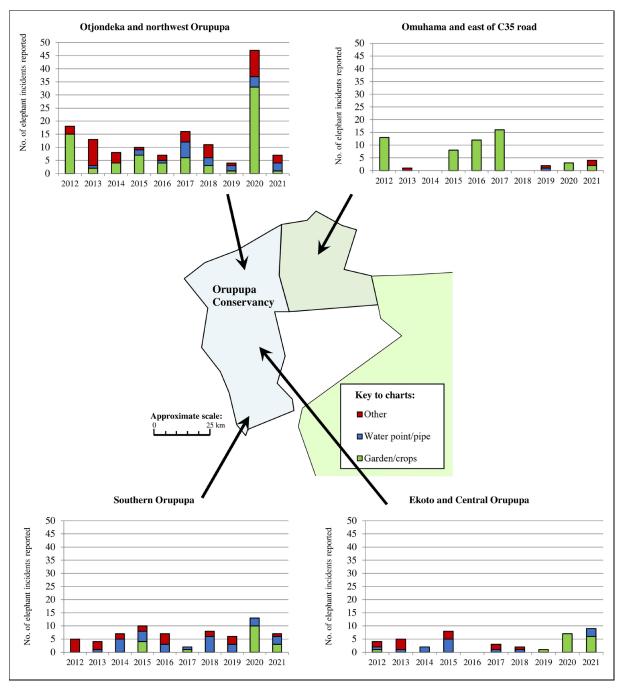


Figure 5: Trends in human-elephant incidents recorded by game guards in different areas of Orupupa Conservancy.

One of the main points of feedback from discussions with game guards in 2021 and 2022 was their perception that human-elephant conflict in Orupupa Conservancy is becoming more serious overall, including at water points and vegetable gardens. The perception of the game guards, based on their own observations and on feedback from local people, is that the number of elephants in the conservancy has been increasing.

DISCUSSION

Water supply infrastructure

The overall frequency of human-elephant conflict incidents reported in Orupupa Conservancy is low, with typically about three incidents reported per month on average. The water points that had the most frequent damage by elephants are Okomuhona, Okazorongua, Ondama and Okauua in the south, and Okarindi in the northeast. The most incidents reported at water points was at Okomuhona village in the southeast, with nine incidents reported over the 10 years. However, even though the frequency of reported incidents is low in these villages, the damage resulting from an incident by elephants at a water point can have a substantial impact on the local community. When water point infrastructure is damaged, in practice it often takes much time to repair, partly because of the large distances to travel to suppliers to buy parts and equipment. For example, for several months in 2021 the water point at Okomuhona village in the southeast of the conservancy was not operational and, although this was not a result of damage by elephants, water had to be transported into the village by truck, which is expensive. The water point at the cattle post at Otjamusirika is an example where the infrastructure was damaged by elephants (Figure 1e), and could not be immediately repaired, so for one month people were having to walk 5km to Otjondeka to obtain water.

Even when elephants have not damaged any infrastructure, but have drunk the water that had been pumped into a holding dam for livestock, this often results in a cost for the village in terms of the diesel needed to pump the extra groundwater. Although such incidents are not recorded in Event Books, they do affect community attitudes towards elephant conservation. The main actions that villagers can take to reduce damage at water points is to ensure that the holding dams are full of water for elephants to drink, because damage often occurs when elephants find no water in the dams but they smell water in the pipes. Ensuring holding dams are full costs the community money at water points with diesel pumps. In the village of Okazorongua the community has constructed an earth dam to store rainfall for livestock and wildlife, which for a few months reduces the costs of diesel fuel at the community water point and the risk of elephant damage. The water supply at Okatjuru is another example of the fragile situation for communities. Several years ago the community decided to close the groundwater borehole because of the costs of diesel fuel for pumping, and instead they use a hand pump. The most effective and sustainable intervention to address these challenges and reduce operational costs is to upgrade the water points to include protection from elephants and to install solar pumps (Figure 1f). Such upgrades tend to be funded by the national government or donor organisations, and are a priority for many villages and cattle posts in Orupupa Conservancy. Investment in converting water infrastructure to include solar pumps and adding walls to protect water points from elephant damage is the main intervention included in the National Elephant Conservation and Management Plan for reduction of human-elephant conflict at water points in the northwest (MEFT 2021).

Vegetable gardens

Between 13 and 40 incidents per year were reported in total (e.g. water points, vegetable gardens, other) across Orupupa Conservancy from 2012 to 2019, but the total then jumped to 70 incidents in 2020. This increase was because of 53 incidents at vegetable gardens in 2020. There was a major reduction in livestock during the drought in 2018-2019. From that time some villages in the Northern Highlands established small vegetable gardens, particularly next to water points or springs. This increased the potential for human-elephant conflict in the area. In the conservancy, several incidents were reported of elephant damage at vegetable gardens in 2020; including in Otjondeka, Okozonguehe Otjihorekangombe in the north, and Okazorongua and Ekoto in the south. This is an example of the changing situation in northwest Namibia. Although typically elephants tend to stay away from villages during the rainy season because they have access to water elsewhere, the setting up of vegetable gardens resulted in some visits of elephants to villages during the rainy season. In Okazorongua, there had been no incidents of elephant damage at the water point between 2012 and 2018, but six incidents were reported during 2019 and 2020. The establishment of vegetable gardens in Okazorongua might have led to the damage at the water point in 2019 and 2020 by tempting elephants into the area.

In 2021 vegetables were not planted at many gardens because of the concern of the local people that this would attract elephants to the villages. The number of incidents at vegetable gardens in 2021 did significantly decrease, except for ongoing incidents at the vegetable gardens at Ekoto in the centre of the conservancy. There are currently few actions that villagers take to reduce incidents at vegetable gardens, apart from making noises to try to scare the

elephants away. The main action taken in 2021 was simply to stop growing vegetables. The National Elephant Conservation and Management Plan identifies the problems with damage at small crop fields and vegetable gardens in the northwest and proposes interventions such as electric fencing and exploring the feasibility of chilli production and use to deter elephants (MEFT 2021).

Trends in reported incidents of human-elephant conflict

The trends shown in Figures 3 and 5 do not confirm the perception of game guards of increases in incidents of elephant damage in Orupupa Conservancy. The marked increase in reported incidents at vegetable gardens in 2020 (Figure 3) is likely to be an outlier compared to the stable trend of similar numbers of cases each year for 2012-2019 and 2021. A detailed analysis of Event Books in other conservancies in the Northern Highlands would provide a more complete picture.

Local community commitment

Namibia has been leading the implementation of the community-based conservancy model to wildlife conservation, which involves a structured legal mechanism that empowers the communities to make decisions on the use of local natural resources. Several studies have concluded that the focus of the conservancy model on supporting communities to gain from the value of wildlife has been a major factor in the increase in wildlife populations in northwest Namibia since the 1990s (Naidoo et al. 2011: Silva & Mosimane 2013: MEFT/NACSO 2021; Störmer et al. 2019; Wenborn et al. 2022). However, Orupupa Conservancy is one of the conservancies that has received no investment in tourism and minimal revenues, and has not gained from local employment and other benefits from wildlife tourism. According to the game guards consulted in our study, this is affecting the commitment of communities wildlife conservation. The local perception of an increase in reported human-elephant conflict, including the high number of incidents in 2020 from which communities lost vegetable crops, is likely to be further negatively impacting the perception of communities on the conservancy model. Competition between humans and wildlife for natural resources is a particular concern given the increasing risks of more severe droughts in future because of climate change (Hunninck et al. 2017; IUCN 2020).

Elephant movements

According to the game guards consulted during this study, some elephants leave Etosha National Park during the rainy season from the northwest area of the park to look for preferred vegetation in the Northern Highlands. In terms of location of reported incidents of human-elephant conflict, there have been a higher

number of incidents in the north of Orupupa Conservancy than the villages in the south. Although this could be partly a result of elephant movements in a corridor out of the northwest area of Etosha National Park, the results are inconclusive. The higher number of recorded incidents in the north is more likely to be because of a combination of other reasons. There are several springs in that area and it might be that elephants are more likely to drink at the springs (at which their dung is often observed), because these springs tend to be further away from households than water points. However, according to game guards, elephants also like to drink at community water points because the water might be cleaner. Also, the higher number of vegetable gardens in the north part of Orupupa Conservancy is likely to be a factor. Finally, the higher number of recorded incidents might simply be because there is a higher human population in the north, and therefore incidents are more likely to be reported. As an example, there were no incidents reported at the water point in Otjondeka from 2012 to 2021. This is the village with the largest human population in the conservancy. The water point is located near an area of many houses, the clinic and the school. Elephants would be expected to choose the easier and quieter options of drinking at Otjondeka Springs, which are further away from the village properties. However, there was an increase in incidents at vegetable gardens in Otjondeka in 2020, with eight incidents reported in the year, indicating that elephants might be willing to take more risks when it comes to opportunities to take vegetables from the gardens. Although there is uncertainty into the reasons for more incidents in some areas of Orupupa Conservancy, the detailed analysis has demonstrated that further such analysis and mapping of data on recorded human-elephant conflict incidents across other conservancies will be useful as one indicator of elephant movements in the Northern Highlands.

The need for identification of elephant herds

The total population of elephants in the Northern Highlands is currently not known and their movements are uncertain. More detailed information on the population and movements is needed to plan specific interventions to conserve the elephant population and reduce human-elephant conflict in line with the National Elephant Conservation and Management Plan. Setting up a system for game guards to identify specific elephant herds would help to generate a reliable estimate of the number of herds and the total population in the Northern Highlands. The perception of the game guards is that a small number of elephants are causing most of the incidents. A system to identify elephant herds would also increase knowledge on elephants that cause incidents more often, and facilitate an early warning system between villages about local movements of elephants. The National Elephant Conservation and Management Plan includes the strategy to enhance monitoring of vulnerable elephant populations in areas of Kunene Region. A method for elephant identification has been developed by Elephant-Human Relations Aid (EHRA), a Namibian NGO, which is testing the method in elephant ranges to the south of the Northern Highlands. Such a system of elephant identification would enhance the data already recorded in the Event Books and increase the usefulness of the monitoring process in terms of knowledge on elephant movements and planning local mitigation actions on human-elephant conflict.

The important role of community game guards

The data in Event Books should be assessed with consideration of the context of the challenges for the game guards. They receive low salaries and lack suitable walking boots and other equipment. On some days, they might lack motivation for keeping proper records in the Event Books. There is significant uncertainty in whether Event Book data provide a comprehensive record of the total number of incidents. It is likely that some incidents go unreported, particularly in villages located far from the villages in which the game guards live. The game guards usually do not have access to a vehicle and have to walk between villages. Some of these points are potentially demonstrated by the fact that 39% of the total recorded incidents in Orupupa Conservancy took place in the six villages in which the game guards live (Otjondeka, Okozonguehe, Omuhama, Ekoto, Okazorongua and Okomuhona). This is disproportionate because there was a total of 33 villages in which incidents were reported between 2012 and 2021. Overall, the data assessed in this study just represents one conservancy in the Northern Highlands and there is some uncertainty in the data. A wider assessment that includes other conservancies in the Northern Highlands would provide useful information, contributing to the development of local management plans.

Namibian conservation NGOs and the Ministry of Environment, Forestry and Tourism analyse and publish much of the data in Event Books, both at an aggregated level and for individual conservancies, although not to the level of detail presented in this study. Our study has demonstrated the important role of community game guards. We have also shown the benefits of co-operation between the hands-on work of experienced game guards in conservancies, researchers and data analysts.

ACKNOWLEDGEMENTS

We would like to acknowledge the support of Mr Beliudt Kavare, Orupupa Conservancy, and Mr Elia Kangombe, Okomuhona Village.

REFERENCES

- BBC (2008) Elephant Nomads of the Namib Desert. Online: https://www.dailymotion.com/video/x6e1lop [Accessed: 11 November 2020].
- BBC (2019) Seven Worlds, One Planet Africa (Episode 7). Online: https://www.bbc.co.uk/iplayer/episode/m000c6pn/seven-worlds-one-planet-series-1-7-africa [Accessed: 18 November 2020].
- Blanc J (2008) Loxodonta africana. The IUCN Red List of Threatened Species 2008. Online: https://www.iucnredlist.org/species/12392/3339343 [Accessed: 15 October 2020].
- Gobush KS, Edwards CTT, Balfour D, Wittemyer G, Maisels F, Taylor RD (2021) *Loxodonta africana*. The IUCN Red List of Threatened Species 2021. Online: https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS. T181008073A181022663.en [Accessed: 22 June 2021].
- GRN (2015) Namibia Poverty Mapping Report. Government of the Republic of Namibia. National Planning Commission. Online: https://www.na.undp.org/content/namibia/en/home/library/poverty/nampovmap.ht ml [Accessed: 18 November 2021].
- Heydinger J (2021) Eserewondo Rozongombe: Livestock as Sites of Power and Resistance in Kaokoveld, Namibia. *Environment and History* 27(2).
- Heydinger J, Packer C, Tsaneb J (2019) Desert-Adapted Lions on Communal Land: Surveying the Costs incurred by, and Perspectives of, Communal-area Livestock Owners in Northwest Namibia. *Biological Conservation* 236: 496–504.
- Hunninck L, Ringstad IH, Jackson CR, May R, Fossey F, Uiseb K, Killian W, Palme R, Roskaft E (2017) Being stressed outside the park conservation of African elephants (*Loxodonta africana*) in Namibia. *Conservation Physiology* 5: 1–11.
- Inman EN, Hobbs RJ, Tsvuura Z (2020) No safety net in the face of climate change: The case of pastoralists in Kunene Region, Namibia. *PLOS ONE* 15(9): e0238982.
- IUCN (2020) IUCN SSC Position Statement on the Management of Human-Wildlife Conflict. IUCN Species Survival Commission (SSC) Human-Wildlife Conflict Task Force. Online: https://www.iucn.org/sites/dev/files/ssc_human_wildlife_conflict_position_statement.pdf [Accessed: 21 October 2021].
- Leggett K, Fennessy J, Schneider S (2003) Seasonal distributions and social dynamics of elephants in the Hoanib River catchment, northwestern Namibia. *African Zoology* 38: 305–316.
- Leggett K, Brown L, Ramey R (2011) Matriarchal associations and reproduction in a remnant subpopulation of desert-dwelling elephants in Namibia. *Pachyderm* 49: 20–32.
- MEFT (2021) National Elephant Conservation and Management Plan 2021/2022-2030/2031. Ministry of Environment, Forestry and Tourism, Namibia.
- MEFT/NACSO (2021) The state of community conservation in Namibia (2019 Annual Report). Online: http://www.nacso.org.na/resources/state-of-community-conservation [Accessed: 21 October 2021].
- NACSO (2020) Registered Communal Conservancies.
 Online: http://www.nacso.org.na/conservancies
 [Accessed: 2 November 2020].
- Naidoo R, Weaver LC, De Longcamp M, Du Plessis P (2011) Namibia's Community-Based Natural Resource Management program: an unrecognized payments for environmental services scheme. *Environmental Conservation* 38: 445–453.

