Foraging ecology of Kelp Gulls in natural and anthropogenically modified environments

By:

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As I watched the seagulls, I thought, that's the road to take, find the absolute rhythm and follow it with absolute trust.

Nikos Kazantzakis

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DECLARATION:

In accordance with Rule G5.6.3, I hereby declare that the above-mentioned thesis is my own work and that it has not previously been submitted for assessment to another University or for other qualification.

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Abstract

Humans are having a profound impact on the natural environment through a myriad of activities, such as land use change or direct exploitation of resources. Some species are able to adapt to these changes and thrive in deeply modified environments. They are often considered winners of global change. Among these are Kelp Gulls *Larus dominicanus* in South Africa, which have a generalist foraging nature. Despite their abundance and potential role in the ecosystem, knowledge on their foraging ecology is limited, with no understanding of the role of natural and anthropogenic food resources during breeding. The aim of this thesis was to assess the foraging movements, diet and health of Kelp Gulls breeding in seven different colonies varying in proximity to landfills. GPS loggers were deployed on incubating adults to assess foraging trip patterns, effort, and habitats. Diet and trophic ecology of adults and chicks was determined during the breeding season by combining conventional diet analysis (i.e. stomach content samples and regurgitated pellets) with stable isotope analysis of blood plasma. Finally, population health was estimated using indices of body condition for adults and chicks, and blood and faecal parasites were examined.

The first successful tracking data from Kelp Gulls in South Africa revealed that birds from all colonies spent more time foraging in natural environments (marine, coastal and terrestrial) than in anthropogenically modified ones, irrelevant of the distance to the nearest landfill, potentially reflecting prey profitability or availability around the breeding colonies. Gulls also had higher foraging effort when foraging at sea (longer travelling distance), which might be balanced by foraging on high energy prey in the marine environment (e.g. fish).

Diet and trophic ecology data confirmed the wide range of resources Kelp Gulls were capable of exploiting. Anthropogenic items were important food sources at some colonies, while annual differences in trophic level targeted were apparent at some other colonies, possibly reflecting varying predation levels on other seabirds. Diet and trophic ecology generally differed between adults and chicks, with chicks being fed a more marine, i.e. fish, and higher trophic level diet, potentially due to the higher energy content of fish being important for chick growth.

Despite differences between colonies in foraging effort and diet, body condition of both adults and chicks was similar across colonies. Birds from one of the urban colonies, foraging at the local landfill, tended to have slightly higher body condition values,

possibly due to the high fat content of anthropogenic items, although this was not significant. Blood parasites were very scarce, with only one genus identified, *Haemoproteus* spp. Parasite abundance was significantly lower in chicks than in adults, implicating that adults might get infected in areas outside the colony. Faecal smears revealed the presence of yeast cells (*Candida* spp.) in birds, coinciding with higher body condition values, possibly linked to foraging habitat choice, as birds might ingest yeast cells when feeding in urban areas contaminated with human excrement.

Kelp Gulls breeding in South Africa forage on a wide variety of resources and habitats, with limited apparent impact on their parasite load and body condition. All colonies foraged to some extend on natural sources, although some colonies located in very urban areas seemed to depend more closely on anthropogenic items as food resource. Therefore, changes in e.g. landfill management might cause changes in population dynamics, with possible repercussions on neighbouring bird populations. Their generalist foraging nature, among others, makes Kelp Gulls winners of global change and is partly responsible for their increased population numbers. As they are often perceived as pests, information on the foraging ecology is important to manage gull populations effectively.

Keywords: *Larus dominicanus*; Foraging movements; Diet; Stomach content; Pellets; Stable isotopes; Health; Body condition; Parasites; Global change

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Preface

The present thesis consists of five chapters, of which three are data chapters. Chapter 2 is written as a research article and has already been published. Chapters 3 and 4 are written as chapters and are intended for publication, thus “we” was used rather than “I”. Repetition of certain contents was unavoidable, e.g. repeated methodologies, and are highlighted in grey. A combined list of references from all the chapters can be found at the end of the thesis. I analysed all the data and wrote all the chapters. Lorien Pichegru and Peter Ryan contributed to all chapters/ papers and are thus recognized as co-authors. Furthermore, several collaborators contributed to different chapters. Nicolas Suarez trained me in the field and advised and reviewed the GPS chapter (Chapter 2). Maëlle Connan helped with stable isotope and diet analysis and reviewed the diet chapter (Chapter 3). Mike Butler analysed the stable isotope data in the lab (Chapter 3).

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Chapter 1: General introduction

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Global change

We currently live in the Anthropocene, a geological epoch characterised by human-dominated impacts on the global environment (Crutzen & Stoermer 2000, Crutzen 2002). Population increases in combination with a myriad of human activities, such as resource use or land use change are no longer affecting the natural environment on a local or regional scale only, but are considered global (Steffen et al. 2004). These global changes are impacting the atmosphere, as well as terrestrial, coastal, and marine systems (Steffen et al. 2004) and can cause, among others, degradation of ecosystem services and loss of biodiversity (Millennium Ecosystem Assessment 2005).

The global land area is widely used and altered by humans and almost a third has been subjected to land use change during the past 60 years (Winkler et al. 2021). Overall, land use can be assigned to different categories, such as agricultural, urban, industrial or forestry (Mayer et al. 2016). Total population growth is one of the main factors for an increase in urbanization, and as of 2018, 55% of the global population is living in urban areas (United Nations et al. 2019). Urban areas can affect ecosystems in several ways through e.g. excess nutrient or pollutant inputs, changes in local climate and weather, increased carbon dioxide emissions, introduction of non-native species, or habitat fragmentation, modification and loss (Foley et al. 2005, Pickett et al. 2011). These impacts have multiple consequences, such as increases in global air temperatures, loss of biodiversity, or changes in water quality in coastal and freshwater ecosystems (Foley et al. 2005). In addition, urban regions can become areas of biotic homogenization by replacing local native with globally similar non-native species, better adapted to anthropogenic conditions (McKinney 2006). Urbanization is usually accompanied by other forms of land use change due to the demands arising from urban living (Grimm et al. 2008), such as agriculture for food production (Foley et al. 2005). Overall, croplands and pastures represent about 40% of the global land surface and can, among others, decrease water quality through the use of fertilizers for agriculture (Foley et al. 2005). Deforestation for agriculture has caused a loss of around 35% of natural forest areas (Mackey et al. 2015). Deforestation itself does not only

diminish carbon uptake (Mackey et al. 2013), but also reduces biodiversity (Wilcove et al. 2013).

With increasing population numbers the demand for resources, such as fossil fuels, raw materials, freshwater, or food from plant or animal sources, is increasing as well (Smail 1997) and a major factor for driving changes in both terrestrial and marine ecosystems (Steffen et al. 2004). Fossil fuels account for 84% of energy consumption worldwide (Ritchie & Roser 2017). Around 9.5 ± 0.5 billion tons of carbon dioxide are released into the atmosphere each year by burning fossil fuels (Friedlingstein et al. 2019), leading to an increase in air temperature on a global scale (Steffen et al. 2004). Freshwater availability is decreasing due to several drivers, such as higher demands from urban areas, or agriculture, land use change and climate change related droughts (Jiménez Cisneros et al. 2014). Freshwater scarcity is not only threatening the supply for drinking water and other urban uses but also for ecosystems and food production, as the majority of freshwater resources is used for agriculture (Koehler 2008). Global food demand is on the rise and most food is supplied from terrestrial sources such as agriculture and land-derived seafood, and only 17% originate from wild fisheries or mariculture (Costello et al. 2020). As freshwater resources are decreasing and suitable land for agriculture is becoming sparse, the growth rate for agriculture is slowing (FAO 2011). Despite the overall low contribution of marine resources to global food supply, 34% of marine fish stocks are overfished (FAO 2020). Fishing pressure is leading to a drastic reduction in biomass not only of fish species directly targeted but also of species caught accidentally i.e. bycatch (Millennium Ecosystem Assessment 2005). Overfishing also reduces food availability for other marine species (Goñi 1998).

The increase in atmospheric carbon dioxide due to the use of fossil fuels, agriculture, and land-use change (IPCC 1996), is another important aspect of global change and possibly the best documented one (Vitousek 1994). Overall, increasing concentrations of atmospheric carbon dioxide are responsible for global climate change, affecting terrestrial, freshwater, and marine ecosystems (Dunn et al. 2020). Terrestrial ecosystems under climate change are faced with e.g. increased temperatures and more frequent extreme weather events (Steffen et al. 2004). Those impacts are not only threatening global food security (Jia et al. 2019), but also the distribution and abundance of species, and ultimately biological diversity (Vitousek 1994). Extreme rainfall events, especially in agricultural regions, are responsible for increased

phosphorus runoff, which can lead to aggravated eutrophication in freshwater ecosystems (Carpenter et al. 2018). The marine environment is affected by increased sea surface temperatures (Bindoff et al. 2007), which in turn can cause, among other, a decrease in sea ice, rising sea levels, or increased ocean stratification (Doney et al. 2012). Changes in sea surface temperatures can lead to changes in distribution and abundance of marine species, which can ultimately change ecosystem structures (Yao & Somero 2014). Elevated carbon dioxide concentrations can also decrease ocean pH levels, resulting in ocean acidification (Doney et al. 2009). Increased acidity in combination with decreased aragonite saturation due to higher carbon dioxide concentrations can cause decalcification of corals (Fine & Tchernov 2007), which in turn can lead to a loss of biodiversity (La Barre 2011).

Winners and losers of global change

Global changes are undoubtedly affecting ecosystems worldwide, and even though impacts are often negative, some species are able to thrive under those altered conditions (Morris & Heidinga 1997). But what defines whether a species is considered a ‘winner’ or a ‘loser’ of global changes? Overall, a species will benefit from, or be adversely affected by global changes based on specific traits (McKinney & Lockwood 1999). Generally, a species able to tolerate a wide range of conditions is able to better adapt to changing environmental conditions (Baskin 1998). More specifically, rapid population growth and high reproduction rates coupled with a widespread distribution, the ability to disperse rapidly, and a generalist foraging nature are some of the traits characterising winners (McKinney & Lockwood 1999). In addition, a high rate of innovation and a high level of risk-taking might be advantageous for living in human-dominated areas (Møller 2009). On the other hand, species less flexible towards changes can be disadvantaged, and are often losers of global changes (McKinney & Lockwood 1999, Thuiller et al. 2005). Losers can be characterised by slow population growth and low reproduction rates, a limited distribution, have slow dispersal patterns, and are specialist foragers (McKinney & Lockwood 1999). In the context of changing environments, specialists are at risk of being replaced by generalists, causing a loss of biodiversity (Clavel et al. 2011).

With about 28% of species being threatened worldwide (IUCN 2021), the ability of a species to adapt, either through behavioural plasticity or genetic change, to global

changes is more important than ever (Running & Mills 2009). Adaptive responses to environmental changes of species in terrestrial, marine, and freshwater ecosystems are diverse and include phenological changes (Root et al. 2003, Thackeray et al. 2010), adaptive evolution (Hoffmann & Sgrò 2011), or changes in distribution (Parmesan & Yohe 2003, Poloczanska et al. 2013), morphology (Gardner et al. 2011, Baudron et al. 2014), and behaviour (Sih et al. 2011, Wong & Candolin 2015).

Phenological shifts have been reported for many taxa and often coincide with spring advancement due to global warming (Parmesan & Yohe 2003), with effects more pronounced in high-latitude areas (IPCC 1996). Phenological adaptations can include changes in the timing of breeding (e.g.Beebee 1995, Dunn & Winkler 1999, Moyes et al. 2011), timing of flowering (e.g. Cayan et al. 2001, Fitter 2002), or timing of migration (e.g. Bradley et al. 1999, Sparks et al. 2005). Phenological changes can lead to a mismatch between species, resulting in changes in food availability or increased predation risk (Visser & Both 2005). Changes in distribution can be another adaptative strategy of species as a response to global changes (Sirami et al. 2017). Movement and range shifts have been reported for many taxa and can be associated with changes in climate, or land use changes (Hockey et al. 2011, Lenoir & Svenning 2015). Range expansions are often linked to habitat generalists with higher dispersal rates and higher colonization ability, whereas range contractions often involve habitat specialists (Travis 2003). Geographic range expansions of alien species into novel habitats might cause a reduction in native species abundance and can consequently lead to a loss of biodiversity and ecosystem functioning (Walther et al. 2009). Species' movements away from stressors might not always be possible due to anthropogenic barriers such as habitat fragmentation (Berry et al. 2013, McGuire et al. 2016). Some species might then go through evolutionary adaptation to cope with changing conditions (Hoffmann & Sgrò 2011). Especially in populations with high genetic variance, natural selection might allow adaptation as a response to global changes (Bell & Collins 2008). Adaptive evolution is more likely to occur in species with specific traits such as rapid growth, short generation times, large population numbers, and high phenotypic and genetic variability (Running & Mills 2009). Changes in morphology, such as body size or colour, might be another mechanism for coping with global changes (Millien et al. 2006, Fuller et al. 2010, Baudron et al. 2014). These might be directly related to the climate, such as temperature (Maloney et al. 2009, Gardner et al. 2011) or, in the case of body size, might be further related to food availability or

quality, resulting from global changes, such as climate or land use change (Gardner et al. 2011). Finally, species can also respond by modifying their behaviour (Wong & Candolin 2015). This can include utilization of new resources and habitats, adjustment to changing global conditions, such as climate or habitat, or avoidance of or adaptation to new abiotic or biotic stressors (Sih et al. 2011). Especially species able to successfully adapt to urban environments often show higher levels of behavioural plasticity than species unable to cope with urban pressures (Lowry et al. 2013, Sol et al. 2013). Global changes to the environment can also lead to maladaptive behaviour, causing a mismatch between environmental cues and behavioural and life-history decisions, resulting in an ecological trap (Schlaepfer et al. 2002, Robertson et al. 2013).

Seabirds and global change

There are over 350 seabird species worldwide (BirdLife International 2021), representing roughly 3.5% of all birds (Croxall et al. 2012). Seabirds are at or near the top of the food chain (Schreiber & Burger 2002) and can have an important role in the ecosystem through nutrient transfer or ecosystem engineering (Sekercioglu 2006). Seabirds are relatively easy to study, especially during the reproductive season, as they depend on land for breeding (Schreiber & Burger 2002). Due to their foraging ecology and life history, seabirds can be used as sentinels of ocean (Piatt et al. 2007, Parsons et al. 2008), and coastal system health (Thibault et al. 2019). They can also be used as indicators for ecosystem pollution due to accumulation of contaminants through the food web (Furness & Camphuysen 1997).

Seabirds represent one of the most threatened groups of birds (Croxall et al. 2012), with 31% of species categorised as critically endangered, endangered, or vulnerable, and another 11% classified as near threatened (BirdLife International 2021). Seabirds are exposed to multiple threats both on land and at sea, including land use change, disturbance by humans, invasive species, pollution, climate change, diseases, overfishing, or incidental mortality in fisheries (Dias et al. 2019). Land use change can lead to habitat loss for seabirds or increase interaction with humans or other predators (Rastandeh et al. 2018), or changes in resource availability (Lee et al. 2020). Disturbance by humans can have negative effects on breeding success, especially in multispecies breeding colonies through predation of eggs or chicks due to nest

abandonment (Anderson & Keith 1980). Likewise, introduced invasive species such as rodents or cats can cause significant declines in adult seabirds or seabird eggs and chicks through direct predation (Jones et al. 2008, Towns et al. 2011). Pollution in the form of chemicals originating from e.g. industries, agriculture or sewage outfalls are mostly ingested through water or food and can affect the development, physiology, and behaviour of seabirds or can even lead to mortality (Schreiber & Burger 2002). Plastic pollution is another major threat for seabirds, mostly due to entanglement and ingestion (Derraik 2002). Entanglement in discarded fishing nets can lead to injuries or mortality, whereas ingestion of plastic items can impact body condition or cause internal injuries (Thiel et al. 2018). Climate change effects such as temperature increases or more frequent extreme weather events like droughts might lead to breeding habitat loss for seabirds (Batianoff et al. 2010, Doney et al. 2012). In addition, climate change can affect seabirds also through spatial and temporal mismatches in prey availability which can ultimately lead to poor breeding success (Durant et al. 2007). Pollution and increased temperatures and water levels due to climate change might further contribute to the spread of parasites and diseases such as botulism in seabirds (Khan et al. 2019). Competition with fisheries is another stressor for seabird populations worldwide, as reduced prey availability can ultimately impact fitness and distribution patterns (Grémillet et al. 2018). Fishing activities can further lead to incidental bycatch of seabirds feeding behind fishing vessels for offal and bait, which can negatively impact population numbers especially of already threatened species (Anderson et al. 2011).