- Ramey R, Brown L (2019) Life History of Desert-Dwelling Elephants. Online: https://desertelephantconservation.org/ [Accessed: 7 October 2020].
- Silva AJ, Mosimane AW (2013) Conservation-based rural development in Namibia: a mixed-methods assessment of economic benefits. *The Journal of Environment & Development* 22(1): 25–50. https://doi.org/10.1177/ 1070496512469193
- Sky Nature (2020) Wild Kingdoms: Desert Survivors. Online: https://www.sky.com/watch/channel/sky-nature/wild-kingdoms/episodes/season-1/episode-1 [Accessed: 24 November 2020].
- Störmer N, Weaver L, Stuart-Hill G, Diggle R, Naidoo R (2019) Investigating the effects of community-based conservation on attitudes towards wildlife in Namibia. *Biological Conservation* 233: 193–200.
- Stuart-Hill G, Diggle R, Munali B, Tagg J, Ward D (2005).The Event Book System: a Community-based

- Natural Resources Monitoring System from Namibia. *Biodiversity and Conservation*, 14: 2611-2631.
- Thouless CR, Dublin HT, Blanc JJ, Skinner DP, Daniel TE, Taylor RD, Maisels F, Frederick HL, Bouché P (2016) African Elephant Status Report 2016: an update from the African Elephant Database. Occasional Paper Series of the IUCN Species Survival Commission, No.60, (IUCN African Elephant Specialist Group).
- Viljoen PJ, Bothma JP (1990) The influence of desert-dwelling elephants on vegetation in the northern Namib Desert, South West Africa/Namibia. *Journal of Arid Environments* 18: 85–96.
- Wenborn M, Svensson MS, Katupa S, Collinson R, Nijman V (2022). Lessons on the Community Conservancy Model for Wildlife Protection in Namibia. *The Journal of Environment & Development* 31(4): 375–394. https://doi.org/10.1177/10704965221121026.

A preliminary comparison of brown hyaena activity patterns at den sites located within a protected reserve and a commercial farmland

H Fischer¹, R Portas², S Edwards¹

URL: https://nje.org.na/index.php/nje/article/view/volume6-fischer

Published online: 7th September 2022

¹ Capel Manor College, Bullsmoor Lane, Waltham Cross, Enfield, UK EN1 4RQ. sledwardsuk@gmail.com

² University of Lubljana, Biotechnical Faculty, Dept. for Forestry, Večna pot 83, SI-1000 Ljubljana, Slovenia; Cheetah Research Project, Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research of Berlin, Alfred-Kowalke-Straße 17, 10315 Berlin, Germany

Date received: 1st November 2021; Date accepted: 13th June 2022.

Abstract

Wildlife activity patterns reflect both internal biological rhythms and adaptations to environmental factors. Studies examining the impact of anthropogenic activities on wildlife, including land-use, have frequently found changes in activity patterns in response to these activities. One species often found in human-dominated landscapes is the brown hyaena (*Parahyaena brunnea*), a large, nocturnal carnivore, endemic to southern Africa, which lives in societal clans that use a communal den. This study compared brown hyaena activity patterns at two den sites: a protected nature reserve and a non-protected commercial farmland in north-central Namibia. Activity curves produced by camera trap monitoring of the two den sites were significantly different and showed a coefficient of overlap of 0.21 (95% confidence intervals 0.19-0.25). Brown hyaena den activity at the protected site was mainly diurnal, whilst activity at the non-protected site showed a higher degree of nocturnal activity. Several potential reasons may explain the differences in den activity between the two sites, including environmental conditions and anthropogenic influences. More studies are needed with larger sample sizes to further investigate the impact of these factors.

Keywords: activity patterns, brown hyaena, Namibia, protected area

Introduction

Wildlife activity patterns, also referred to as diel activity patterns, reflect both internal biological rhythms and adaptations to environmental factors experienced by an individual, which may vary on a daily and/or seasonal basis (Kolowski *et al.* 2007; Ordiz *et al.* 2017). The period of day in which an individual is active can be adapted to exploit their environment, and major drivers of activity patterns include resource availability, predator avoidance and intraspecific interactions (Kitchen *et al.* 2000), and as such, changes to activity patterns may incur indirect fitness costs for a species (Kolowski *et al.* 2007; Kruuk 2014). Documenting wildlife activity patterns can therefore provide valuable ecological insights as well as helping to reveal the impact of anthropogenic activities on wildlife populations (Frey *et al.* 2017). Studies examining the impact of anthropogenic stress on wildlife have frequently found that wildlife modified their activity patterns (Di Bitett *et al.* 2008; Gaynor *et al.* 2018a; Morales-Gonzalez *et al.* 2020). More specifically, human activity has been suggested to be the cause of decrease in diurnal activity (Shamoon *et al.* 2018); for example, elephants (*Loxodonta africana*) have been found to restrict diel activity in areas with higher levels of human disturbance (Gaynor *et al.* 2018b).

Given the current increasing rate of anthropocentric land-utilisation across Africa, which has led to the conversion of natural habitats into heterogenous agricultural landscapes, documenting the impact of land-use on wildlife activity patterns is likely to be important for conservation management of endangered species. Studies have shown that wildlife species alter activity patterns in response to human land-use (Gaynor *et al.* 2018a). Several African ungulate species, including sable (*Hippotragus niger*) were found to increase their nocturnal use of waterholes in response to human hunting pressure (Crosmary *et al.* 2012). Similarly, serval (*Leptailurus serval*) have been recorded to increase nocturnal activity levels on farmlands which is suggested as a mechanism to avoid daytime activity of humans (Ramesh & Downs 2013).

In addition to being sites of increased human activity, farmlands may also represent areas where carnivore persecution takes place. This is because of the real or perceived threat carnivores pose towards livestock and/or human life (Kent & Hill 2013; Ramesh & Downs 2013). Human persecution imposes a stimulus to which an individual animal cannot become habituated, and wild carnivores often respond to anthropogenic activity by avoidance (Gaynor *et al.* 2018a; Kitchen *et al.* 2000). Previous studies have shown that human disturbance can cause an increase in nocturnal activity in diurnal carnivore species such as brown bear (*Ursus arctos*, Morales-Gonzalez *et al.* 2020) and nocturnal and crepuscular carnivore species such as serval (Kitchen *et al.* 2000).

Brown hyaena (*Parahyaena brunnea*) is a species commonly found on farmland, and therefore its sympatric overlap with humans may impact its activity pattern (Mills & Hofer 1998; Owens & Owens 1978; Wiesel 2015). The brown hyaena is a large-sized (~45 kg) mammalian carnivore endemic to southern Africa with an estimated total population size of < 10,000 individuals and is listed as Near Threatened by the International Union for Conservation of Nature (Wiesel 2015). The species experiences deliberate or incidental persecution in the form of shooting, trapping, and poisoning. This is usually

due to farmers perceiving brown hyaenas to be a threat to livestock despite them rarely preying on livestock, being primarily a scavenger (Kent & Hill 2013; Mills 1990; Wiesel 2015; Winterbach *et al.* 2017). As a consequence, human persecution has led to the local extinction of brown hyaenas in southern parts of Namibia (Wiesel 2015).

Within protected areas of the southern Kalahari, brown hyaenas are predominantly nocturnal, with activity peaks observed after sunset and just before sunrise (Mills 1990). The species is social and lives in clans of up to 13 individuals, consisting of related females, their offspring of both sexes and non-natal males. Approximately 8% of the population consists of nomadic individuals which have no lasting relationships with conspecifics (Mills 1990). Although clan members forage solitarily, individuals within a clan share the same home range and communal dens, which function as the centres of social activity and are visited by all clan members (Mills 1990). Cubs are raised at a communal den, from three months old, with the involvement of all clan members (Mills 1990). Communal denning, given that food availability is sufficient, provides several benefits: clan members cooperate in ways that appear to increase the direct and indirect fitness of individuals, including increased food supply by several individuals, which in turn enhances breeding and cub survival rates (Alcock & Rubenstein 2019; Mills 1990; Owens & Owens 1978). Dens also function as protection for the cubs during periods when adults are absent (Mills 1990; Owens & Owens 1978).

In this study, we compared the activity patterns of two brown hyaena clans at their communal den sites located in areas differing in level of formal protection to investigate the potential anthropogenic impact on activity patterns. We predicted that den activity at the protected site would show a higher degree of nocturnality compared to the non-protected site due to the higher risk of persecution on farmlands.

Materials and Methods

Study sites

The protected site, Okonjima Nature Reserve (ONR) is a privately-owned reserve, situated 50 km south of Otjiwarongo, north-central Namibia. The 200 km² reserve is fully enclosed by a 2.4 m-high electrified fence of 7-10 kilovolt, erected in 2010 and comprises a 180 km² area reserved for wildlife and a 20 km² area containing buildings for human activity, such as non-consumptive tourism. Brown hyaena density within ONR was estimated at 24.01 brown hyaena/100 km² (Edwards et al. 2019). ONR also contains a leopard (*Panthera pardus*) population estimated at a density of 14.51 leopards/100 km² (Noack et al. 2019). No active carnivore management has taken place since the establishment of the fence. The brown hyaena den on ONR was monitored as part of an ongoing study.

The farmland site, Gross Okandjou Farm (GOF) is a commercial farm totalling 90 km², situated 30 km west of the town of Omaruru in central-western Namibia. The farm is divided into camps where a total of 80-120 cattle (*Bos taurus*) and 60 horses (*Equus caballus*) graze. Farm activities include non-consumptive tourism (horse-riding) and sustainable hunting of antelope for meat production, predominantly kudu (*Tragelaphus strepsiceros*) and gemsbok (*Oryx gazella*). No carnivore persecution takes place directly at the farm; however, large carnivores in the area are likely to range over several neighbouring farms, which may differ in tolerance towards carnivores, due to their perceived or real threat to livestock. The brown hyaena den was located inside a cave within mountainous habitat and was found and monitored opportunistically.

Data collection

A brown hyaena clan, consisting of a collared female with three 7-month-old cubs, two adults and one sub-adult was monitored using a camera trap at ONR. A single Cuddeback X-change 11339 infra-red camera trap (Non Typical Inc., Wisconsin, USA), housed in a 'Cuddesafe' protective housing was mounted approximately 50 cm from the ground on a metal pole, focused on the main den entrance. The camera trap was programmed to take three images per trigger, with no delay between triggers and an image quality of 20 mega-pixels and the sensor set to high sensitivity (Edwards *et al.* 2020). On GOF, the den, used by a clan consisting of two adults and one cub estimated to be nine months old, was monitored using a Reconyx PC900 HyperFire (Reconyx Inc, Holeman, Wisconsin, USA) motion sensor camera trap, positioned to capture all den entrances. The motion sensor was set to high sensitivity, with three image per trigger and no delay interval between triggers.

Adults often stayed for prolonged periods of time at the dens (maximum time = 5 h 28 min). Thus, to ensure that time stamps were temporally independent, a random sub-sample comprising 50% of the records from each den was selected and included in the analysis (c.f. Edwards *et al.* 2021). The time stamps of independent events were then used to produce activity curves. Data used for this study were collected from 21 June 2020 to 22 July 2020, with a total of 24 and 25 active camera trap nights achieved for ONR and GOF respectively. To avoid temporal bias, days where the camera trap was not active for the entire 24-cycle (due to batteries running out of power) were removed from the analysis.

Data analysis

Camera trap data from each site were filtered to remove any images not showing brown hyaena presence; these may have been triggered by unrelated movements such as other species or wind-related movements (Trolliet *et al.* 2014). The package 'overlap' (Ridout & Linkie 2009) in statistical program R (R Development Core Team 2014) was used to non-parametrically estimate and plot the probability function of the time distribution for each site, producing a visual representation of the activity pattern, the 'activity curve'. In this approach, events (time stamps from camera traps), were viewed as a random sample taken from an underlying continuous temporal distribution, describing the probability of an event occurring at any given time (Ridout & Linkie 2009).

The 'overlap' package was also used to calculate coefficients of overlap between the activity curves produced, using estimator Δ , a continuous variable between o and 1, where o indicates no overlap, and 1 indicates total overlap. The coefficient is defined as the area under the curve formed by taking the minimum of each density function of the two compared cycles at each time point (Monterroso *et al.* 2014). Estimator Δ_4 was used as this is suggested the most applicable for sample sizes of > 75 (Ridout & Linkie 2009). Confidence intervals for coefficients of overlap were calculated using 1 000 bootstraps. A Watson Wheeler test in R package 'circular' (Lund & Agostinelli 2013) was used to test for homogeneity in the two activity patterns. The test detects differences in the mean angle of the circular temporal data indicative of differences in activity peaks (Batschelet 1981).

Results

After filtering of images not showing brown hyaena presence and removal of incomplete camera trap nights, a total of 897 image files from ONR and 18 161 image files from GOF were obtained. This resulted in a random sub-sample of 50% of each data set of n = 448from ONR and n = 9.080 from GOF being used for analysis. The probability overlap plot showed a clear peak in brown hyaena den activity at ONR during the mid-afternoon, which corresponded to a mean activity period of 14h56, whilst at GOF, a bimodal activity curve was seen with peaks around o5hoo and 22hoo (Figure 1, Table 1). The coefficient of overlap between the two sites was 0.21 (95% confidence intervals 0.19-0.25). The Watson-Wheeler test indicated a significant difference in the activity patterns between each site (W = 714, d.f. = 2, p < 0.001).

Table 1: Circular descriptive statistics for brown hyaena den activity at Okonjima Nature Reserve (ONR) and Gross Okandjou Farm (GOF).

Variable	ONR	GOF
Sample size	448	9 080
Mean vector	14h52	01h23
Length of mean vector	0.77	0.45
Circular variance	0.21	0.54
Circular standard deviation	02h43	04h46
Standard error of mean	ooho5	ooho2
95% confidence interval	14h45-15h07	01h28-01h38

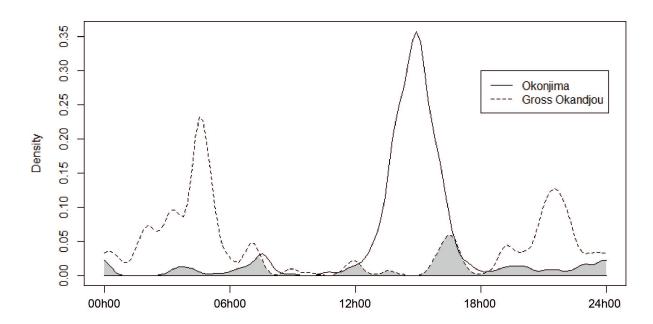


Figure 1: Overlap plot showing the activity curves for brown hyaena at den sites on Okonjima Nature Reserve and Gross Okandjou Farm. Grey area represents the overlap in activity.

Discussion

Wild carnivores have been recorded shifting diel activity patterns and increasing nocturnal activity in response to human activity both in the form of land-use, and the corresponding increases in human activity, and direct persecution (Gaynor *et al.* 2018a). Given the increase in human land-utilisation in Africa, interactions between humans and wildlife are likely to occur more frequently, thus understanding the outcomes of such interactions is important for conservation management (Kolowski *et al.* 2007; Wiesel 2015). We compared brown hyaena den activity at two sites in Namibia and found a significant difference in activity patterns between a protected reserve and a non-protected farmland. Brown hyaenas at the protected site displayed higher levels of diurnal den activity than those in farmland, with a peak in activity during midafternoon at the protected site, in comparison to activity peaks around 05hoo and 22hoo in farmland. Although data collection was limited to one den per site, these results may suggest that differences in the environmental conditions between the two sites may be causing brown hyaenas to change their den activity patterns.