Seabirds can be categorised as either generalist or specialist species depending on their diet (Le Bohec et al. 2013). Generalist species are less sensitive towards changes in resource availability as they are able to exploit a wide variety of resources and are thus able to switch to alternative resources when preferred prey becomes less available (e.g. Votier et al. 2004a, Mendes et al. 2018). Specialist species on the other hand are more sensitive towards changes as they often rely on specific food resources such as small fish or plankton (e.g. Ancona et al. 2012, Crawford et al. 2015). Consequently, specialists might change distribution patterns or show population declines when experiencing food shortages (Avery et al. 1993, Crawford et al. 2011). In parallel, however, with global changes the availability of supplementary food resources from fisheries bycatch or landfill sites has increased, often favouring species with a generalist foraging nature (Oro et al. 2013). These supplementary food

resources are often predictable and highly abundant, allowing easy access and exploitation (Oro et al. 2013, Noreen & Sultan 2021). However, these resources can also be considered as “junk food” as they provide less energy (Grémillet et al. 2008) or have greater fat content than more natural food (Pierotti & Annett 1991, O’Hanlon et al. 2017). Prey quality in the marine environment might be further affected through climate induced range shifts or overfishing of energy-rich prey fish (Furness 2003, Scopel et al. 2019). Foraging on lower quality resources can have negative effects for population numbers, especially for species with limited prey handling capacity, energetically high foraging behaviour, or low digestive efficiency (Österblom et al. 2008). Food quality can not only affect chick development and subsequent survival (Wanless et al. 2005, Kitaysky et al. 2006), but can also impact body condition of adult birds and lead to higher plasma cholesterol levels (Marteinson & Verreault 2020). Feeding on human-derived food from e.g. landfills can increase the risk of ingesting plastic or other debris (Seif et al. 2018, Lopes et al. 2021), and might also lead to higher blood parasite loads as vector density might be higher, further inland and away from the coast (Quillfeldt et al. 2011). Seabirds feeding on human refuse are also exposed to pathogens (Plaza & Lambertucci 2017) and can be carriers of e.g. *Salmonella* (e.g. Fenlon 1981, Fenlon 1983, Monaghan et al. 1985). The increased availability of easily accessible and abundant supplementary food resources has led to population increases in many generalist seabirds (Crawford et al. 1995, Wanless et al. 1996, Votier et al. 2004a, Oro et al. 2013, Noreen & Sultan 2021). Especially artificially inflated gull (*Larus* spp.) populations in urban areas are often perceived as a nuisance, and conflicts arise due to noise, mess, aggressive behaviour, hazards to aircraft, or transmission of diseases (Belant 1997, Rock 2005). Anthropogenically inflated generalist populations can also cause problems for other seabirds through direct predation of adults, chicks, or eggs, when supplementary food resources become less available (e.g. Regehr & Montevecchi 1997, Votier et al. 2004a). Predation of other species can cause population decreases and is especially concerning for already threatened species (Vidal et al. 1998, Votier et al. 2004b, de Ponte Machado 2007). Furthermore, a reduction in human-derived food can also adversely affect generalist seabird population sizes (Duhem et al. 2008, Bicknell et al. 2013), when they depend heavily on anthropogenic resources (Votier et al. 2004a, Bicknell et al. 2013, Ouled-Cheikh et al. 2021).

Study species: The Kelp Gull

Figure 1.1: Kelp Gull *Larus dominicanus* during incubation on Jutten Island.

Distribution and status

The Kelp Gull is distributed throughout much of the southern hemisphere and is mostly found in coastal areas and on islands (BirdLife International 2018a). Six subspecies have been recognized: *L. d. judithae* (southern Indian Ocean islands), *L. d. austrinus* (breeding on the Antarctic Peninsula), *L. d. antipodus* (New Zealand), *L. d. melisandae* (Madagascar), *L. d. dominicanus* (southern South America) and *L. d. vetula* (southern Africa) (Jiguet et al. 2012). Kelp Gulls are 50-65 cm in length and have a red spot on the lower mandible of the bright yellow bill (Hockey et al. 2005). The African subspecies *L. d. vetula* has an orange-yellow orbital ring, somewhat variable leg colour ranging from dull blue grey in young birds to blue grey through greenish to yellow in adults, and a dark grey iris, with considerable individual variation, with some having whitish or pale yellow eyes (Jiguet et al. 2001).

Kelp Gulls are currently listed as 'least concern' in the International Union for Conservation of Nature (IUCN) Red List for threatened species with an increasing population trend with a global estimate of 3.3 to 4.3 million individuals (BirdLife International 2018a). Population numbers in South Africa increased drastically from 20 000 individuals to 42 000, following intense population growth in the mid 1980s after protection from persecution (Crawford et al. 2009a) and the availability of supplementary food sources from fishery discard and landfills (Steele & Hockey 1990, Steele 1992). Juvenile Kelp Gulls are often found in areas where human refuse is

abundant and easily available, possibly leading to an increased post-fledging survival, which in turn might be responsible for the population increase in Kelp Gulls (Steele & Hockey 1990). Currently the population in South Africa is estimated at 35 000 individuals (Whittington et al. 2016), after numbers decreased mainly due to intense predation on Kelp Gull chicks by Great White Pelicans *Pelecanus onocrotalus* (de Ponte Machado 2007, Mwema et al. 2010).

Diet

Kelp Gulls are opportunistic feeders and forage on a wide variety of natural prey as well as food derived from human activities (Steele 1992, Bertellotti & Yorio 1999, Ludynia et al. 2005, Silva-Costa & Bugoni 2013). In South Africa, Kelp Gulls feed on macrozooplankton, isopods, amphipods, crabs, echinoderms, polychaetes, sponges, molluscs (especially cuttlefish *Sepia* spp), fish, insects, berries, frogs, snakes, small mammals and carcasses of birds and seals (Hockey et al. 2005). They also feed on various crustacean species such as Cape Rock Lobsters *Jasus lalandii,* swarming crustaceans, or goose barnacles (*Lepas* spp), and several bivalves, for example white mussels (*Donax* spp), Black Mussels *Choromytilus meridionalis*, Ribbed Mussels *Aulacomya ater*, and the invasive Mediterranean Mussel *Mytilus galloprovincialis* (Hockey et al. 2005). Kelp Gulls often scavenge from landfills, open-air rubbish tips, fishing harbours and croplands (Hockey et al. 2005). In addition, they can scavenge scraps from Cape Fur Seals *Arctocephalus pusillus* and kleptoparasitise from conspecifics and others (Hockey et al. 2005).

They are natural predators of seabirds, feeding on chicks and eggs of African Penguins *Spheniscus demersus*, Cape Gannets *Morus capensis*, Cape Cormorants *Phalacrocorax capensis*, Bank Cormorants *P. neglectus*, Crowned Cormorants *Microcarbo coronatus*, and White-breasted Cormorants *P. lucidus* in southern Africa (Du Toit et al. 2003), with most of these species considered ‘endangered’ (BirdLife International 2018b, BirdLife International 2018c, BirdLife International 2018d, BirdLife International 2020). Increasing gull populations are known to have negative effects on the breeding success of other seabird species by competing for nesting space, kleptoparasitism and predation (Furness & Monaghan 1987). Competition for nesting space might result in the displacement of other species to less favourable areas and could adversely affect breeding (Burger 1979). Kleptoparasitism by gulls on other adult seabirds while feeding chicks can have additional negative effects on chick survival as

it can reduce time spent on foraging, and thus feeding, to avoid pirates (Hulsman 1976). Kelp Gulls can also affect other species and have been observed to predate on newborn and juvenile Cape Fur Seals *Arctocephalus pusillus pusillus* in Namibia (Gallagher et al. 2015) and on Southern Right Whales *Eubalaena australis* in Argentina (Fazio et al. 2012).

When populations of a seabird predator, such as the Kelp Gull, are artificially increased via supplementary food, the reduction of such food can in turn increase the predation pressure on other species (Votier et al. 2004a, Fazio et al. 2012). Switching to predation might buffer population size effects for the predator, while potentially causing population declines or harm for the prey species (Votier et al. 2004a, Fazio et al. 2012). The ability of a generalist to switch to other available prey might buffer population level consequences of reduced food availability but Kelp Gulls preying on threatened species like the endangered African Penguin and Cape Gannet can adversely affect these threatened species' population levels (Du Toit et al. 2003). Management interventions, such as culling, to control Kelp Gull numbers can become necessary to preserve other species (Fazio et al. 2012, Pichegru 2013).