The potential persecution of carnivores across the larger farmland landscape is a possible reason for the differences in activity patterns seen between the two sites. A study examining the impact of persecution on coyotes (*Canis latrans*) found nocturnal activity increased when persecution was present compared to no persecution (Kitchen *et al.* 2000). The same study also showed that eight years after anthropogenic persecution had ceased, coyotes adopted a more diurnal activity pattern, indicating that anthropogenic persecution influenced coyote diel activity pattern, and was able to conclude that nocturnal activity of coyotes increased with the presence of persecution (Kitchen *et al.* 2000). Furthermore, a study focusing on sika deer (*Cervus nippon*) found a higher degree of nocturnality during a culling program than prior to its start (Ikeda *et al.* 2019). Additionally, a study found that red brocket deer (*Mazama americana*) were more nocturnal in areas with persecution compared to areas with higher level of protection (Di Bitett *et al.* 2008). However, given the unknown levels of persecution on the farmlands surrounding the GOF, further research would be needed to investigate how persecution of brown hyaena and/or sympatric carnivores impacts brown hyaena activity patterns across Namibian farmlands.

Another potential factor which may explain the differences in brown hyaena den activity seen between the two sites is differences in activity patterns of sympatric apex predators. Brown hyaenas are a scavenging species and comparison of brown hyaena and leopard diet via scat analysis on Namibian farmlands found a high degree of overlap, suggesting the species may benefit from the presence of leopard (Stein et al. 2013). Indeed, brown hyaenas on ONR have frequently been observed scavenging from leopard kills, and even kleptoparasitising leopard kills (Edwards pers. obs.). Scavengers may benefit from being sympatric with efficient predators (Creel et al. 2001) and, to maximise this benefit, brown hyaenas may align their activity patterns with leopards to access their kills before other scavengers such as vultures (Accipitridae species) do, although this could also increase interference competition (Creel et al. 2001). However, activity patterns of leopards on both farmlands and protected areas also containing brown hyaenas would need to be compared in order to fully examine if differences in apex predator activity patterns could explain the differences in brown hyaena activity patterns observed in this study.

This study is limited to just one den at each study site, between which differences in cub age and clan structure were seen, which may have impacted how often and when adults visited the den. The three cubs on ONR were seven months old, compared to a single cub of nine months old on GOF. Mills (1990) observed an increase in the time spent suckling as cubs grew, however between four and nine months old mothers visited cubs at the den once per 24 hours during the night. Brown hyaena cubs receive solid food at the den from four months of age, which is brought back by clan members, but are not weaned until 12-16 months of age (Mills 1990). Therefore, cubs at both dens were in similar phases of development regarding their diet. The single cub at GOF was provided food by two adults, in comparison to the three cubs on ONR which had two adults and a sub-adult within their clan. The three cubs at ONR may have required more frequent food deposits from adults than the single cub at ONR, which may explain the increased diurnal activity at the site. In addition, prey density and food availability may differ in both study sites, which may also affect the activity patterns of brown hyaenas. Future studies which include a range of sites, clan sizes and cub ages are needed to fully assess the impact of clan size and cub age on timing of visits to the den under different environmental conditions.

Conclusion

Although limited to a small sample size, the findings of this study suggest that the brown hyaena den site within a commercial farmland had higher levels of nocturnal activity and a significantly different activity pattern to a den within a protected reserve. These findings are consistent with several former studies showing an increased nocturnal activity due to anthropogenic activity and/or persecution on other carnivore and prey species such as coyotes, servals, bears and red brocket deer. The consequences of higher levels of brown hyaena nocturnal den activity at GOF compared to ONR are currently unclear. More studies are needed to understand the specific implications of higher nocturnal den activity at the farmland site compared to the protected site on brown hyaena populations and fitness of individuals on a long-term basis.

Acknowledgements

We would like to thank the Ernest Kleinwort Charitable Trust, the Namibian Wildlife Conservation Trust, Varta Consumer Batteries, the AfriCat Foundation, AfriCat UK and Okonjima Lodges CC for supporting the project. We thank the Vogel family from the farm Gross Okandjou for their interest and support in wildlife research and conservation. We also thank the Ministry of Environment, Forestry and Tourism in collaboration with the National Commission on Research, Science and Technology for granting the relevant permits for this research. Thank you to Nikolaos Karantanis and Thomas Logan for their input on the design of this study.

References

- Alcock J, Rubenstein DR (2019) Animal Behaviour (Eleventh edition). Oxford University Press, Oxford
- Batschelet E (1981) Circular statistics in biology. Academic Press, London
- Creel S, Spong G, Creel NM (2001) Interspecific competition and the population biology of extinction-prone carnivores. In Gittelman JL, Funk SM, MacDonald D, Wayne R (ed) *Carnivore Conservation*, pp. 35–60. Cambridge University Press, Cambridge.
- Crosmary WG, Valeix M, Fritz H, Madzikanda H, Côté SD (2012) African ungulates and their drinking problems: Hunting and predation risks constrain access to water. *Animal Behaviour* 83(1): 145–153. https://doi.org/10.1016/j.anbehav.2011.10.019
- Di Bitetti MS, Paviolo A, Ferrari CA, De Angelo C, Di Blanco Y (2008) Differential responses to hunting in two sympatric species of brocket deer (*Mazama americana* and *M. nana*). *Biotropica* 40(5): 636–645.
- Edwards S, Noack J, Heyns L, Rodenwoldt D (2019) Evidence of a high-density brown hyaena population within an enclosed reserve: The role of fenced systems in conservation. *Mammal Research* 64(4): 519–527.
- Edwards S, Noack J, Heyns L, Rodenwoldt D (2021) Are camera traps a reliable method for estimating activity patterns? A case study comparing technologies for estimating brown hyaena activity curves. *Remote Sensing in Ecology and Conservation* 7(2): 129–138.
- Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using cameratrap data: challenges and opportunities. *Remote Sensing in Ecology and Conservation*: 1–10. https://doi.org/10.1002/rse2.60
- Gaynor KM, Hojnowski CE, Carter NH, Brashares JS (2018a) The influence of human disturbance on wildlife nocturnality. *Science* 360(6394): 1232–1235.
- Gaynor KM, Branco PS, Long RA, Gonçalves DD, Granli PK, Poole JH (2018b) Effects of human settlement and roads on diel activity patterns of elephants (*Loxodonta africana*). *African Journal of Ecology* 56: 872–881. https://doi.org/10.1111/aje.12552
- Ikeda T, Takahashi H, Igota H, Matsuura Y, Azumaya M, Yoshida T, Kaji K (2019) Effects of culling intensity on diel and seasonal activity patterns of sika deer (*Cervus nippon*). *Scientific Reports* 9(1): 1–8. https://doi.org/10.1038/s41598-019-53727-9.
- Jacobson AP, Gerngross P, Lemeris JR, Schoonover RF, Anco C, Breitenmoser-Würsten C, Durant SM, Farhadinia MS, Henschel P, Kamler JF, Laguardia A, Rostro-Garcia S, Stein AB, Dollar L (2016) Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 2016 4:e1974. https://doi.org/10.7717/peerj.1974. PMID: 27168983
- Kambongi T, Heyns L, Rodenwoldt D, Edwards S (2021) A description of daytime resting sites used by brown hyaenas (*Parahyaena brunnea*) from a high-density, enclosed population in north-central Namibia. *Namibian Journal of Environment* 5: B1-
- Kent VT, Hill RA (2013) The importance of farmland for the conservation of the brown hyaena *Parahyaena brunnea*. Oryx 47(3): 431–440.
- Kitchen AM, Gese EM, Schauster ER (2000) Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78(5): 853–857.

- Kolowski JM, Katan D, Theis KR, Holekamp KE (2007) Daily patterns of activity in the spotted hyaena. *Journal of Mammalogy* 88(4): 1017–1028.
- Lund U, Agostinelli C (2018) CircStats: circular statistics, from Topics in Circular Statistics, R package version 0.2-6. https://CRAN.R-project.org/package=CircStats
- Mills G, Hofer H (1989) Hyaenas. Status Survey and Conservation Action Plan. IUCM/SSC Hyaena Specialist Group. IUCN, Cambridge. http://www.carnivoreconservation.org/files/ actionplans/hyaenas.pdf
- Mills MGL (1994) Kalahari hyaenas: Comparative behavioural ecology of two species. The Blackburn Press, New Jersey.
- Monterroso A, Conde C, Gay C, Gómez D, López J (2014) Two methods to assess vulnerability to climate change in the Mexican agricultural sector. *Mitigation and Adaptation Strategies* for Global Change 19(4): 445–461.
- Morales-Gonzalez A, Ruiz-Villar H, Ordiz, A, Penteriani V (2020) Large carnivores living alongside humans: Brown bears in human-modified landscapes. *Global Ecology and Conservation* e00937. https://doi.org/10.1016/j.gecco.2020.e00937
- Ordiz, A, Sæbø S, Kindberg J, Swenson JE, Støen, O (2017) Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? *Animal Conservation* 20: 51–60. https://doi.org/10.1111/acv.
- Owens MJ, Owens DD (1978) Feeding ecology and its influence on social organization in brown hyaenas (*Hyaena brunnea*, Thunberg) of the Central Kalahari Desert. *African Journal of Ecology* 16(2): 113–135.
- R Development Core Team (2014) *R: a language and environment for statistical computing; Version 3.1.1.* R Foundation for Statistical Computing, Vienna.
- Ramesh T, Downs CT (2013) Impact of farmland use on population density and activity patterns of serval in South Africa. *Journal of Mammalogy* 94(6): 1460–1470.
- Ridout MS & Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics* 14(3): 322–337.
- Shamoon H, Maor R, Saltz D, Dayan T (2018) Increased mammal nocturnality in agricultural landscapes results in fragmentation due to cascading effects. *Biological Conservation* 226: 32–41. https://doi.org/10.1016/j.biocon.2018.07.028
- Stein AB, Fuller TK, Marker LL (2013) Brown hyaena feeding ecology on Namibian farmlands. *African Journal of Wildlife Research* 43(1): 27–32. https://doi.org/10.3957/056.043.0115
- Trolliet F, Huynen MC, Vermeulen C, Hambuckers A (2014) Use of camera traps for wildlife studies. A review. *Biotechnology, Agronomy and Society and Environment* 18(3):446-454
- Wiesel I (2015) Parahyaena brunnea: Wiesel I.: The IUCN Red List of Threatened Species 2015: e.T10276A82344448 [Data set]. International Union for Conservation of Nature.
- Winterbach CW, Maude G, Neo-Mahupeleng G, Klein R, Boast L, Rich LN, Somers MJ (2017) Conservation implications of brown hyaena (*Parahyaena brunnea*) population densities and distribution across landscapes in Botswana. *Koedoe* 59(2) a1441.

Provisional atlas of breeding birds of Henties Bay in the coastal Namib Desert G Kopij

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-kopij

Published online: 7th March 2022

Department of Integrated Environmental Science, Ogongo Campus, University of Namibia. Private Bag 5520 Oshakati, Namibia. Department of Vertebrate Ecology, Wrocław University of Environmental & Life Sciences, ul. Kozuchowska 5b, 51-631 Wroclaw, Poland.

Date received: 17th December 2021; Date accepted: 28th January 2022.

Abstract

Fourteen species were recorded breeding in the town of Henties Bay (345 ha) in 2016/17 austral summer, six of which made up 85.4% of all breeding birds. The dominant species were Laughing Dove *Streptopelia senegalensis*, Common Waxbill *Estrilda astrild*, House Sparrow *Passer domesticus*, Southern Masked Weaver *Ploceus velatus*, Cape Sparrow *Passer melanurus*, and Rosy-faced Lovebird *Agapomis roseicollis*. The breeding avifauna in Henties Bay is similar to that in Swakopmund and Walvis Bay.

Keywords: bird, breeding, community ecology, Namibia, population density, urban ornithology

Introduction

Studies on various biota in urban environments constitute a rapidly growing sub-discipline of ecological research. However, this sub-discipline is growing unevenly. For example, over 100 urban bird atlases are at present available in Europe (Luniak 2013, 2017), but only a few in Africa, mostly from the southern part of this continent (Kopij 2018). In Namibia, several provisional urban ornithological atlases have been completed recently in the following towns: Katima Mulilo (Kopij 2016), Outapi (Kopij 2019a), Swakopmund (Kopij 2018) and Walvis Bay (Kopij, in press). The two latter towns are located on the Atlantic Coast in the Namib Desert. In this paper, a provisional ornithological atlas is presented for Henties Bay (centred on about 22.1 South, 14.3 East), another coastal town situated in this desert.

Study area and methods

The Namib Desert is one of the oldest and most hyper-arid deserts in the world. It is unusual in that due to its location along the Atlantic Ocean, it is often covered by dense fog which brings water to all living organisms (Mendelsohn et al. 2009). There are only a few distinct towns along the coast: Lüderitz, Walvis Bay, Swakopmund and Henties Bay. From ecological point of view, these towns may be considered as artificial oases connected by wide ephemeral river valleys with savanna biomes further to the east. Henties Bay is situated near the Omaruru River mouth, 70 km N of Swakopmund $(S 22^{\circ}11'84'', E 14^{\circ}28'24''E)$ in the Erongo Region. Henties Bay is a tourist town, located along a high bank of the Atlantic Ocean, stretching today over almost 8 km. The study area was confined to the town lying between the ocean and the main Omaruru road (Figure 1). The town was founded in 1965 as a small tourist village, but by 2017 the population had reached c. 3 000 citizens and up to 7 000 tourists visit annually. The older parts of the town



Figure 1: The location of Henties Bay in Namibia (inset), and the town with the study area demarcated with a broken yellow line (main panel).



Figure 2: Views of Henties Bay.

are well-vegetated with palms, araucarias, figs, all sorts of shrubs, succulents and herbs (Figure 2). There are numerous bird feeders installed in some yards, where seeds and nuts are provided on a regular basis throughout the year.

Studies were conducted in the austral summer of 2016/17. The simplified version of the mapping method (Bibby *et al.* 2012, Sutherland 1996) was employed to assess population densities and structure of community of birds breeding in the town. The formal, more vegetated and older part of the town was surveyed twice; the first survey was conducted between 20 December 2016 and 10 January 2017, the second survey between 15 January 2017 to 15 February 2017. For details regarding the methodology see Kopij (2018).

Results and discussion

A total of 14 breeding bird species were recorded in the town of Henties Bay in the study period (Table 1, Appendix 1). The dominant species were Laughing Dove, House Sparrow, Common Waxbill, Southern Masked Weaver, Cape Sparrow and

Rosy-faced Lovebird. Together, they comprised 85.4% of all breeding birds (Table 1). There were only two subdominant species, viz. Cape Wagtail and Speckled Pigeon. They comprised 8.3% of all breeding birds. The remaining six species comprised 6.2% (Table 1).

In Swakopmund, also located on the Atlantic coast, 18 breeding species were recorded in the same austral summer (2016/17). Six species were classified as dominants: Cape Sparrow, House Sparrow, Southern Masked Weaver, Common Waxbill, Laughing Dove and Rock Dove (Kopij 2018). In Walvis Bay, just south of

Table 1: Breeding bird community in Henties Bay in the 2016/17 austral summer.

Species	Pairs (n)	Density (pairs/10 ha)	Dominance (%)
Laughing Dove Streptopelia senegalensis	251	7.3	29.4
House Sparrow Passer domesticus	141	4.1	16.6
Common Waxbill Estrilda astrild	124	3.6	14.6
Southern Masked Weaver Ploceus velatus	90	2.6	10.6
Cape Sparrow Passer melanurus	63	1.8	7.4
Rosy-faced Lovebird Agapornis roseicollis	60	1.7	7.1
Cape Wagtail Motacilla capensis	37	1.1	4.3
Speckled Pigeon <i>Columba guinea</i>	34	1.0	4.0
African Marsh Warbler Acrocephalus baeticatus	14	0.4	1.6
Dusky Sunbird Cynniris fuscus	11	0.3	1.3
Helmeted Guineafowl Numida meleagris	11	0.3	1.3
Red-faced Mousebird Urocolius indicus	10	0.3	1.2
Cape Glossy Starling Lamprotornis nitens	3	0.1	0.4
Rock Kestrel Falco rupicolus	2	0.1	0.2
Total	851	24.7	100.0

Swakopmund, 17 breeding species were recorded in this same austral summer. Six species (Cape Sparrow, House Sparrow, Southern Masked Weaver, Common Waxbill, Laughing Dove, Rock Dove and Specked Pigeon) were also dominant and comprised 88.2% of all breeding pairs recorded (Kopij, in press). Therefore, avian communities are very similar in Henties Bay, Swakopmund and Walvis Bay.

By contrast, in the town of Outapi, situated in the savanna biome of the northern Namibia, 29 breeding species were recorded (Kopij 2019a). Only three dominant species were distinguished, comprising only 65.4% (Kopij 2019a). Similarly, in the town Ongwediva, located in the same biome, 30 breeding species were recorded, with dominant species comprising 69.3% (Kopij 2021). Furthermore, 122 breeding bird species were recorded (with dominants comprising 42.5%) in the town of Katima Mulilo, situated in Zambezi Riparian Forest and Kalahari Woodland (Kopij 2016). This shows that towns located in savanna biomes contain greater bird diversity than those located on the arid Atlantic coastline.

Acknowledgements

 $I would \ like \ to \ express \ my \ thanks \ to \ Ms. \ The resia \ Gebhardt \ and \ Mr. \ Tony \ Nsio \ who \ assisted \ me \ in \ the \ field \ study.$

References

Bibby CJ, Burgess ND, Hill DA, Mustoe S (2012) *Bird Census Techniques*, 2nd ed. Academic Press, London.

Kopij G (2016) Birds of Katima Mulilo town, Zambezi Region, Namibia. *International Science & Technology Journal of Namibia* 7: 85-102.

Kopij G (2018) Provisional atlas of breeding birds of Swakopmund in the coastal Namib Desert. *Lanioturdus* 51(2):

Kopij G (2019a) Population density and structure of birds breeding in an urban habitat dominated by large baobabs (*Adansonia digitata*), Northern Namibia. *Biosystem Diversity* 27(4): 354-360.

Kopij G (2019b) Structure of avian communities in a mosaic of built-up and semi-natural urbanised habitats in Katima Mulilo town, Namibia. Welwitschia International Journal of Agricultural Sciences 1: 68-75.

Kopij G (2020) Structure of the breeding bird community along the urban gradient in a town on Zambezi River, Northeast Namibia. *Biologija* 66(1): 1-9.

Kopij G (2021) Population density and structure of a breeding bird community in a suburban habitat in the Cuvelai drainage system, northern Namibia. *Arxius de Miscellania Zoologica* 19: 313-320.

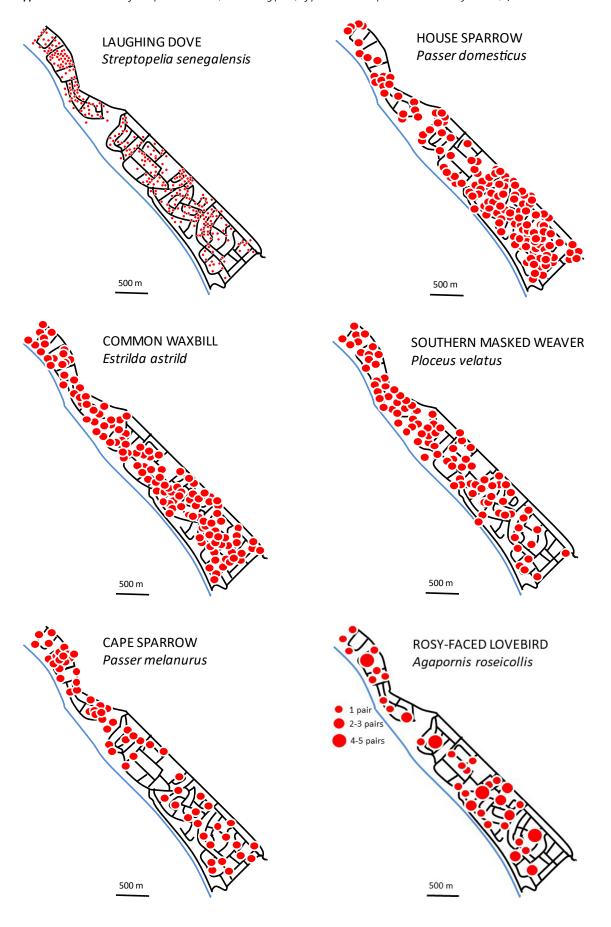
Luniak M (2013) Kartograficzne atlasy awifauny miast w Europie – przegląd badań. *Ornis Polonica* 54: 40–49.

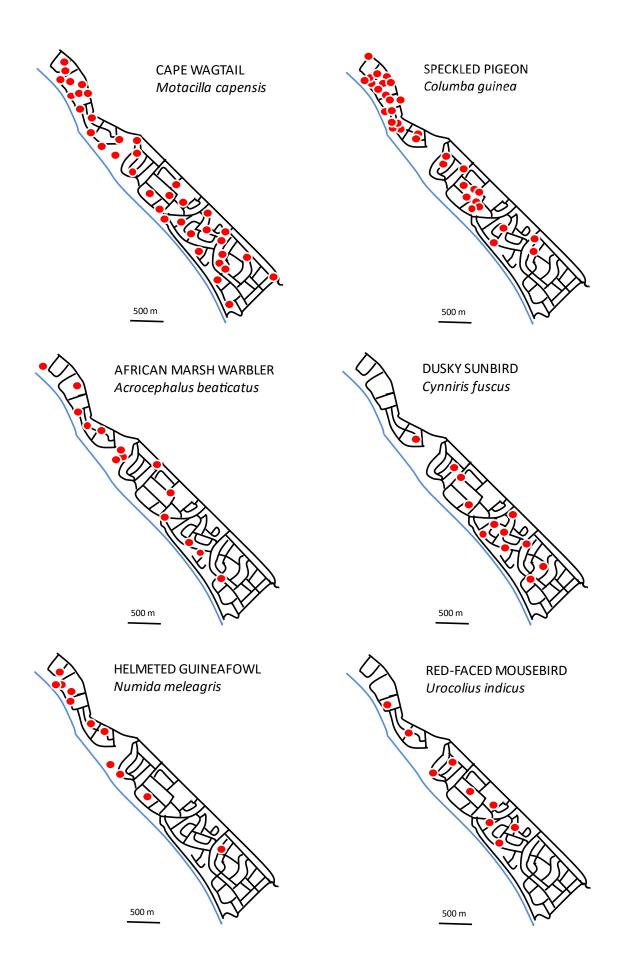
Luniak M (2017) Urban ornithological atlases in Europe: a review. In: Murgui E. and Hedblom H. (eds.). Ecology and conservation of birds in urban environments. Springer, Heidelberg. p. 209-223.

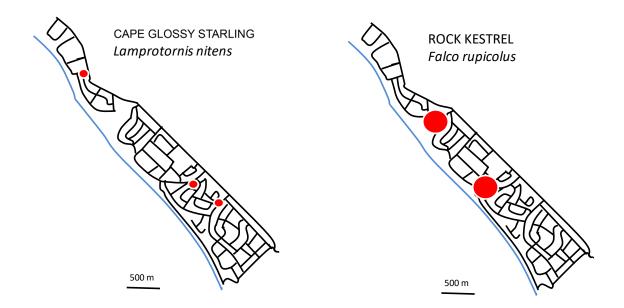
Mendesohn J, Jarvis A, Roberts C, Robertson T (2009) Atlas of Namibia. A Portrait of the Land and its People. Sunbird Publishers, Windhoek.

Sutherland WJ (ed.) (1996) Ecological census techniques. A handbook. Cambridge Univ. Press, Cambridge (UK).

 $\textbf{\textit{Appendix 1.}} \ \textit{Distribution of occupied territories (i.e. breeding pairs) of particular bird species in Henties Bay in 2016/17 austral summer.$







Range extension of *Crotaphopeltis hotamboeia* (Laurenti, 1768) in Namibia F Theart¹, TJ Ping², K Engelking¹, FS Becker³

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-theart

Published online: 25th May 2022

- ¹ Namibia University of Science and Technology, Faculty of Natural Resources and Spatial Sciences, Windhoek, Namibia. francois.theart@gmail.com.
- ² Tyrone Ping Exploring Southern African Herpetofauna, Cape Town, South Africa.
- ³ School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa; National Museum of Namibia, Department of Natural Sciences, Windhoek, Namibia

Date received: 7th March 2022; Date accepted: 9th May 2022.

Abstract

While Namibia has a high diversity of reptiles (Herrmann & Branch 2013), it is deficient in records for most reptile species, and several distributions are still poorly understood. We extend the known range for *Crotaphopeltis hotamboeia* by more than 700 km southwest from the nearest published Namibian record, and more than 150 km southeast from the nearest recorded museum record. This represents one of the most arid records for the species.

Keywords: Crotaphopeltis hotamboeia, Namibia, range extension

Background

Crotaphopeltis hotamboeia is a medium-sized, rear-fanged colubrid which feeds largely on amphibians. It is widely distributed throughout Southern Africa and inhabits most biomes with the exception of rainforests and hyper arid regions (Engelbrecht et al. 2020). This species is typically associated with areas with a high annual rainfall or permanent sources of water (Ping pers. obs.). Crotaphopeltis hotamboeia is known in Namibia from a few localities in the far northeast. Previous publications indicate its presence in the Otjozondjupa Region (Griffin 2003, Branch 1994), although the exact locations were not previously published. It may also occur in the Kavango, Omusati, and Oshikoto regions (Bauer pers. com. 2021).

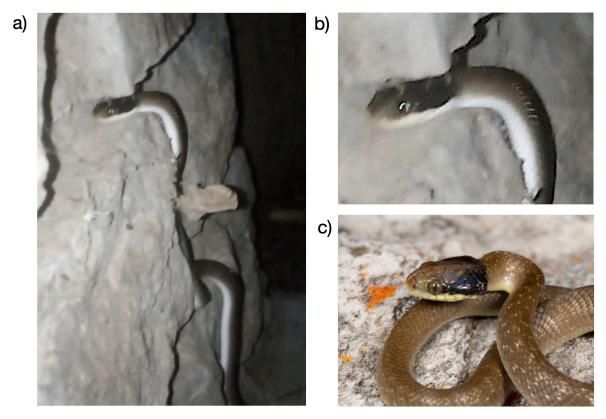


Figure 1: The original image as supplied by the observer is shown in panel a. The head is shown enhanced in panel b, clearly showing the dark temples, which are unique to Crotaphopeltis hotamboeia. Panel c presents an image of the same species, shown here for comparison (photo: T Ping).

Results

On the evening of 21st of March 2021 shortly after sunset, the owner of Exito Safaris observed a small snake near their home. Unable to identify the species the farmer sent an image of the snake to FT (see Figure 1). Despite the poor quality of the image, FT was able to confidently identify the snake as *Crotaphopeltis hotamboeia* due to the presence of dark temples on the head, a pale colour on the upper and lower lip, a creamy white belly and a slate grey body. Considering the area, size of the snake and the head colouration, there are no other likely candidate species for this photograph. The closest other species in terms of appearance would be the black-headed centipede eater (*Aparallactus capensis*), which does not have a brown tip to the snout, pale upper lip, or a similar head shape; the body of *A. capensis* is also of notably more slender build. Scale counts and Snout-Vent Length measurements were not taken as the snake was relocated by the observer shortly after the photos were taken. This observation (S21.664188 E18.778358) serves as the first confirmed

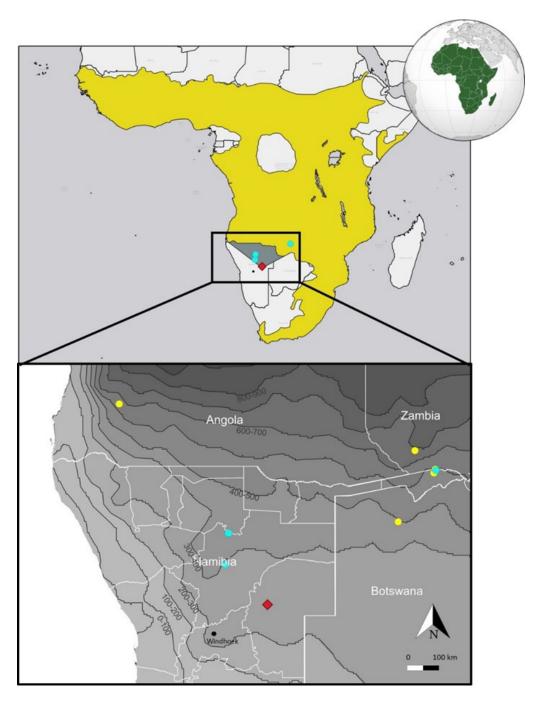


Figure 2: The current range of Crotaphopeltis hotamboeia in yellow, and the suggested range update in dark grey (upper panel); the new record is indicated by a red diamond; previously unpublished records from the National Museum of Namibia as blue circles; the nearest Global Biodiversity Information Facility (GBIF, 2022) records as yellow circles; mean annual rainfall is indicated in grey, with isohyets labelled in dark grey text (bottom panel).

record from the Omaheke Region, which is at the lower end of the annual rainfall range in which this species is known to occur (Wagner *et al.* 2021; see Figure 2). This record lies approximately 158 km southeast of the nearest record in the National Museum of Namibia (NMNW) Herpetology Collection, which was collected from the adjacent Waterberg (Figure 2; NMNW R1990). This record, and other records from the NMNW, have not been published before but were presumably those referred to in Griffin (2003).

Acknowledgements

We would like to thank the owner of Exito Safaris for providing us with the photographs and the co-ordinates for this record. We would like to thank Professor Aaron Bauer of Villanova University for providing the known localities for *Crotaphopeltis hotamboeia* and for confirming the identification and range extension of the snake.

References

Branch WR (1994) Field guide to snakes and other reptiles of Southern Africa, [2nd ed.]. Struik Publishers, Cape Town.
Engelbrecht HM, Branch WR, Greenbaum E, Burger M, Conradie W, Tolley KA (2020) African Herald snakes, *Crotaphopeltis*, show population structure for a widespread generalist but deep genetic divergence for forest specialists. *Journal of Zoological Systematics and Evolutionary Research* 58(4): 1220—1233. https://doi.org/10.1111/JZS.12361.

Griffin M (2003) Annotated Checklist and Provisional Conservation Status of Namibian Reptiles, *Namibia Scientific Society*, pp160.

Herrmann HW, Branch WR (2013) Fifty years of herpetological research in the Namib Desert and Namibia with an updated

and annotated species checklist. *Journal of Arid Environments* 93: 94–115. https://doi.org/10.1016/J.JARIDENV.2012.05.003 GBIF (2022) *Crotaphopeltis hotamboeia* (Laurenti, 1768). https://www.gbif.org/species/9176658. Accessed on 18 April 2022.