Breeding cycle

The age at first breeding in South African Kelp Gulls varies between three (Whittington 2007) and four years (Crawford et al. 2000). They breed annually from late August to early February with most clutches being laid by the middle of November (Crawford et al. 1997). Even though Kelp Gulls have three brood patches, the clutch size varies between one and three eggs, with a mean clutch size of 2.1 eggs (Williams et al. 1984). Nest sites are generally in areas with a minimum slope and maximum rock or vegetation cover (Burger & Gochfeld 1981). The nesting habitat as well as the nesting material can be quite variable. Kelp Gulls can breed in cliff or rock stacks, over rock formations, among large boulders, in gullies, on sandy beaches or in vegetation up to one meter in height (Crawford et al. 1982). Nesting material can be derived from feathers, grass, twigs, small stones, kelp, mollusc shells (Crawford et al. 1982) as well as anthropogenic debris (Witteveen et al. 2017).

The incubation period lasts around 26 and 27 days and chicks are semi-precocial with down feathers and able to leave the nest after a few hours (Williams et al. 1984). Time until fledging varies and lies between 46 and 73 days (Williams et al. 1984). Chicks are fed by both parents (Hockey et al. 2005) and even though adult Kelp Gulls feed

opportunistically throughout the year, chicks seem to be fed mostly natural prey, e.g. fish, by parents during the breeding season (Steele, 1992). This selective behaviour might be related to the fact that natural prey has a higher nutritional value and can be easier handled by chicks (Annett and Pierotti, 1989).

Ethics statement

Kelp Gull handling, GPS tracking, and blood and diet sample collection were undertaken with ethical clearance from the Nelson Mandela University Research Ethics Committee (Animal): A17-SCI-ZOO-011, permission from the Department of Environmental Affairs with permit number RES2017/101, and permission from the South African National Parks with permit numbers CRC/2017-2018/011--2017/V1 and CRC/2018-2019/011--2017/V1.

Thesis rationale and structure

Humans have profoundly modified environmental conditions, both on land and at sea, through e.g. land use change, over-exploitation of resources (Steffen et al. 2004), or excess production of carbon dioxide resulting in a global climate change (IPCC 1996). These global changes are known to affect density and distribution, phenology, morphology and behaviour of different species (Root et al. 2003).

For example, some populations of opportunistic and scavenging seabirds have grown exponentially in several parts of the world, while trends of more specialized species, for instance targeting small pelagic fish, have declined (e.g. Paleczny et al. 2015). Population trends of many large gulls (*Larus* spp.) have increased since the 1970s, due to cessation of control and increased human food subsidies, such as fishery wastes and open refuse tips (Lisnizer et al. 2011, Oro et al. 2013), although increasing trends have reversed recently in some populations (Anderson et al. 2016).

In the Benguela upwelling system, recent major ecological changes (Blamey et al. 2015) strongly affected the population of the endemic endangered Cape Gannets *Morus capensis* and African Penguins *Spheniscus demersus* (BirdLife International 2018b, BirdLife International 2020). Gannet and penguin populations in South Africa plummeted by 45 and 60% respectively since the start of the 21st century (Sherley et al. 2019, Sherley et al. 2020), mostly because of decreased food availability following

an eastward shift of their main pelagic prey, anchovies and sardines (Pichegru et al. 2010, Crawford et al. 2015). By contrast, Kelp Gulls *Larus dominicanus* are thriving in South Africa (Whittington et al. 2016). They are natural predators of seabirds, but their impacts have recently been distorted through human activities (Crawford et al. 2009b) and strong management interventions have been put in place on some seabird colonies to limit their impacts on threatened seabirds (Pichegru 2013, Whittington et al. 2016).

Knowledge of Kelp Gull foraging ecology in South Africa remains very limited, with little understanding of the different habitats used over the breeding cycle. The lack of knowledge of Kelp Gull foraging ecology during their breeding season prevents an understanding of the impact of anthropogenic and natural food availability on foraging movements, diet, and health and ultimately population dynamics and its potential impact on other seabird colonies. This thesis explored the foraging ecology of Kelp Gulls across their breeding cycle at several colonies in South Africa, which differed in their habitat, from natural to highly anthropogenically modified. We compared their foraging ecology (foraging movements, diet, trophic ecology) and health status (body condition, parasite load and diversity) to assess to what extent South African Kelp Gulls rely on anthropogenic food and explore the potential implications of their diet on the health status.

Chapter 2 investigated the foraging movements of incubating Kelp Gulls breeding at six different colonies in South Africa with varying proximity to landfills. Individual gulls were equipped with miniaturized GPS loggers and tracked for 24 to 96 hours. Foraging effort was extracted and foraging habitats identified. Kelp Gulls are generalists and able to exploit a wide variety of resources, ranging from natural to anthropogenic (Steele 1992, Hockey et al. 2005). Foraging habitat choice can differ based on the availability of suitable foraging habitats within the foraging range (O'Hanlon et al. 2017). Food from anthropogenic resources, such as landfills, can be more predictable and easily accessible (Horton et al. 1983), than food from e.g. the marine environment (Weimerskirch 2007). We expected 1) birds from colonies located closer to urban areas or landfills to have reduced foraging effort, and 2) birds breeding closer to urban areas or landfills to rely more on anthropogenic food.

Following the results from Chapter 2, Chapter 3 investigated the diet and trophic ecology of incubating Kelp Gulls and their chicks during two consecutive breeding

seasons in seven colonies varying in their proximity to landfills. The diet was assessed by analysing stomach content samples from both adults and chicks and regurgitated pellets collected both during incubation and chick-rearing. Stable isotope analysis of blood plasma from both adults and chicks provided an indication of the trophic ecology. As central place foragers during the breeding season, Kelp Gull diet depends on resource availability in the vicinity of the breeding site (Orians & Pearson 1979). Even though Kelp Gulls might feed opportunistically for themselves, chicks are often fed with a more natural energy-rich diet (Steele 1992). This switch is probably linked to specific dietary requirements of chicks (Spaans 1971, Annett & Pierotti 1999) and easier handling of natural food resources in comparison to anthropogenic ones (Annett & Pierotti 1989). We expected 1) spatial differences in resource use and trophic ecology, with gulls feeding more on anthropogenic resources with increasing proximity of colonies to landfills; 2) temporal differences in diet and trophic ecology between years; and 3) a distinct diet between incubating adults and chicks, with chicks being fed a more natural energy-rich diet on a higher trophic level.

Following the results from Chapter 3, we then investigated whether colony location and subsequently diet could affect body condition and parasite load and diversity in Chapter 4. This was achieved by calculating an index of body condition using morphometric measurements. Blood and faecal samples were analysed for parasite prevalence and identification. Foraging habitat choice and thus diet might affect both body condition and parasite load (Bosch et al. 2000, Auman et al. 2008, Quillfeldt et al. 2011). Especially supplementary food resources of anthropogenic origin, from e.g. landfills, can have higher energy density, and protein and fat content (Pierotti & Annett 1991, O'Hanlon et al. 2017), and thus affect body condition, resulting in heavier birds (Auman et al. 2008). In addition, foraging in areas such as landfills might cause higher and more diverse blood parasite infections, as vector density might be higher (Quillfeldt et al. 2011), but might in turn lead to less helminth diversity than when feeding in marine or coastal areas (Bosch et al. 2000, Diaz et al. 2011). We expected 1) generally higher body condition in birds breeding in colonies closer to landfills; 2) higher blood parasite loads for birds in colonies closer to landfills; 3) lower helminth load and diversity for gulls breeding closer to landfill areas, reflecting increased use of anthropogenic resources; and 4) lower body condition values for gulls with high parasite loads.

Chapter 5 summarised the key findings of each chapter and discussed the perspectives arising from the results in the broader context of global change. In addition, we made suggestions for future studies on Kelp Gulls.

Chapter 2: Foraging movements of breeding Kelp Gulls in South Africa

Chapter 2: Foraging movements of breeding Kelp Gulls in South Africa

Reusch K, Suárez N, Ryan PG, Pichegru L (2020) Foraging movements of breeding Kelp Gulls in South Africa. Movement Ecology 8: 36.

Abstract

Kelp Gulls *Larus dominicanus* are one of the most abundant gulls in the Southern Hemisphere and can play an important role in their ecosystem. Understanding their foraging ecology is therefore important, especially in the context of anthropogenic changes of the environment. Over 35 000 Kelp Gulls breed in South Africa but little is known about their habitat use. It has been hypothesised that foraging mainly occurs in natural habitats while provisioning chicks to ensure high quality food, but knowledge on their foraging ecology during the incubation period remains poor. We tracked incubating Kelp Gulls from six colonies distributed along the coast of South Africa, varying in their distance to urban areas and landfills, and compared foraging trip patterns and habitat selection between colonies. Gulls from west coast colonies, generally located further from landfills than the other studied colonies, travelled farther from their breeding sites (11.7 ± 9.9 – 17.8 ± 21.7 km, n = 3 colonies) than birds from Cape Town and south and east coast colonies (1.7 ± 0.8 – 3.1 ± 3.7 km, n = 3) with birds travelling farthest when foraging at sea. Gulls from all colonies spent more time foraging in marine, coastal, and natural terrestrial environments than scavenging in strongly modified habitats while incubating. Our results suggest that Kelp Gulls in South Africa are able to exploit various resources from different foraging habitats, regardless of colony location and seem to rely less on anthropogenic habitats than expected.