Wagner P, Penner J, Rödel M-O, Luiselli L, Branch WR, Chirio L, Howell K & Malonza PK (2021) *Crotaphopeltis hotamboeia*. The IUCN Red List of Threatened Species 2021: e.T13264994A13265005. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T13264994A13265005.en. Accessed on 18 April 2022.

First records for Namibia of Lesser Masked Weaver *Ploceus intermedius* subsp. beattyi

W Swanepoel^{1,2}, RW Becker¹, V De Cauwer¹

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-swanepoel

Published online: 2nd September 2022

- ¹ Biodiversity Research Centre, Department of Agriculture and Natural Resources Sciences, Namibia University of Science and Technology, Windhoek, Namibia.
- ² Independent Researcher, PO Box 21168, Windhoek, Namibia. wessel@kaokosafari.com

Date received: 13th August 2022; Date accepted: 28th August 2022.

Abstract

The presence in Namibia along the Kunene River and border of Angola of the *beattyi* subspecies of *Ploceus intermedius* (Lesser Masked Weaver) is reported for the first time. Observations suggested that *beattyi* probably grades into birds of the *cabanisii* subspecies from Epupa Falls and further upstream along the Kunene River, while typical *cabanisii* occurs south of the Kunene River.

Keywords: Lesser Masked Weaver, Namibia, Ploceus intermedius subsp. beattyi, range extension

In January 2020, the Namibia University of Science and Technology (NUST) arranged a biodiversity survey of the Namibian side of the Kunene River mouth and upstream to about 15 km inland. The riverine vegetation upstream from the mouth consists of *Phragmites* reeds with woody shrubs, trees and climbers, and annual herbs as undergrowth. The river valley is rocky and narrow with the steep slopes mostly covered with sand from the adjacent sand sea located to the south.

A significant result of the avifauna survey was the first record for Namibia of the *beattyi* subspecies of Lesser Masked Weaver *Ploceus intermedius*. This species occurs from eastern Africa south to northern South Africa and west to Botswana, Namibia and western Angola. In Namibia, it occurs locally from central to northern Namibia, including the Zambezi Region. In north-western Namibia, the weavers inhabit riverine vegetation along the major ephemeral rivers and the perennial Kunene River. Since the first Southern African Bird Atlas Project (SABAP1; Harrison *et al.* 1997) the species has expanded its range to reach the coast where the birds have been recorded in Swakopmund and Henties Bay (SABAP2 data & W. Swanepoel [pers. obs.])

Three subspecies are currently recognised (Oschadleus 2004, 2005):

- Ploceus intermedius intermedius from Ethiopia and Somalia to central Tanzania. Breeding males have the black
 forehead and forecrown merging with the dark brown hind crown; nape and sides of neck are golden yellow
 tinged brown; lower breast, belly and flanks bright yellow, upper breast washed brown.
- **P. i. cabanisii** from coastal Tanzania southwards to southern Africa, including Namibia and the interior of southern Angola. Breeding males differ from nominate *intermedius* in having the hind crown and breast brighter yellow, less washed with saffron.
- *P. i. beattyi* from western Angola, north of Benguela. Breeding males differ from nominate *intermedius* in that the chestnut wash on the hind crown is darker, extending over the hind neck; the chestnut wash on the breast is also darker, extending over the flanks. The chestnut wash around the mask is conspicuous (Oschadleus pers. com.).

On 29 January 2020 two male Lesser Masked Weavers were seen and photographed some 11 km upstream of the Kunene River's mouth. Their foreheads and forecrowns were black, the bills black, the eyes bluish white, and the bellies yellow – all features of the Lesser Masked Weaver. However, these birds differed from Lesser Masked Weavers normally seen in Namibia which belong to subsp. *cabanisii* (Figure 1) in that the Kunene birds had a chestnut wash around the black mask, the hind crown was chestnut, extending over the hindneck, and the breast had a chestnut wash which extended over the flanks – perfectly matching the description of *beattyi* from coastal Angola. Images of the birds (Figure 2) were sent to Dieter Oschadleus from SAFRING in South Africa, who confirmed the identity of the birds as indeed being *Ploceus intermedius beattyi* (Oschadleus pers. com.).

The finding of *Ploceus intermedius beattyi* prompted us to have a careful look at other Lesser Masked Weavers along the Kunene River and north-western Namibia. Breeding colonies were subsequently found further inland along the Kunene River at Otjinhungwa (September 2020 and April 2021) (Figure 3) and at Epupa Falls (September 2020) (Figure 4), indicating that the subspecies probably occurs all along the Kunene River, possibly as far as Ruacana (Figure 5). Breeding males from Otjinhungwa had the same features as the birds from the Kunene River mouth area although with less

pronounced chestnut colouration. Birds from Epupa lacked the chestnut wash over the flanks although some individuals still had the chestnut wash around the mask as in *beattyi*. Unlike the breeding males from these colonies, breeding males (March 2020) from the Galton Gate at Otjovasando in the Etosha National Park (200 km to the south of the Kunene River) (Figure 1b), had little if any chestnut wash on the hind crown or chest. This indicates that the birds at Otjovasando belong to *cabanisii* and might mix with birds from Epupa (and probably further upstream).



Figure 1: Ploceus intermedius cabanisii. Note pure yellow underparts and lack of chestnut wash around mask. a) Henties Bay, January 2018. b) Otjovasando (Galton Gate), Etosha National Park, March 2020. Photographs: W. Swanepoel.



Figure 2: Ploceus intermedius beattyi. a) Note chestnut wash over breast, extending to flanks. b) Note chestnut wash on the hind crown, extending over hind neck. Kunene River Mouth, January 2020. Photographs: W. Swanepoel.





Figure 3: Ploceus intermedius beattyi. Variation in extent of chestnut on crown, nape and flanks. a) Bird well-washed with chestnut (early morning light caused the effect of an orange filter). b) Bird with less pronounced chestnut wash. Otjinhungwa, Kunene River, September 2020. Photographs: W. Swanepoel.



Figure 4: Ploceus intermedius intermediate between beattyi and cabanisii. a) Bird nearer to subsp. cabanisii; note the narrow chestnut wash around the mask b) Bird nearer to subsp. beattyi; note the faint chestnut wash around mask and over breast; chestnut over flanks is lacking. Epupa Falls, September 2020. Photographs: W. Swanepoel.

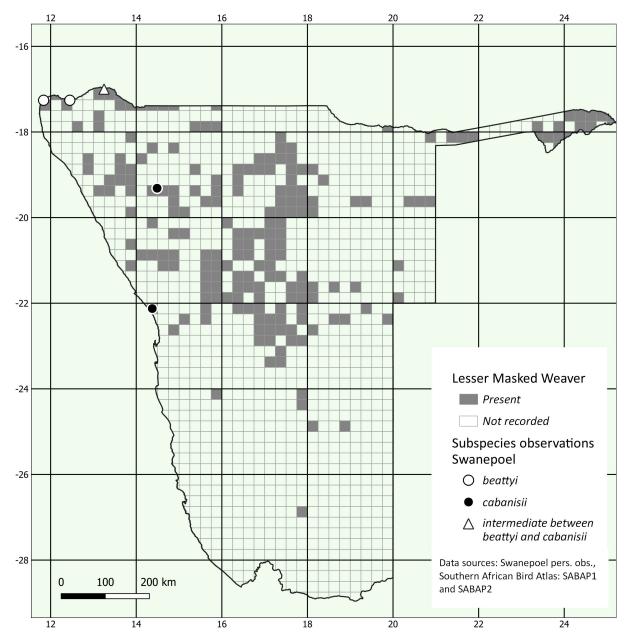


Figure 5: The distribution of Lesser Masked Weaver in Namibia and the location of records of subspecies described here.

Acknowledgements

We would like to acknowledge the European Union for funding this expedition through the SCIONA project (grant agreement FED/2027/394-802), as well as Johan van Rooyen from the Northern Namibia Development Corporation for hospitality and logistical support.

References

Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V & Brown CJ (eds) (1997) The atlas of southern African birds Vol 2: Passerines. Birdlife South Africa, Johannesburg.

Oschadleus D (2004) Lesser Masked Weaver. In: Fry CH & Keith S (eds) The Birds of Africa Vol 7 pp 142-145. Christopher Helm, London.

Oschadleus, D (2005) Lesser Masked Weaver In: Hockey PAR, Dean WRJ & Ryan PG (eds) Roberts - Birds of southern Africa 7th edition pp 1010-1011. The Trustees of the John Voelcker Bird Book fund, Cape Town.

White-crowned Shrike (Eurocephalus anguitimens) A. Smith, 1836: comparative biometrics, moult data and criteria for the determination of age

U Bryson¹, DM Paijmans²

URL: https://www.nje.org.na/index.php/nje/article/view/volume6-bryson Published online: 4th March 2022

Date received: 20th September 2021; Date accepted: 12th October 2021.

CONTENTS

ABSTRACT	2
1. INTRODUCTION	2
2. SITES AND METHODS	2
3. CHALLENGES FACED 3.1 Terminology 3.2 Age categories in the Palaearctic and in the Afrotropical Region. 3.3 Age description. 3.4 Age distinction.	3 4
4. SPECIES DETAILS 4.1 Taxonomy 4.2 Measurements	4
5. MOULT AND BREEDING	5
6.TIMING OF BREEDING AND OVERLAP WITH MOULT	5 6
7. MOULT AND DETERMINATION OF AGE	6
8. DEVELOPMENT FROM JUVENILE TO ADULT	7
9. FURTHER CRITERIA FOR DETERMINING THE AGE 9.1. Development of the front bristles and of the colouration of the bill 9.2. Feather ring around the eye 9.3. Colouration of the underparts of juvenile, immature and adults 9.4. Variation of grey or brown colouration 9.5. Wing feathers and wing moult in young and adults: shape, length, colour and density 9.6. Residual feathers from a former plumage	9 10 10 11
10. SITE FIDELITY, LONGEVITY, RECAPTURES AND GROUP COHESION 10.1. Site fidelity 10.2. Longevity 10.3. Recaptures 10.4. Group cohesion	13 13 13
11. FURTHER RESEARCH	14
REFERENCES	
Appendix 1: Site descriptions	18
Amondiy 2: Mathoda	21

 $^{^1\,}$ Becker-Gundahl-Str. 8, 81479 Munich, Germany. ursula@thomas-bryson.de $^2\,$ 22 Elizabeth Street, Hobart, Tasmania, 7000, Australia

ABSTRACT

We present measurement and moult data on the nominate subspecies of the White-crowned Shrike *E. a. anguitimens* from Namibia and South Africa and discuss plumage development through the different age groups. We compare our Namibian observations of the moult process and our records of active brood patches with breeding records (Brown *et al.* 2015) to gain a better understanding of the year's cycle of the species. For South Africa, we show the progress of moult over the months, and note an overlap of moult and breeding in both Namibia and South Africa. We found three distinct plumages in the Southern White-crowned Shrike. Based on photographic evidence, we describe in detail the plumage development through the discernible age groups, from nestling to juvenile and immature to adult and describe criteria to determine a more exact age. We discuss variation in colouration and present observations on site fidelity, longevity and other aspects. This monograph is intended to supplement published data and encourage further discussion and research on plumage, moult and breeding, social structure and site fidelity.

Keywords: age; biometrics; brood patch; white-crowned shrike; Eurocephalus anguitimens; moult; plumage; sex

1. INTRODUCTION

Species and subspecies of Namibian birds are underrepresented in research and literature of southern African birds. To help address this shortcoming, we present our observations and our measurements and moult data on White-crowned Shrike (*Eurocephalus anguitimens*; Figure 1), supplementing the information available for this data deficient species and its nominate subspecies. Additionally, we compare our Namibian moult records with breeding data in Brown *et al.* (2015) to place the moult process into the annual life cycle of the species.

We have included data collected by selected colleague ringers, who generously gave us access to their records and with whom we share the same precise method of measurement. In this article we present measurement and moult data from 55 Southern White-crowned Shrikes of the nominate subspecies *E. a. anguitimens*, 22 of them being from Namibia and 30 from South Africa. The research

was conducted under a ringing permit issued by the Namibian Ministry of Environment, Forestry and Tourism, and the South African Bird Ringing Unit (SAFRING) permit number 1240, respectively.

2. SITES AND METHODS

Our data on the Southern White-crowned Shrike in Namibia were collected mainly south of the Waterberg (Farm Hamakari), in the Erongo Mountains and the Kunene region (Figure 2). The data on the South African birds were collected in the Northern Province, close to the Botswana border.

2.1 Distribution and sites

Southern White-crowned Shrikes were ringed in **Namibia** near Otavi (19°37'S, 17°11'E), in the Erongo mountains (21°29'S, 15°52'E), near Omaruru (21°20'S, 16°04'E), at the Farm Hamakari (20°36'S, 17°20'E), along the Kunene River, and in **South Africa** at various locations in the Northern Province, mainly in D'Nyala Nature Reserve (23°44'S, 27°45'E) and Platjan (22°29'S, 28°50'E)



Figure 1: Adult Southern White-crowned Shrike. July 2003, D'Nyala Nature Reserve, South Africa.

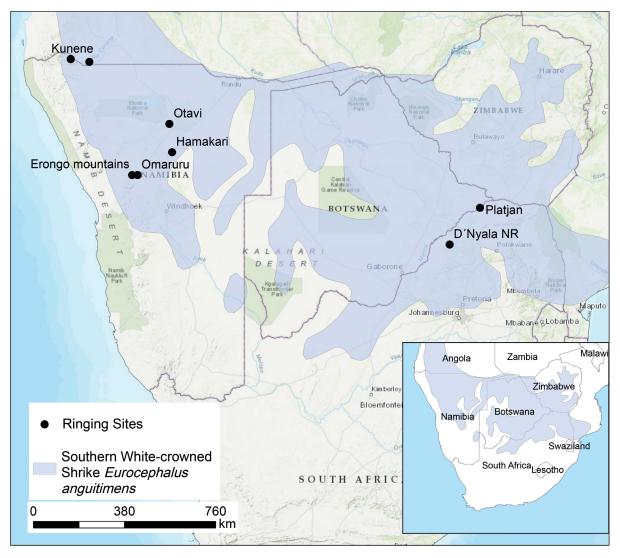


Figure 2: Distribution of the Southern White-crowned Shrike in southern Africa, downloaded from www.iucnredlist.org on 18 May 2019. Black dots designate sites where data were gathered.

(Figure 2). Site descriptions and photos are provided in Appendix 1.

2.2 Bird ringing and measurements

Birds were ringed and measured and moult scores were taken in accordance with the guidelines of the South African Bird Ringing Unit's (SAFRING) Bird Ringing Manual (de Beer *et al.* 2001, based on Svensson 1984). The birds' sex was determined, if possible, by the shape and position of the pelvic bones, by cloaca and the brood patch, while being aware of brood patches being found in helpers and smaller patches also in males.

3. CHALLENGES FACED

In Afrotropical species literature, we find considerable gaps in descriptions of plumage by age categories and a lack of more supportive criteria and precise terminology for the ageing of Namibian shrikes. Thus, we oriented ourselves on the

Palaearctic literature, concerning ageing and age development.