Keywords: Seabird ecology, *Larus dominicanus*, bio-logging, anthropogenic food

Introduction

Humans are having increasingly profound impacts on the environment through a myriad of activities including urbanization, contributing towards global changes (Steffen et al. 2004). Some species show greater tolerance towards anthropogenic

changes than others, for example by being less specialised in terms of habitat or diet and can benefit from altered conditions. Such species are considered 'winners' of global changes (e.g. McKinney & Lockwood 1999). By comparison, more specialised species with more sensitive requirements tend to be limited in their capacities to adapt to changes, and often experience population and range decreases as a result of global changes (e.g. McKinney & Lockwood 1999, Thuiller et al. 2005, Clavel et al. 2011).

Seabirds are particularly threatened by global changes with 28% of seabirds being categorised as either critically endangered, endangered or vulnerable (Croxall et al. 2012). As seabirds use both marine and terrestrial habitats (Croxall et al. 2012, Sydeman et al. 2012), threats include overfishing inducing depletion of their prey, bycatch in fisheries, pollution, introduced species in their breeding sites, anthropogenic disturbance, and habitat loss (Croxall et al. 2012). Populations of specialist feeders in particular tend to have declined (e.g. BirdLife International 2018b, BirdLife International 2018c, BirdLife International 2020) due to major ecological changes (Blamey et al. 2015), as well as competition with fisheries (Crawford 1998). By contrast, opportunistic and scavenging species are generally advantaged and some of their populations are growing exponentially in several parts of the world (e.g. Furness & Monaghan 1987, Neubauer et al. 2006, Lisnizer et al. 2011, Cotter et al. 2012). Opportunistic seabirds that are able to switch to alternative food sources can become a problem for other seabirds through competition for prey or direct predation, when extensively used food sources, like fishery discards (Votier et al. 2004a) or offal (de Ponte Machado 2007) are reduced.

Many large gulls (*Larus* spp.) are opportunistic foragers, able to exploit a wide variety of food sources ranging from marine to intertidal, terrestrial, or anthropogenic (e.g. Duhem et al. 2003a; Yoda et al. 2012). Their ability to forage on human-derived food, such as fishery waste and open refuse tips, as well as cessation of population control measures has led to an increase in population numbers for many species since the 1970s (Lisnizer et al. 2011, Oro et al. 2013). Food derived from anthropogenic sources can be more predictable and easily accessible (Horton et al. 1983) than food derived from e.g. the marine environment, which can often be patchily distributed (Weimerskirch 2007). Even though many gull species feed opportunistically throughout the year, there seems to be a switch in diet during the chick-rearing period to more natural prey, e.g. fish (Annett & Pierotti 1989, Smith & Carlile 1993). This selective

behaviour might be related to the fact that natural prey has a higher nutritional value and is more easily handled by chicks (Annett & Pierotti 1989).

The Kelp Gull *Larus dominicanus* is distributed in coastal areas and on islands at mid- to high-latitudes throughout much of the southern hemisphere (BirdLife International 2018a). Kelp Gull populations are generally increasing, with a global estimate of 3.3 to 4.3 million individuals (BirdLife International 2018a). Population increases in both South America (Yorio et al. 2016) and South Africa (Whittington et al. 2016) have been attributed to increased feeding opportunities mostly from anthropogenic sources (Yorio & Caille 2004, Whittington et al. 2006, Lisnizer et al. 2011). Kelp Gulls are opportunistic feeders that forage on a wide variety of natural prey as well as food derived from human activities (Steele 1992, Bertellotti & Yorio 1999, Ludynia et al. 2005, Silva-Costa & Bugoni 2013). In South Africa, the breeding population is estimated at about 17 500 pairs (Whittington et al. 2016) and they are known to feed on invertebrates, fish, insects, berries, frogs, snakes, small mammals and carcasses of birds and seals as well as seabirds' eggs and chicks including conspecifics (Hockey et al. 2005). They also scavenge from rubbish dumps, fishing harbours and croplands (Hockey et al. 2005).

Knowledge of Kelp Gull foraging ecology is limited in South Africa and information exists mostly on abundance (e.g. Crawford et al. 1997; Whittington et al. 2016) and distribution patterns (e.g. Steele & Hockey 1990; Whittington et al. 2006), as well as their general diet (e.g. Steele 1992; Hockey et al. 2005). As Kelp Gulls can have an important role in their ecosystem due to their abundance it is important to understand their foraging ecology. Kelp Gulls are generalists and can be predators of other seabirds, so variations in the availability of their main food sources could affect other seabirds. In addition, a decrease in the availability of supplementary food sources could cause population declines, as seen in other gull species (Duhem et al. 2008, Washburn et al. 2016). Gulls tend to switch to a more natural diet during chick-rearing (e.g. Annett & Pierotti 1989, Smith & Carlile 1993), therefore the incubation period may provide the opportunity to get a more comprehensive insight into the wider range of foraging habitats exploited, and to identify the relative importance of anthropogenic resources for adult Kelp Gulls. In this study we investigated the foraging behaviour of Kelp Gulls breeding at six colonies in South Africa, varying in their proximity to urban areas and landfills. We deployed GPS loggers on incubating adults to explore: 1)

whether colony location in relation to anthropogenic areas influenced foraging effort, and 2) whether foraging habitat choice (e.g. oceanic, terrestrial or anthropogenic, like landfills) differed among colonies. We expected birds from colonies located closer to urban areas or landfills to have reduced foraging effort and to rely more on anthropogenic food.

Methods

Field sites

The foraging behaviour of incubating adult Kelp Gulls was investigated at six colonies, three on the west coast, one within Cape Town, one on the south coast and one on the east coast of South Africa (Figure 2.1).

The Dwarskersbos colony (DW; 32°43'S, 18°12'E) is located on the west coast of South Africa in a salt works 4 km south of Dwarskersbos. This small coastal village with 670 inhabitants is 25 km from the closest landfill. The colony had some 1 200 Kelp Gull breeding pairs in 2018 (L. Upfold, pers. comm.).

Malgas Island (MA; 33°03'S, 17°55'E) and Jutten Island (JU; 33°05'S, 17°57'E) are small islands in the West Coast National Park in the mouth of Saldanha Bay on the west coast of South Africa. Malgas Island had 113 breeding pairs of Kelp Gulls in 2018 (B. Dyer, pers. comm.). The 8.3 ha island lying 850 m offshore, is home to colonies of Cape Gannets *Morus capensis*, Bank *Phalacrocorax neglectus*, Cape *Phalacrocorax capensis*, and Crowned Cormorants *Microcarbo coronatus*. The closest towns are Saldanha and Langebaan, with 28 000 and 8 000 inhabitants, respectively, with the closest landfill 15 km from the colony.

Jutten Island (JU; 33°05'S, 17°57'E; 46 ha), 3.7 km southeast of Malgas Island, had ca 1 200 Kelp Gull breeding pairs in 2018 (B. Dyer, pers. comm.) and is roughly 12 km away from the closest landfill. Other seabirds breeding on the island include Crowned, Cape and Bank Cormorants.

The Strandfontein colony (ST; 34°05.4'S, 18° 32.1'E) is located within the city of Cape Town with 3.4 million inhabitants. The colony is located in sandy dunes between Strandfontein sewage works and False Bay and is only 3 km from the large Coastal Park landfill site. It had ca 1 060 breeding pairs in 2018 (B. Dyer, pers. comm.).

The Keurbooms Lookout Beach colony (KE; 34°03'S, 23°22'E) is located on a sandbank at the western side of the Keurbooms Estuary, in Plettenberg Bay on the south coast. The colony is situated 1 km from Plettenberg Bay with 32 000 inhabitants and 51 km from the closest landfill. The colony is the smallest colony sampled with 100 Kelp Gull breeding pairs (pers. obs. 2017), but lies adjacent to a much larger colony of some 1 300 pairs on the Keurbooms Peninsula (Whittington et al. 2016).

Finally, the Swartkops Estuary colony (SW; 33°51'S, 25°34'E) is located in Port Elizabeth, a city of approximately 1.2 million inhabitants, on the Swartkops Estuary on the east coast. This estuary is generally in poor condition due to various anthropogenic sources of pollution, including sewage discharges (Adams et al. 2019). The colony is 3 km from the nearest landfill and has some 500 Kelp Gull breeding pairs (P. Martin 2019, pers. comm.).

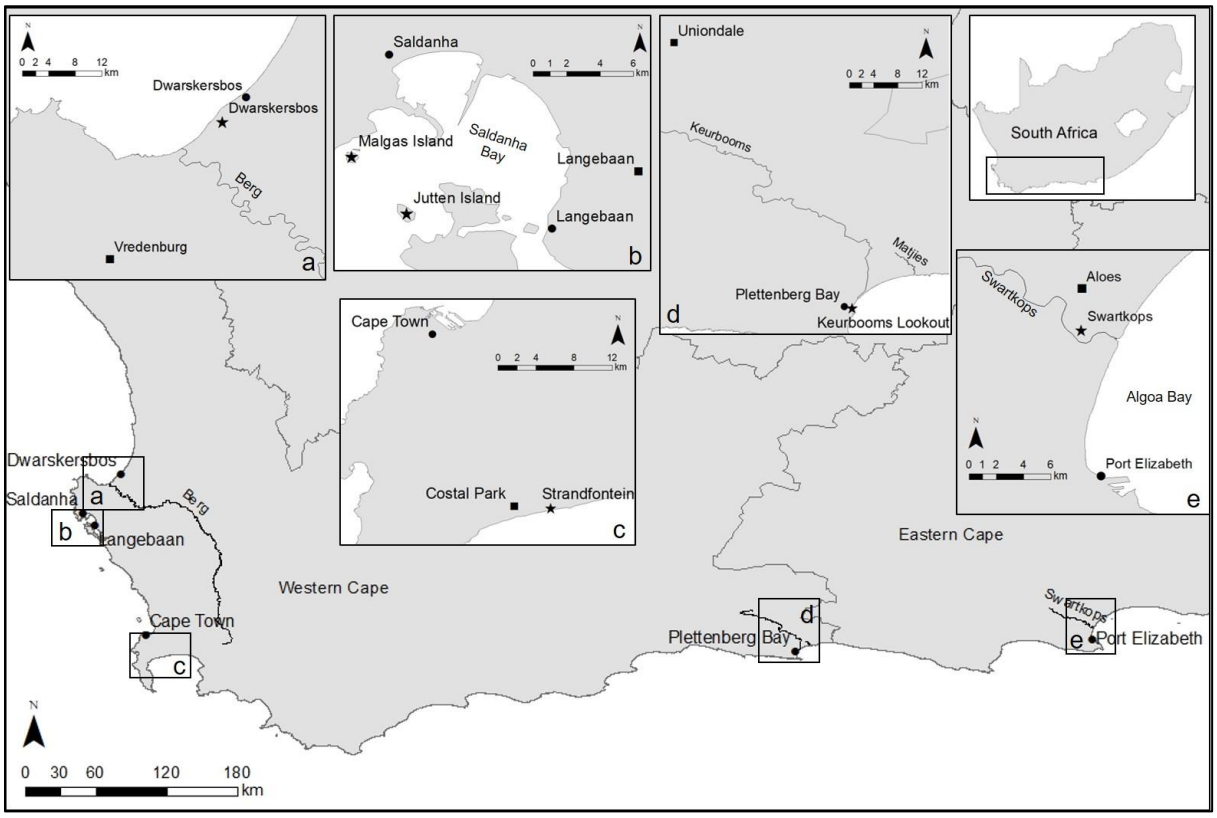

Figure 2.1: Map of the study areas showing the locations of the six Kelp Gull colonies in South Africa (stars), closest cities (circles), and closest landfills (squares).

GPS deployment and analyses

Miniaturized GPS loggers (CatTrack/I-gotU 44.5 x 28.5 x 13mm, Perthold Engineering LLC/Mobile Action) were deployed on one incubating Kelp Gull per nest at 6 colonies in October-November 2017 and at four colonies in October 2018 (see Table S2.1). Birds were captured initially with a walk-in trap and recaptured with a noose placed over the nest after a period of 24 to 96 hours. Upon capture, all gulls were weighed and GPS loggers were taped to the back feathers with Tesa tape®, which causes limited damage to the plumage (Wilson et al. 1997). GPS loggers weighed ~20 g, representing ≤ 2.7% of the birds' body weight (730-1200 g, Torlaschi et al. 2000), and were programmed to record a position every 30 seconds in 2017 and every three minutes in 2018. This longer interval was set to increase the battery life of the loggers and record additional foraging trips. Handling time was ~ 5 minutes for GPS deployment. Upon release all birds were marked with non-toxic animal dye to allow identification. Upon recapture, GPS loggers were removed, gulls were re-weighed and measured: head length, bill length and depth, and tarsus length to the nearest 0.1 mm with Vernier callipers, and wing length (flattened chord) to the nearest 1 mm using a stopped wing ruler. Due to additional samples collected for another study, handling time after recapture was ~ 10-12 minutes. To test whether GPS deployment and handling may have a detrimental effect on the birds, we compared their weight prior to GPS deployment and after recapture with a paired t-test. The differences were not significant ($n = 69$; $t = -70$; $p > 0.05$), implying that the effect of our study was negligible on the birds. In addition, we observed that most birds stayed on the colony after release and started incubating within 10 minutes.

GPS data were uploaded into ArcMap 10.5.1 (Esri, 2018) to identify foraging trips. We only considered trips away from the colony lasting >10 minutes as foraging trips <10 minutes were mostly within 1 km of the breeding site and were most likely for comfort behaviours (i.e. bathing, roosting; Figure S2.1). All GPS data were filtered for erroneous GPS locations following (McConnell et al. 1992), based on a maximum flying speed of 70 km h^{-1} (Shaffer et al. 2017). As the sampling interval differed between GPS tracks in 2017 and 2018, tracks were interpolated to a common interval of 3 minutes using the function redisltraj in the R package adehabitatLT (Calenge 2019) allowing comparisons between years. For each trip, maximum distance from the colony (greatest distance from last point on colony), path length (sum of distance between all

consecutive GPS locations) and trip duration (time between last and first location on the colony before and after a trip) were calculated.

Habitat analysis

In order to identify foraging areas, we used an Expectation-Maximization Binary Clustering (EMbC) algorithm for behavioural annotation using the R package EMbC (Garriga et al. 2016). This algorithm used turning angle and speed between successive GPS locations to assign each location to one of four behavioural categories: low velocity and low turns (LL), high velocity and low turns (HL), low velocity and high turns (LH), and high velocity and high turns (HH) (Garriga et al. 2016). We considered that an animal was flying when the velocity was high and the turning angle low (HL) and potentially foraging in all other three categories (LL, LH, HH). Foraging locations were then uploaded into ArcMap 10.5.1 and an Imagery Basemap was used to associate them with a defined foraging habitat. Foraging habitats were categorised as follows: oceanic, coastal, terrestrial natural and terrestrial anthropogenic. Oceanic habitat was defined as any point in the marine environment >60 m from the shore. Coastal habitats included the shore (beach and up to 60 m from the shoreline). Terrestrial natural habitats consisted of unmodified terrestrial habitats such as nature reserves, and terrestrial anthropogenic habitats were defined as transformed areas (e.g. artificial water bodies, parks), urban areas, landfills, and agricultural fields.

Statistical analysis

All statistical analyses were carried out in R (version 3.5.2; R Core Team 2020). To compare foraging trip parameters (maximum distance from the colony, trip duration, path length) between colonies and years, we fitted models using the lmer function from the lmerTest package (Kuznetsova et al. 2017). Trip parameters were log transformed to obtain normality and homoscedasticity and set as the response variable, while year and colony were the explanatory variables, with bird ID as a random factor to account for multiple trips per bird. The MuMIn package (Barton 2019) was used for averaging the different models and selecting the best fit model based on the Akaike Information Criterion (AIC). We performed post hoc Tukey tests on the explanatory variable of each model to allow pair-wise comparisons using the multcomp package (Hothorn et al. 2020).