3.1 Terminology

In general, the terminology to describe the age of birds is far from consistent or clearly defined. Several core terms are used arbitrarily in both a general and a restricted sense. It is hence not standardised and differs across Africa and widely between the continents (Schulze-Hagen 2019). We tried to be consistent in the terms used and as clear as possible, primarily following Harris & Franklin (2000), Jenni & Winkler (2012, 2020) and Shirihai & Svensson (2018).

3.2 Age categories in the Palaearctic and in the Afrotropical Region

The description of the age of Palaearctic birds falls into categories that follow the major seasonal changes. All Palaearctic passerines breed in the northern summer and start moulting thereafter.

Through clear distinction of summer and winter, a clear distinction of the age differences of plumage can be made and named. Young birds can be categorised after calendar years, and at any stage clearly distinguished from adults based on plumage differences.

These categories cannot be simply transferred to the Afrotropical region, since breeding times are variable in many passerine species dependent on a variety of factors, mostly precipitation and the subsequent abundance of food. We use the terms juvenile, immature and sub-adult for birds in their first year of life, and the term "second year of life" for birds with features that allow, as we assume, this specification (see 7. Moult and determination of age).

3.3 Age description

For defining the exact and often approximate age of a bird, the plumages of different developmental stages of Namibian birds, and African birds in general, are not yet adequately researched and described. As first described by Stresemann & Stresemann (1966, p. 10), some species grow, before adulthood, a second set of juvenile feathers, some even a third, which changes into immature plumage during the post-juvenile moult. In some species, the post-juvenile moult sets in before the growth of the juvenile plumage is completed (Dorsch 1993). When handling Afrotropical birds, one can observe how in some species the different plumages can be well distinguished, while in others the moult progress looks more like a continuous process (pers. obs.) (as described for Palaearctic species by Roselaar, pers. com. 2021). These details of juvenile

feather growth and moult have not yet been addressed in the African literature.

3.4 Age distinction

The literature on Afrotropical birds generally does not differentiate between the two quite distinctive plumages of juvenile and immature birds, if two different plumages are described at all. For the Southern White-crowned Shrike we could identify two distinct plumages during the first year of life after the nestling age: a juvenile and, after the post-juvenile moult, an immature plumage, which we describe in this article.

A glossary of the terms used for ageing can be found in Appendix 2.

4. SPECIES DETAILS

4.1 Taxonomy

Of two southern African subspecies, only the Southern White-crowned Shrike of the subspecies *E. a. anguitimens* is found in Namibia (N and NE). It also occurs in SW and S Angola and eastwards to Botswana (except SW), in extreme S Zambia, on the central plateau of Zimbabwe, and in N South Africa (W Limpopo and N North West Provinces) (Yosef & International Shrike Working Group 2019, del Hoyo *et al.* 2016).

4.2 Measurements

Table 1 presents the measurements of our samples of the Southern White-crowned Shrike of the subspecies *E. a. anguitimens* taken in Namibia and in South Africa.

Table 1: Average measurement data (including standard deviation [SD], minimum and maximum) of adult Southern White-crowned Shrikes (E. a. anguitimens). Measurements are grouped by sex and location of adult (SAFRING Code Age 4) birds.

Grouping	Parameter	Wing (mm)	Tail (mm)	Tarsus (mm)	Culmen (mm)	Head (mm)	Mass (g)
Adults	Mean ± SD	136.4 ± 3.7	105.0 ± 3.7	25.9 ± 1.2	22.5 ± 2.9	47.5 ± 1.1	64.5 ± 5.4
SAFRING Code	Min-max	129-152	97-114	24.4-30.7	17.9-27.6	43-49.7	48.2-76.8
Age 4	n	52	51	46	46	49	51
A 1 1	Mean \pm SD	136.3 ± 4.0	104.4 ± 3.4	26 ± 1.3	21.6 ± 2.7	47.5 ± 1.3	64.3 ± 5.9
Adults Unknown Sex	Min-max	129-152	97-114	24.4-30.7	17.9-27.6	43-49.7	48.2-76.8
Ulikilowii Sex	n	41	40	35	35	38	40
A 1 1/	Mean \pm SD	136 ± 1.4	108.5 ± 6.4	26 ± 0.6	25.8 ± 0.6	47.3 ± 0.6	62.6 ± 1.8
Adult Males	Min-max	135-137	104-113	25.5-26.4	25.3-26.2	46.8-47.7	61.3-63.8
iviales	n	2	2	2	2	2	2
A 1 1/	Mean \pm SD	137.1 ± 2.8	106.6 ± 4.2	25.6 ± 0.7	25.1 ± 1.6	47.5 ± 0.3	65.7 ± 3.2
Adult Females	Min-max	133-142	101-112	24.5-26.6	21-26.3	46.9-48	61-72
Telliales	n	9	9	9	9	9	9
A 1 1/2	Mean ± SD	135.6 ± 2.8	105.4 ± 3.8	25.9 ± 0.8	23.9 ± 2.7	47.1 ± 1.2	62 ± 5.2
Adults in Namibia	Min-max	130-140	100-113	24.5-27.8	17.9-27.6	43-48.6	48.2-68
INallifola	n	22	22	19	19	22	22
A doubter in Countle	$Mean \pm SD$	137 ± 4.3	104.7 ± 3.7	26 ± 1.4	21.5 ± 2.6	47.8 ± 1	66.4 ± 4.7
Adults in South Africa	Min-max	129-152	97-114	24.4-30.7	18.1-26.8	45.9-49.7	58.3-76.8
Allica	n	30	29	27	27	27	29

Table 2: Extent of primary feather moult of adult Southern White-crowned Shrikes from Namibia. Values are average moult scores of each primary for n number of birds per month sampled. The colour gradient is shown on the side. The tail (t), head (h), body (b) and brood patch (bp) are expressed as a percentage of birds assessed showing signs of moult. Nest count values of the Southern White-crowned Shrike for Namibia are taken from Brown et al. (2015). No moult records were collected during the months marked in grey.

Month	n	P1	P2	Р3	P4	P5	Р6	P7	Р8	Р9	P10	t	h	b	bp	Nests	Moult
Jul	0															0	Score
Aug	3	0	0	0	0	0	0	0	0	0	0					0	0
Sep	1	0	0	0	0	0	0	0	0	0	0					0	
Oct	•															2	1
Nov	0															5	
Dec																6	2
Jan	1	5	4	2	0	0	0	0	0	0	0				100%	7	
Feb	4	5	5	5	4	3	0	0	0	0	0		0%	0%	50%	5	3
Mar	8	5	5	5	5	4	4	2	0	0	0	13%	0%	0%	100%	4	
Apr	0															4	4
May	0															0	
Jun	4	5	5	5	5	5	5	5	5	3	3					0	5

5. MOULT AND BREEDING

Breeding is usually followed by a complete moult, as replacing the plumage is costly. The limited energy resources are invested sequentially in the establishment of territory, mating, egg-laying, breeding and feeding the young. Moult should occur when no other activity has priority (Jenni & Winkler 2020, p. 178). Thus, moult is strongly related to breeding, and mostly indicates the actual status of the bird in its annual cycle. Similar to all sedentary shrikes, the White-crowned Shrike generally should undergo a single complete post-breeding moult (Yosef 2008). The sequence follows the normal passerine descending pattern (Tables 2 and 3).

Young Southern White-crowned Shrikes fledge about 38 days after egg-laying, following 18-20 days of incubation (20 days considered being too long by Tarboton 2014) and 19-20 days for the



Figure 3: Southern White-crowned Shrike on its nest in the Etosha National Park in August, which is a breeding event out of the recorded season for Namibia. August 2017. Photo courtesy of Billi A. Krochuk.

nestling period (Harris & Franklin 2000, Tarboton 2014).

6.TIMING OF BREEDING AND OVERLAP WITH MOULT

Moult onset varied between the Southern Whitecrowned Shrike populations in Namibia, Botswana and South Africa. The samples were small, and many variables may play a role, particularly occurrence and beginning of precipitation in different regions and years, and individual differences in the annual reproduction cycle.

6.1 Namibia

6.1.1. Nesting dates

In Namibia, egg laying has been recorded between October and April (Brown et al. 2015; Table 2). In the data base of Jarvis et al. (1999), eggs were recorded from November to early May, while the majority of records, 49 of 57, were from January to May.

We found one photographic record of an adult breeding in August in the Etosha National Park which is an exceptional early timing for the species (Figure 3).

The females in our study had fully active brood patches from the end of January until mid-March (Table 2) which corresponds with the nesting data of Brown *et al.* (2015). We did not collect data for this species in April.

6.1.2. Overlap of nesting dates and moult

At the same time we observed that the process of moult in our sample, as depicted in Table 2,

overlapped with the egg laying data of Brown *et al.* (2015).

6.1.3. Overlap of brood patches and moult

This corresponds with our findings from the months January to March when we examined ten females and males for brood patches, all of which were in moult. Of 21 adults, the moult of the first primary feather was completed in January. Five of these were displaying full brood patches, while the other five showed receding ones.

6.1.4. Post-breeding moult and brood patches in family/helper groups with young

In Namibia, we recorded family/helper groups, with one or two begging young, from the beginning of February to mid-March.

On 3 February 2010, one young bird was observed together with five adults. Three adults were ringed and showed primary moult: two with a moult score of 25 (5555410000) and one with a moult score of 20 (5554100000) (mean score 23), while the young, in partial juvenile moult, showed no primary moult. This group was not checked for brood patches.

On 13 March 2019 one begging young was seen with four adults. Two of the adults were ringed and showed a moult score of 31 (5555542000) and 29 (5555540000) (mean score 30) and still a brood patch, which we considered on our scale as "fully" active by colour, swelling and skin quality. By recording the moult, it became clear that one of them was a full, older adult, while the second must have been a younger adult, maybe a helper. (See the discussion and figures below in 9.5. Wing feathers and wing moult in young and adults: shape, length, colour and density).

This second bird showed the same quality of brood patch as the older adult, the possible dominant female. From these parallels in brood patches we formed the hypothesis that, during the breeding and fledgling period, the hormonal status in helpers corresponds with those of the egg laying and breeding birds. Active brood patches can be seen in individuals which are not the main breeders, such as males in several species (Thiede 1985, p. 118-122, pers. obs.), and in parasitising cuckoos that do not brood at all (pers. obs.).

On 4 March 2020, from a group of eight adults and three young, six adults and two young, were ringed. All adults were moulting the wing, five with decreasing, one with still fully expressed brood patch. Two individuals had four new primaries, four individuals six, and one seven primaries fully replaced (moult scores from 26 to 39, mean score 32).

6.2. Botswana

For northern **Botswana**, Traylor (1965, p. 369) reported that "breeding appeared [to be] over in mid-January" and that wing and tail moult was half completed. This is when the nesting records for the Namibian birds start to peak, and when the birds in our sample had completed the moult of their first primary feather (Table 2).

Skinner (1995 in Dean 2005) collected eight breeding records from October to January, and again one for April. This sequence of timing can be understood with rainfall starting later the further west and south, and thus the length of time it takes from the start of the rainy season to achieve a certain cumulative amount of rain. In higher rainfall areas the amount of rain effective enough to trigger breeding is achieved more quickly - often in the first month. In more arid areas it may take two or three months of cumulative rain to reach the "effective" tipping point - which compounds the delay in breeding (Chris Brown, pers. com. 2021).

6.3. South Africa

In the NE of South Africa, where both southern African subspecies occur (*E. a. anguitimens* in the west and *E. a. niveus* in the east), Tarboton *et al.* (1987, p. 237) recorded egg-laying only in October, November and December. More recently Tarboton (2014) notes that the laying dates are mainly October to December with extension from September to April, earlier than in Namibia. We noted in our study that the primary moult in **South African** birds also started earlier than in Namibian birds (compare Table 2 and Table 3). Here too, our moult data show an overlap of moult with the breeding data of Tarboton (2014), like in our Namibian sample.

Our sample of moulting Southern White-crowned Shrikes in South Africa is small and prone to reduced statistical significance when one individual shows irregular moult. The overall pattern matches the findings from Namibia, with breeding in the southern summer months and the usual post breeding moult starting during the breeding activity. No moult has been observed during the southern winter months (August/September and July/August). These samples of breeding and moult are very small and more research is needed.

7. MOULT AND DETERMINATION OF AGE

The plumage and moult features particularly, give clues about the age of a bird.

First year phases and corresponding plumages in typical shrikes (Laniinae) are: nestling, juvenile, post-juvenile moult (Cramp & Perrins 1993, p. 443) and post-juvenile plumage, which we call immature

Table 3: Extent of primary feather moult of adult Southern White-crowned Shrikes of the subspecies E. a. anguitimens from South Africa. Values are average moult scores of each primary for n number of birds per month sampled. The colour gradient is shown on the side. No moult records were collected during the months marked in grey.

Month	n	P1	P2	Р3	P4	Р5	Р6	P7	Р8	Р9	P10	t	h	b	bp	Nests	Moult
Jul	17	0	0	0	0	0	0	0	0	0	0						Score
Aug	1	0	0	0	0	0	0	0	0	0	0						0
Sep	0																
Oct	0																1
Nov	2	3	4	3	1	0	0	0	0	0	0						
Dec	0																2
Jan	2	5	5	5	5	4	1	0	0	0	0						
Feb	3	5	5	5	5	5	4	2	1	1	0						3
Mar	0																
Apr	0																4
May	0																
Jun	0																5

plumage following Harris & Franklin (2000, p.50). Passerines reach adulthood and maturity when entering their second year of life (Bub & Dorsch 1988, p. 7).

In their first year, young Southern White-crowned Shrikes are clearly distinguishable as non-adults by the colouration of bill and gape flange, plumage features (colour, quality, density, existing abrasion and wing moult limits or lacking thereof, shape of wing and tail feathers) and other features like leg colour and quality of the skin, softness of the skeleton, behaviour and wear of the bill.

With a complete moult of birds of all ages after the breeding period of the adults, generally young passerines tune into the moult cycle of adults, although with much variation.

Occasionally, residual feathers of the juvenile plumage can be found in a freshly moulted adult bird. These indicate the age, the second year, of this individual. From the third year on, it appears that the features of the plumage can no longer be used to identify the exact age of Southern White-crowned Shrikes.

8. DEVELOPMENT FROM JUVENILE TO ADULT

All the photographs below if not otherwise credited were taken by the authors and show Southern White-crowned Shrikes (*E. a. anguitimens*).

8.1. First year

First year development is only occasionally described for passerine species in southern Africa. This includes the time frames in which young Southern White-crowned Shrikes pass through the different phases and plumages over the first year, and how the plumage develops through the months.

The sequence in which the different areas of plumage are moulted during ageing has yet to be examined, and whether there is a determined sequence at all.

Harris & Franklin (2000, p. 140) describe juvenile and immature plumage of the White-crowned Shrike, both descriptions being merged in Dean (2005). It appears that in the White-crowned Shrike the transition from juvenile to adult plumage is a continuous one (pers. obs.). This concurs with Palaearctic Laniinae as stated by Cramp & Perrins (1993, p. 443) and Kees Roselaar (pers. com. 2021) who describe the post-juvenile moult of Palaearctic Laniinae as "very gradual", starting "shortly after fledging", while later growing feathers are "progressively resembling adult breeding plumage more closely." See more details on this transition in Jenni & Winkler (2020, pp. 43-45).

During this development from juvenile and immature, the age of the Southern White-crowned Shrike is recognisable by such features as the beak colour, the colouration and extent of the gape flange, the extension of the black ear coverts, and the colour and growth of the bristles above the beak. Additionally, the crown of the head and underbelly change colour.