We then compared the use of different foraging habitats (oceanic, coastal, terrestrial natural, terrestrial anthropogenic) between colonies and whether foraging parameters

were influenced by foraging habitat choice. A correlation matrix was used to assess the level of correlation between trip parameters in order to avoid any effect of collinearity in our results. The “Pearson” method with the Hmisc package (Alzola & Harrell 2006) was used to obtain significance levels for correlations. As trip parameters were strongly correlated (r values between 0.6–0.99 and p values < 0.001), trip duration and path length were removed from habitat choice analysis. In order to maximise the accuracy of the model, maximum distance was used, as it showed more significant differences between colonies. Only the dominant habitat (i.e. that most visited during a foraging trip, >50% of foraging time) was considered in each trip. Habitats were combined when an individual spent an equal amount of time in more than one habitat. We used a conditional inference tree with the function ctree of the party package (Hothorn et al. 2006) to estimate what influenced habitat choice and used the type of habitat as response variable and maximum distance and colony as explanatory variables. We used the default setting to build the tree and set statistical significance at $p \leq 0.05$. To estimate model accuracy, we set the seed at 1234 and divided the data set into a training (70% of data) and testing data set (30% of data). Model accuracy was obtained by calculating the misclassification error rate on the testing data set following Jawaharlal (2014).

Results

Of the 85 incubating Kelp Gulls equipped with GPS loggers, 75 were recaptured. All 10 birds that eluded recapture were observed alive. Of the 75 recaptured birds, one GPS logger was damaged and data could not be retrieved, two loggers did not record data in a consistent way and one bird had lost the GPS. In addition, in 2017 three birds did not leave their colony. As a result, data were collected from 68 birds, which completed 316 foraging trips (Table S2.1).

Trip parameters

Foraging trip parameters did not vary between years (lmer, $p > 0.05$), allowing data from both years to be pooled for comparisons between colonies. Birds from Jutten Island foraged farthest from their colony, with an average maximum distance ± SD of 17.8 ± 21.7 km (Range = 0.03-78.2 km; n=56), compared to averages varying between 1.7 ± 0.8 and 11.8 ± 15.9 km (Range = 0.07-80.7 km; n=206) at the five other colonies (Figure 2.2). Gulls from Cape Town and south and east coast colonies, Strandfontein,

Keurbooms, and Swartkops, all foraged close to their colony, i.e. 1.7 ± 0.8 to 3.1 ± 3.7 km (Range = 0.07-13.66; n= 138) from their breeding sites, with birds from Swartkops travelling the shortest distances. Maximum distances and path lengths varied significantly between colonies (lmer, $p < 0.001$), with birds from west coast colonies, Dwarskersbos, Malgas and Jutten travelling farther and with longer path lengths than birds from the three other colonies. Trip durations also differed between colonies with trips from Strandfontein being significantly shorter than trips from the west coast colonies (lmer, $p < 0.001$; Table 2.1). Trip durations ranged from a minimum of 12.6 min at Swartkops up to a maximum of 28.7 h in Dwarskersbos and foraging distances from 30 m from the colony at Jutten, up to 80 km at Malgas.

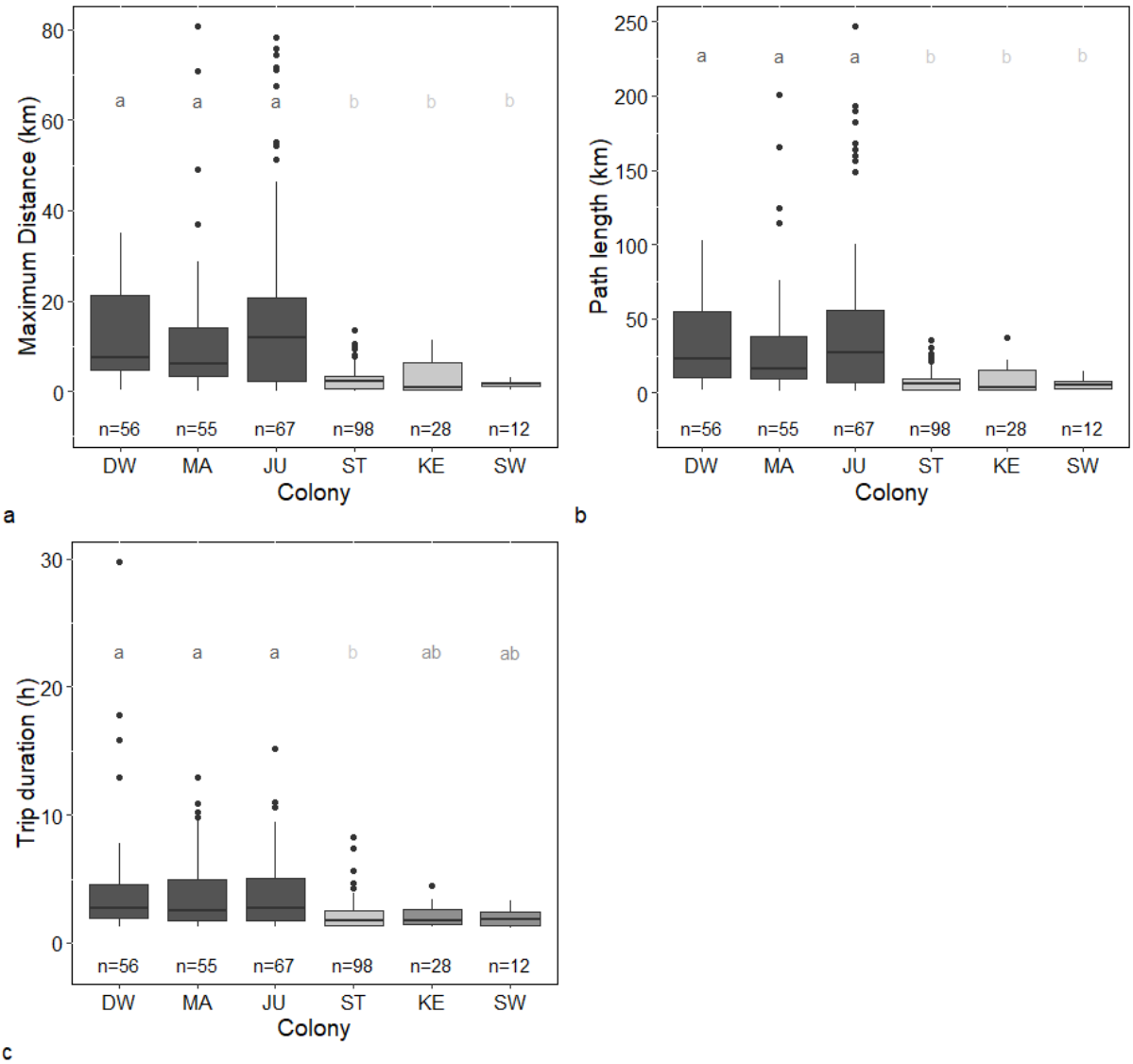

Figure 2.2: Box plots representing foraging trip parameters **a)** maximum distance (km), **b)** path length (km), and **c)** trip duration (h) of incubating Kelp Gulls from six South African colonies (DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST =

Strandfontein, KE = Keurbooms, SW = Swartkops) in 2017-2018. The boxes show the median values and standard deviation. Boxes and letters above with different shades of grey are significantly different from Tukey test results.

Table 2.1: Summary statistics of colony influence on maximum distance (km), path length (km), and duration (h).

Model	Fixed factors	Model estimates ± SE	AIC_c	DF	R^2m	R^2c
Log(Max distance) ~ Intercept			1152.41	3		
Log(Max distance) ~ Colony	Intercept DW	1.94 ± 0.21	1108.95	8	0.26	0.31
	Colony MA	-0.17 ± 0.30				
	Colony JU	0.07 ± 0.28				
	Colony ST	-1.66 ± 0.27				
	Colony KE	-1.79 ± 0.36				
	Colony SW	-1.58 ± 0.48				
Log(Path length) ~ Intercept			1161.91			
Log(Path length) ~ Colony	Intercept DW	2.86 ± 0.20	1118.01	5	0.25	0.28
	Colony MA	-0.16 ± 0.29				
	Colony JU	0.05 ± 0.27				
	Colony ST	-1.63 ± 0.26				
	Colony KE	-1.78 ± 0.35				
	Colony SW	-1.48 ± 0.47				
Log(Trip duration) ~ Intercept			906.09			
Log(Trip duration) ~ Colony	Intercept DW	0.55 ± 0.15	888.43	5	0.14	0.21
	Colony MA	-0.03 ± 0.22				
	Colony JU	-0.01 ± 0.20				
	Colony ST	-0.80 ± 0.20				
	Colony KE	-0.71 ± 0.27				
	Colony SW	-0.88 ± 0.35				

Notes: We used linear mixed-effect models with colony as fixed factors and bird ID as random intercept. All response variables were log transformed. Intercept DW is the intercept and the estimate for the Colony DW. Model estimates and standard errors are shown for the six colonies. We provided the marginal R^2 which represents the variance explained by the fixed factors alone, and the conditional R^2 which describes the variance explained by both the fixed and random factors. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, KE = Keurbooms, SW = Swartkops.