8.1.1. Juvenile age

The juvenile plumage is described in Harris & Franklin (2000, p.140) as brown with pale ashbrown head and back and cream coloured nape and underparts. The brownish-black face mask is still much reduced and lacks the dark ear coverts, while the bill is pale. We observed that the nestling shows a light-yellow bill and a light brown chest well divided from a white belly (Figure 4). It seems that these differences belong to different stages in the development of the juvenile. Of interest might be studies about the possible second and third set of

juvenile feathers (Gwinner 1969, Berthold *et al.* 1970, p. 311, Dorsch 1993), and the result in the phenomenology of the birds.

When out of the nest, the juvenile bird acquires continuously more and more adult features: a darker bill, bristles on the forehead, which are still dark, first markings of the black mask and of a white chest. We estimate, by gape flange, beak



Figure 4: The nestling, about two weeks old and still in the nest, shows a dark mask, grey cap, buff chest and belly, white underbelly, dark brown wings, orange-yellow beak and protruding bright orange gape flange. Etosha National Park, November 2016. Photo courtesy of John Drummond.



Figure 5: A juvenile in transition to immature plumage during its post-juvenile moult. The cap is mainly moulted from grey to white, the first black ear coverts are appearing, throat and chest show the immature, and later adult, white feathers, while the belly is still mainly juvenile ash brown. February 2010.

colouration, plumage features and behaviour, that the birds shown in Figures 5 and 6 were only a few weeks old. The sequence of the body areas undergoing moult and the exact allocation of plumage to determine the age will be possible only through continuous observation.

8.1.2. Post-juvenile moult and immature age

Immature birds have passed their post-juvenile moult, but still show features of young birds in the first year of life (Figure 7).

With growing age, the gape flange recedes, and the bill gains a uniform blackish colour. Main plumage features which distinguish this age group from juveniles are the black ear coverts and the white bristles above the beak. The white chest and brownish underbelly show a distinct contrast, and the median coverts start moulting (Figure 8).

8.2. Adult

Passerines older than one year, with predominantly final plumage, are called adult birds (Bub & Dorsch 1988, p. 7). Adult White-crowned Shrikes display a brown, white and blackish plumage (Figure 9) although variations occur. During proceeding age, certain features become more expressed (for example the black frontal bow of the wing in male Cape Sparrows *Passer melanurus* pers. obs.), while





Figure 6: (A) Under- and (B) upperparts of two juvenile White-crowned Shrikes with brown plumage, buffy edged tail feathers, wing with buff fringes on primaries, secondaries, primary coverts and mantle feathers; still lacking dark ear coverts; yellow gape, beak dark horn with lighter base. March 2020 and February 2010.

other features fade away due to the hormonal processes in advanced age (for example the red colouration of the breeding male of the Southern Red Bishop (*Euplectes orix*).

At this point of knowledge and research, we can only hypothesise that the differences in adult plumage are related to the age of the bird, in our understanding between second year and older birds. Other hypotheses extend to the dominance in the group, which again, could be related to age, rank and the breeding experience of the individuals.



Figure 7: First year bird in transition to adult with receding gape flange and white bristles on the forehead. The uniformly coloured bill is still horn, not black as in immatures and adults, the dark neck band is developing. A distinction of white upper and light brownish underbelly is visible. Botswana, February 2006. Photo courtesy of Grant Reed.



Figure 8: First year bird after its post-juvenile moult: the two dark and only thinly fringed new inner median coverts contrast clearly in colour and abrasion from the neighbouring coverts. The crown is now all white and well formed, as are the fresh black ear coverts with a few tiny whitish residual juvenile feathers in between. The front bristles are almost all white, but still short, the bill is still not black. Waterberg, Namibia, May 2019. Photo courtesy of Augusto Faustino.

9. FURTHER CRITERIA FOR DETERMINING THE AGE

For the White-crowned Shrike we document with photographic evidence the development of the front bristles and of the colouration of the bill. The subsequent features, too, were identified during our field observations and for further discussion and research: the feather ring around the eye, the colouration of the underparts, the variation of grey and brown colouration, shape, length, colour and density of wing feathers and residual feathers from a former plumage.

9.1. Development of the front bristles and of the colouration of the bill

With the birds in the hand, we could feel the feather structure above the bill towards the crown. Adult Southern White-crowned Shrikes as well as adult Magpie Shrikes (*Urolestes melanoleucus*) have stiff bristles. In juveniles, these bristles are dark and softer, in adults white and hard, possibly increasing in length with age (Figures 10A and 10B).

In fledglings, the bill is orange yellow (Figure 4), while in juveniles it turns horn coloured, often with darker tip (Figure 10A). In adults, the bill is fully black (Figure 10B).

9.2. Feather ring around the eye

The white ring of tiny feathers around the eye (orbital feather ring), is absent in juveniles. First, the upper half grows, then the feathers behind and below the eye. It is never a complete circle. We counted in full adults mostly seven or eight white feathers in the back of the lower half, which might create a quarter of a circle, while presumably younger adults throughout showed only a few of these feathers (Figure 11). It is unclear at what age the growth is completed (Figure 12).



Figure 9: Adult White-crowned Shrikes in early February in post-breeding moult in plain, light and dark brown and white plumage with black bill and face mask, white, long front bristles and plain wing. The median coverts and the alula are already moulted, as are some primaries. Primary moult score 22 (5554300000). Otavi, Namibia, February 2005.

In the process of moulting, the orbital feathers are replaced and thus cannot serve as an additional criterion for ageing during this time (Figure 13).

9.3. Colouration of the underparts of juvenile, immature and adults

We observed that the underparts are changing in colouration throughout the first year from a light brown chest with white belly in the nestling (Figure 4) through a uniform grey-brown underbelly in juvenile (Figure 6A) to a white chest, creating a clear contrast to the ash-brown underbelly in immatures (Figures 14A and 14B), which appears to darken with age (Figure 15).

Adults do not show strongly contrasting edges of the wing feathers, but mostly a plain wing and a continuous band from the mask over the neck to the mantle (compare the immature from Figure 14B with the adults from Figure 15). We hypothesise that the intensity of the underbelly might be a sign of age, thus 15A being a second year bird with pale and 15B being an older adult with clearly brown underbelly. See also the discussion below in 9.4. Variation of grey and brown and 9.5. Wing feathers and wing moult in young and adults.





Figure 10: Comparison of (A) a juvenile in transition to immature and (B) an adult Southern White-crowned Shrike. The juvenile is in post-juvenile moult with bright yellow gape flange and horn coloured bill; head white with remaining brown juvenile feathers and very first feathers of immature black ear coverts and mask; front bristles dark. The adult has a black bill, a white crown, black lores and ear coverts, a brown neck, a white throat, and white front bristles. Compare also the smooth, shiny surface of the bill in the juvenile with the battered one of the adult, and the shape difference of head and bill. February 2005.

9.4. Variation of grey or brown colouration

Adults show almost plain lighter backs and plain darker wings with thin light edges on the feathers, best visible from close by. The mask is blackish, the crown white, the bill jet black.

We observed a colour variation between brownish and greyish individuals (as in Figures 16A and 16B). More research is needed to define if this variation is due to age, season and wear and moult, genetics, group or individual differences, sun bleaching or other causes.

During further studies, at the same location, during the same ringing session and in the same group, we found substantial colour variations in two adults (Figure 17). This raised the question of this being the possible expression of two different age groups. The moult progress was almost identical (with primary moult score of 29 and 31 (Figure 17). See also the discussion in 9.5. Wing feathers and wing moult in young and adults.

It would be interesting to follow these individuals through longer time periods to see if the colour is a constant feature or if is subject to change.

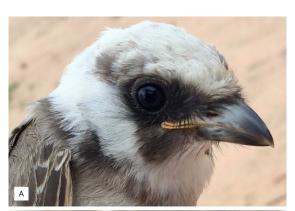




Figure 11: Comparing the orbital feather ring: (A) Juvenile, still without orbital white feathers. March 2020. (B) Adult with three growing orbital feathers in the lower half. This is presumably a second year bird, since one residual median covert from the first year is still present after a complete moult. Both Waterberg area, Namibia, March 2019.

9.5. Wing feathers and wing moult in young and adults: shape, length, colour and density

The overall view of the wing and the features of its feathers hold information for determining the age of a bird. These features are signs of moult, like moult limits or lacking thereof; contrast of colour between feather groups or individual feathers; bleaching, abrasion and general wear; the quality, mainly the density, of the individual feathers and the shape of the wing and the tail feathers.

In juvenile and immature Southern White-crowned Shrikes, the fringes and tips of all coverts and the



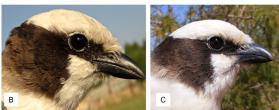


Figure 12: (A) Compare the presumably young adult (from Figure 10A) showing two tiny white orbital feathers in the lower half with two fully grown adults, with more complete orbital feathering. Waterberg area, Namibia, March 2020. (B) Otavi, Namibia, February 2005. (C) Hoedspruit, South Africa, July 2010. Photo courtesy of Kobie Raijmakers.



Figure 13: We ringed this adult during its complete moult in mid-February. The alula is moulting (2-0-1), as is the wing with primary moult score 25 (5555410000). Some coverts, now dark, have been replaced. Of the lower orbital feathers just one was fully grown, while the one further up was in pin. Erongo, Namibia, February 2010.

tips of the remiges are distinctly contrasting, while in adults the fringes are expressed only slightly.

During the nestling and juvenile development, the whole wing grows quickly.

Consequently, the feathers are similar in colour, shape, size and state of abrasion. The feathers on the brownish rump are fringed buff (Figure 18). Additionally, the wing shape seems to change with age: Before adulthood, the outer primaries are considerably longer than the inner primaries (compare Figures 18 and 19 for juvenile vs. adult wing).

In adults, we did observe noticeably different moult features during the same month.

From a family/helper group in mid-March 2019, with one young still being fed, two fully grown birds were caught. Although the primary moult scores were close, 29 and 31, the wings showed major differences, which made us hypothesise about two different age groups (Figures 20A and 20B). Considering its plumage features, we presume that 20A is a second year bird, while 20B appears to be an older adult.





Figure 14: Comparison of the colouration of the underparts of two first year birds: (A) Underparts of a still begging juvenile with soft, loose feathers: pale brown from the white throat to the tail coverts. March 2020, Waterberg area, Namibia. (B) Underparts of an independent, self-feeding immature, age determined by the prominent fringes on the ends of the coverts, the completely white chest and clearly separate pale grey-brown underbelly; bill all blackish, still with thick, by now darkening, gape flange. Etosha, Namibia, July 2004. Photo courtesy of Augusto Faustino.

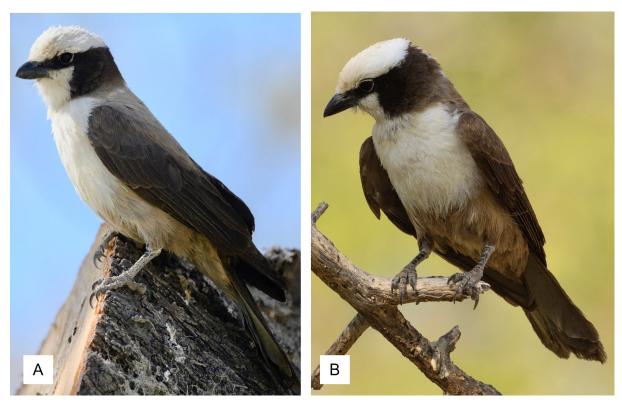


Figure 15: Comparing the underparts of two adults from end of August: (A) with pale and (B) with darker, well contrasting brown underbelly. Etosha National Park and Oshikoto, Namibia, August 2019. Both photos courtesy of Peter Hawrylyshyn.





Figure 16: Comparison between two adult Southern White-crowned Shrikes: (A) Adult with brown plumage and a distinctive brown underbelly vs. white chest in post-breeding moult. March 2020, Botswana. Photo courtesy of Grant Reed. (B) Presumably younger individual with grey plumage. Mokuti Lodge, Oshikoto, Namibia, August 2017. Photo courtesy of Billi A. Krochuk.

In the open wing one can see the differences of shape and colour of the primaries and secondaries, including the tertials: Compared to 19B, the bird of Figure 19A shows paler unmoulted primaries (P7 to P10) while the already moulted primaries (P1 to P6) are more pointed and slimmer. Especially the secondaries, including the tertials, show



Figure 17: Two adults from the same family/helper group: (A) with brown and (B) with greyish overall plumage. Both Waterberg area, Namibia, March 2019.

considerable difference in shape, becoming broader and rounder with age. Also, the moulted remiges of 20A are still more transparent and don't yet have not yet the dark colouration of the second bird. It is known that the typical juvenile wing shows in most passerines "slim and pointed" versus "broad and round" remiges in adults, while a great variation of these expressions is possible (Pascal Eckhoff, pers. comm. 2021).

9.6. Residual feathers from a former plumage

In migratory Laniinae, we quite often find residual feathers in the freshly moulted plumage, which help to determine the birds first two years of life. From the third year on, plumage differences seem to have abated, so that a precise ageing is no longer possible.

Although not as common as in the migratory Laniinae, which are subject to a stricter time regime due to the migratory windows, we found old feathers in a fresh plumage, mainly in the lesser coverts.

10. SITE FIDELITY, LONGEVITY, RECAPTURES AND GROUP COHESION

All our data refer to small samples and thus give only a first view into this quite unexplored field of the White-crowned Shrike.

10.1. Site fidelity

Southern White-crowned Shrikes are sedentary (Lefranc & Worfolk 1997). This reflects in the records of recaptured birds in the SAFRING database: Out of 460 individuals ringed prior to 2020, 19 were retrapped. All but three were found at the very same location as the first ringing. One had moved an astonishing 392 km in 141 days, one 5.5 km in 980 days, and one was recovered 253 km from the ringing site after 849 days.

10.2. Longevity

Three birds were refound in the first seven days, five in the first year, four in the second and third year, one in the fourth, two in the fifth year and finally one after six years and 2 months (2,248 days).

10.3. Recaptures

Four of the 19 were recaptured twice, all at the original site. The bird with the SAFRING ring number 594922 after 352 and 2,248 days, number 4A17216 after 371 and 1,140 days, number 4H47937 after 1,773 and 1,774 days, and number D93836 after 713 and 857 days.

10.4. Group cohesion

Two individuals ringed together on 17 January 2002, Safring ring number D49154 and D49155, were both retrapped at the same location seven months later, on 31 August 2002.



Figure 18: Wing of a juvenile, the same individual as in Figure 6B, with uniformly coloured, only slightly abraded primaries, secondaries and coverts with contrasting fringes and tips and pointed, fringed tertials. The feathers on the rump still show lighter coloured fringes. February 2010



Figure 19: Compare the wings of these two individuals which were ringed on the same day in mid-March and belonged to the same group. (A) This wing of a possibly second year bird shows a moult score 29 (5555540000), secondary moult (410455) and tertial moult (5-1-1). (B) This wing shows a presumably older adult of unknown age with primary moult score 31 (5555542000), secondary moult (540005) and completed tertial moult (5-5-5). The moulted primaries and secondaries, including the tertials, are visibly broader and rounder than in (A). Also, the feathers are darker and less transparent, which hints to a higher feather density, a sign of an older bird. Both Waterberg, Namibia, March 2019.





Figure 20: Comparing the coverts of two birds out of the same family/helper group, ringed at the same day. (A) Example of pale and worn residual feathers in the lesser coverts from the former first year plumage. This fact indicates that this individual is in its second year, as does the low number of orbital feathers. (B) Uniform coverts of a presumably also second year bird. Both Waterberg area, Namibia, March 2020.

11. FURTHER RESEARCH

Much is still unknown about this species and for a fuller understanding further research is needed on issues like the occurrence of moult over the course of a calendar year; the overlap of moult and breeding; residual feathers from a former plumage; the feather ring around the eye; the development of wing feathers to full adulthood; the colouration of the underparts and factors for differences in the overall tone of the plumage colouration; the plumage and the feather quality of second year birds; the development of well distinguished plumages vs. a continuous moult progress, the sequence of the body areas undergoing moult. Furthermore, questions about the social structure of this species need research concerning hierarchy in the family groups, the age of the helpers (second year birds or older adults), breeding pair fidelity, duration of group cohesion, site fidelity and longevity.

ACKNOWLEDGEMENTS

We are thankful to many people who supported us in many ways: Pascal Eckhoff from the Museum of Natural History, Berlin, for discussions on moult; Raffael Winkler, Lukas Jenni, and Kees Roselaar for kindly sharing their expertise on moult; Mark Boorman, Joseph Heymans, Kobie Raijmakers and Shonie Raijmakers for photographs and data on measurements and moult. Our thanks go toJohn Drummond, Augusto Faustino, Pete Hancock, Peter Hawrylyshyn, Billi A. Krochuk, and Grant Reed from Letaka Safaris who generously ceded their photos for our studies and for publication; to Holger Kolberg from the Ministry of Environment and Tourism (MEFT), Windhoek, for the data from the Namibian Avifaunal Data Base; to Kim Hunt from SAFRING for providing the data on recaptures; and to the librarians Janine Dunlop and Phelisa Hans from the Niven Library in the FitzPatrick Institute of African Ornithology at the UCT for supplying us fast, efficiently and friendly with all the literature we had asked for. We also want to express our gratitude to the Namibian farmers who generously hosted us during our studies, allowing us to move and catch freely on their properties, especially Sabine and Wilhelm Diekmann from the Farm Hamakari, Birgit and Winnie Ritzdorf from the Farm Dabib and the owner of the Erongo Wilderness Lodge. The research was done under the South African Bird Ringing Unit (SAFRING) permit number 1240 and all birds were captured and handled under a ringing license issued by the Namibian Ministry of Environment, Forestry and Tourism (Enquiries: Holger Kolberg).

REFERENCES

de Beer SJ, Lockwood GM, Raijmakers JHFA, Raijmakers JMH, Scott WA, Oschadleus HD, Underhill LG (2001) The bird in the hand. In: *SAFRING bird ringing manual*: 44–66. Online: https://safring.birdmap.africa/downloads/ringers-manual.pdf.

Berthold P, Gwinner E, Klein H (1970) Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, Sylvia borin, und eines weniger ausgeprägten Zugvogels, S. atricapilla. *Vogelwarte* 25: 297–331. Online: https://www.zobodat.at/pdf/Vogelwarte_25_1970_0297-0331.pdf.

Brown C, Bridgeford P, Braine S, Paxton M, Versfeld W (2015) Breeding data on the birds of Namibia: laying months, colony and clutch sizes and egg measurements. Online: http://oo.adu.org.za/content.php?id=185. [Accessed 16 September 2018].

Brown C, Franke-Bryson U (2016) The use of brood patches in birds to estimate the approximate date of egglaving. *Lanioturdus* 49(3): 14–16.

Bub H (1981) Kennzeichen und Mauser europäischer Singvögel. Stelzen, Pieper und Würger (Motacillidae und Laniidae). Ziemsen, Wittenberg.

Bub H, Dorsch H (1988) Kennzeichen und Mauser europäischer Singvögel. Cistensänger, Seidensänger, Schwirle, Rohrsänger. (Cisticola, Cettia, Locustella, Acrocephalus). Ziemsen, Wittenberg.

Clancey P (1965) Variation in the White-crowned Shrike Eurocephalus anguitimens Smith 1836. Arnoldia 1(23): 1-3

Cramp S, Perrins C (1993) Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic. Flycatchers to shrikes. Royal Society for the Protection of Birds. Oxford University Press, Oxford.

Dean W (2005) Southern White-crowned Shrike (White-crowned Shrike) *Eurocephalus anguitimens*. In: Hockey

- P, Dean W, Ryan P (eds) *Roberts Birds of Southern Africa*, 7th ed.: 730–731. Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Dorsch H (1993) Zur Entwicklung der dritten Federgarnitur bei Jungvögeln einiger Passeres-Arten. Development of the third set of body feathers for young birds of several Passeres species. *Vogelwarte* 37: 19–25.
- Duquet M, Reeber S (2020) Die Mauser. Das Praxisbuch für Ornithologen, 1st ed. Haupt, Bern.
- Grimes LG (1976) The occurrence of cooperative breeding behaviour in African birds. *Ostrich* 47(1): 1–15. Online: https://doi.org/10.1080/00306525.1976. 9639530.
- Gwinner E (1969) Untersuchungen zur Jahresperiodik von Laubsängern. *Journal für Ornithologie* 110(1): 1–21. Online: https://doi.org/10.1007/BF01671132.
- Harris T, Franklin K (2000) Shrikes and Bush-shrikes. Including wood-shrikes, helmet-shrikes, flycatcher-shrikes, philentomas, batises and wattle-eyes. Christopher Helm, London.
- del Hoyo J, Collar N, Christie D, Elliott A, Fishpool L, Boesman P, Kirwan G (2016) *HBW and BirdLife International Illustrated checklist of the birds of the world. Passerines*. Lynx Edicions in association with BirdLife International, Barcelona.
- Jarvis A, Robertson A, Brown C, Simmons R (1999) Namibian Avifaunal Data Base, unpublished. National Biodiversity Programme. Unpublished report: Ministry of Environment and Tourism (MEFT). Maintained by Holger Kolberg, Windhoek.
- Jenni L, Winkler R (2012) Moult and ageing of European passerines, 2nd edition. Christopher Helm, London.
- Jenni L, Winkler R (2020) *The biology of moult in birds*. Helm, Bloomsbury, London.
- Kasparek M (1981) Die Mauser der Singvögel Europas. Ein Feldführer. (The moult of the passerines of Europe. A fieldguide.). Dachverband Deutscher Avifaunisten, no location

- Lefranc N, Worfolk T (1997) Shrikes. A guide to the shrikes of the world. Pica Press, Sussex.
- Pittaway R (2000) Plumage and moult terminology. *Ontario Birds* 18(1): 27–43.
- Schulze-Hagen K (2019) Oskar Heinroth, Erwin Stresemann und die Geschichte der Mauserforschung (Oskar Heinroth, Erwin Stresemann and the history of research on moult). *Vogelwarte* 57: 1–12.
- Shirihai H, Svensson L (2018) Handbook of Western Palearctic birds. Passerines: Larks to Phylloscopus warblers. Helm, London.
- Skinner N (1995) The breeding seasons of birds in Botswana 1: Passerine families. *Babbler* 29/30: 9–23.
- Stresemann E, Stresemann V (1966) Die Mauser der Vögel (The moult of birds). *Journal für Ornithologie* 107. Sonderheft (Special volume).
- Svensson L (1984) *Identification guide to European passerines*. Stockholm.
- Tarboton W (2014) Roberts nests and eggs of southern African birds. A comprehensive guide to the nesting habits of over 720 bird species in southern Africa. The Trustees of the John Voelcker Bird Book Fund, Cape Town
- Tarboton W, Kemp M, Kemp A (1987) *Birds of the Transyaal*. Transyaal Museum, Pretoria.
- Thiede W (1985) Der Brutfleck. In: Bub H (ed) Kennzeichen und Mauser europäischer Singvögel. Allgemeiner Teil: 111–137. Ziemsen, Wittenberg.
- Traylor MA (1965) Birds of Barotseland and Bechuanaland. *Ibis* 107: 137–172.
- Yosef R (2008) Laniidae (Shrikes). In: del Hoyo J, Elliott A, Christie D (eds) *Handbook of the Birds of the World*. 13: 732–773. Lynx Edicions, Barcelona.
- Yosef R, International Shrike Working Group (2019) Southern White-crowned Shrike *Eurocephalus* anguitimens. Online: https://www.hbw.com/node/ 60497. [Accessed 17 April 2019].

APPENDIX 1: SITE DESCRIPTIONS

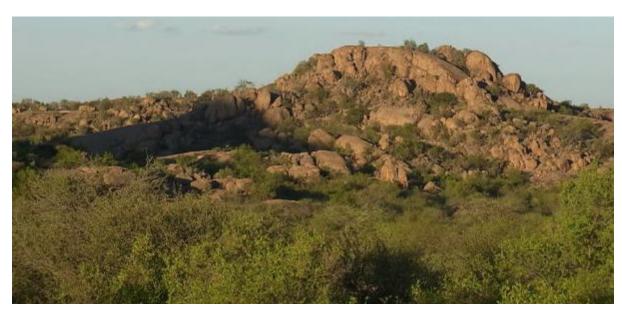
The locations are sorted by country, then in alphabetical order. Site descriptions and dates are noted below each photograph.

1.1. NAMIBIA

1.1.1. Erongo Mountains (21°29'S, 15°52'E)



Landscape 1: Arid savanna with dry riverbeds after good rains. March 2017.



Landscape 2: Mountain valley in the Erongo Mountains. January 2016.

1.1.2. Farm Hamakari, south of the Waterberg (20°36'S, 17°20'E)



Landscape 3: Savanna and mixed woodland. February 2019.



Landscape 4: Riverine growth. February 2019.

1.1.3. Kunene region

Otjitafel (17°11'S, 13°35'E) Hippo Pools (17°24'S, 14°13'E) Ehomba (17°30'S, 13°49'E)

1.1.4. Otavi, Farm Dabib (19°37'S, 17°11'E)



Landscape 5: Savanna, brushland-woodland mixture and grassland. June 2007.

1.2. SOUTH AFRICA

1.2.1. D'Nyala Nature Reserve (23°44'S, 27°44'E)

Savanna and mixed woodland.

APPENDIX 2: METHODS

For more detailed descriptions see Svensson (1984) and de Beer et al. (2001).

2.1. MEASUREMENTS

The following biometric measurements were taken:

Wing: Stop rule used to measure longest extent of the flattened wing (mm).

Tail: Rule used to measure from the tip of the rectrices to the root of the central pair (mm). **Head:** Callipers were used to measure from the back of the head to the tip of the beak (mm).

Culmen: Callipers were used to measure from the skull to the tip of the beak (mm).

Tarsus: Callipers were used to measure from the notch of the intertarsal joint to the end of the tarsometatarsal

bone, bending the foot downwards to approximately 90 degrees to the tarsus (mm).

Mass: An electronic gem scale was used (to the nearest 0.1 g).

For biometric measurements, recaptures were not reported.

2.2 MOULT

The following moult scores were recorded whenever possible:

Active moult of the 10 primary feathers, given by a score of 0 to 5. Active moult of head, tail and body, based on absence or presence of moult (yes/no).

2.3 SEX

Sex was determined by distance and shape of the pelvic bones, existence and size of a brood patch, and, if possible, by the cloacal shape. When the **brood patch** was scored, it was determined as absent, or during its development, as starting, full and post-breeding. For the determination of sex, we used only the data of a fully developed, active brood patch.

The brood patch is likely to develop shortly before incubation starts, in females always, but also in males to an extent that, often but not always, corresponds with their active participation in breeding. The brood patch lies between the two ventral feather tracts (*pterylae*) and is not feathered or only irregularly with downs (*apteria*) (Duquet & Reeber 2020, p. 20, Thiede 1985, p. 112). The skin of the area, on which the bird has contact with the eggs, falls naked and looks swollen, as it thickens and non-inflammatory oedema develop, and, as the blood vessels increase in size and number, the skin turns dark red. When the young have hatched, the area starts returning to normal conditions. The naked patch shrinks, the skin becomes paler and finely wrinkled; then dry scales appear. Shortly after fledging of the young, the skin has returned to normal, while the new feathering on the belly will occur only during the next complete, post-breeding moult, which might start soon after breeding (Svensson 1984, p. 38-39, and pers. observations).

From the quality of a brood patch the timing of breeding can be estimated and calculated (Brown & Franke-Bryson 2016).

For more information on the position, timing, functions and other details see Thiede (1985).

2.4 AGE

2.4.1 General determination of age

Age was determined by plumage features (colour and pattern of feathers; moult features, abrasion, feather quality, shape of remiges and rectrices, colour and development of frontal bristles); beak colouration, shape and wear; gape flange colour, extent and quality; leg skin colouration and its softness/dryness, and mainly by a combination of the above features.

Feather quality

The first plumage, in its first and second feather generation, is often still of lower quality. This shows in more transparency of the flight feathers and shafts less stiff than those of adult birds. The body plumage is less dense

and smooth, but softer and more uneven. The barbs of the individual feathers are looser. On the head, chest, flanks and rump the feathers are fluffy ("hairy"), and thinner and shorter in the neck.

Even in second year birds, the plumage quality seems still lower than in older adult birds. We deduct this from the observed density of feathers and the more intense wear and bleach of our presumably second year birds compared to full adults. It would need specific research to confirm or reject this hypothesis.

2.4.2 Glossary for ageing and moult

The glossary is a summary, among others, of Stresemann & Stresemann (1966), Bub (1981), Kasparek (1981), Shirihai & Svensson (2018). See there for more details, or also Jenni & Winkler (2012).

"Adult" describes a mature bird with clearly defined plumage. This term corresponds to the SAFRING ageing code of 4.

"Juvenile" refers to an individual with its first feathered plumage after down plumage, or as Pittaway (2000) puts it: "Juvenile has a precise meaning: It is the first immature plumage."

In the process of acquiring their final plumage, birds can grow a **second generation of juvenile plumage** (Bub 1981, p. 119, Jenni & Winkler 2012, p. 29). In a more general sense, as often found in the literature, the term "juvenile" is also used to distinguish young from adult plumage.

"Partial moult" refers to the moult of only parts of the plumage, mostly of the body or contour feathers, without the greater feathers of tail and wing.

"Complete moult" means that the whole plumage is being replaced, including the remiges and rectrices.

"Post-juvenile moult" refers to the first moult of a bird, when the plumage, grown during nestling and juvenile period, is moulted. This moult may start even before the juvenile plumage is fully grown. It can be partial or complete, though seems to be consistently partial in the Laniinae. The following plumage is generally the immature one which is similar to the adult plumage but still shows features of a younger bird like lighter fringes and tips or generally fainter colouration.

"Immature" describes a young bird of unspecified age, but still not adult. This term is used to describe a variety of plumage stages following juvenile plumage sensu stricto. It can include the juvenile stage if the precise age is not known (Harris & Franklin (2000, p. 50).

We used the term strictly for a distinct plumage after the juvenile plumage with its possible two or three growth phases.

"Sub-adult" describes the last stage of the immature plumage before reaching full adulthood.

2.5 SAFRING CODES

Age 0 = Age unknown

Age 1 = Pullus

Age 2 = Juvenile

Age 3 = Immature

Age 4 = Adult

Age 5 = 0 to 1/2 year

Age 6 = 1/2 to 1 year

Age 7 = 1 to 2 years

Age 8 = 2 to 3 years

Age 9 = > 3 years