Habitat analysis

Birds from all six colonies spent 75-87% of their time within the colony, 10-17% foraging and 1-6% flying (Figure 2.3). Trips < 10 minutes outside the breeding colony are represented as “other” (0.5 to 3% of time). Overall, birds from Dwarskersbos and Malgas Island spent the longest time away from the colony foraging (17%), while birds from Swartkops foraged for only 10% of the time.

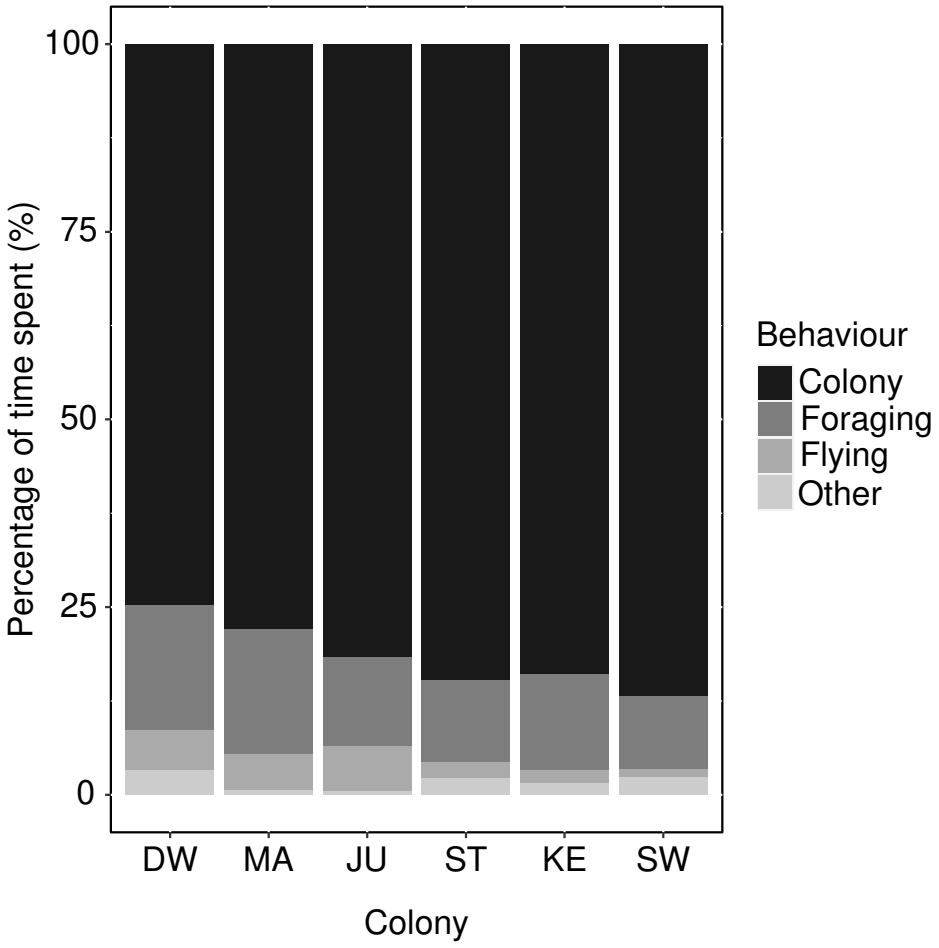

Figure 2.3: Percentage of time spent by incubating Kelp Gulls at the colony, foraging, flying, or other (i.e. trips < 10 minutes outside the breeding colony) for each of the six South African colonies (DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, KE = Keurbooms, SW = Swartkops).

Foraging habitats, as identified by the EMbC, varied widely across colonies (Figure 2.4, Table S2.2). Gulls from Dwarskersbos, Malgas, and Jutten Island, i.e. the west coast colonies, mostly foraged in oceanic habitats (37-52% of their foraging time), whereas birds from Keurbooms foraged mainly in coastal habitats (57%) and from

Swartkops in terrestrial natural areas (65%; Figure 2.5). Birds from Strandfontein showed more diverse habitat choices, foraging in oceanic, coastal, terrestrial natural and terrestrial anthropogenic habitats. Birds from all colonies fed to some extent in terrestrial anthropogenic areas (4-41% of their time), with birds from Malgas Island (41%) and Strandfontein (33%) spending the highest amount of time. Birds from Malgas spent more time on artificial water bodies (19%) and agricultural fields (16%) compared to birds from Strandfontein which frequented the sewage works (15%) and nearby landfill (15%). However, much of this time at wetlands could be spent roosting, bathing, or in other comfort behaviours, which could indicate that time spend foraging in these areas was overestimated.

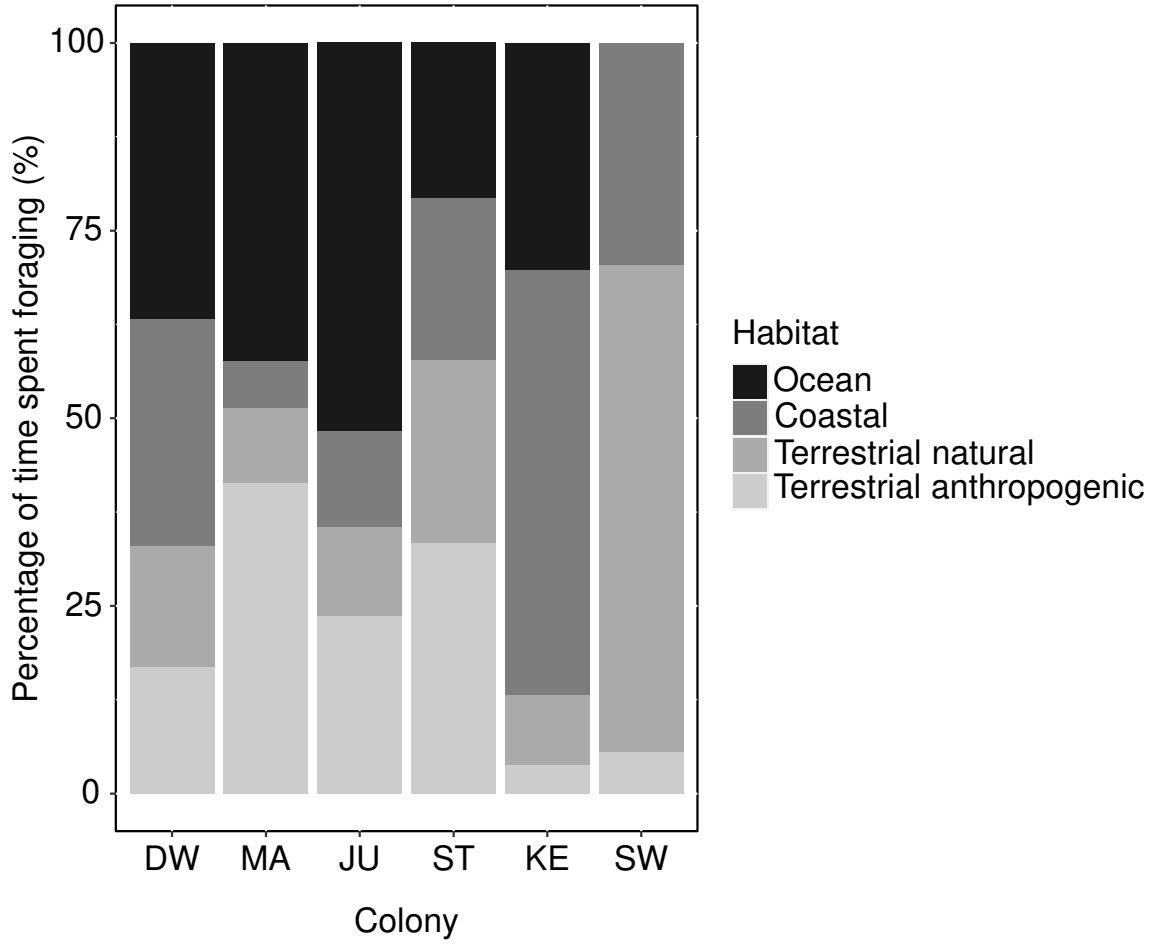

Figure 2.4: Percentage of time spent by incubating Kelp Gulls in each of the four foraging habitats for each of the six studied colonies in South Africa (DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, KE = Keurbooms, SW = Swartkops).

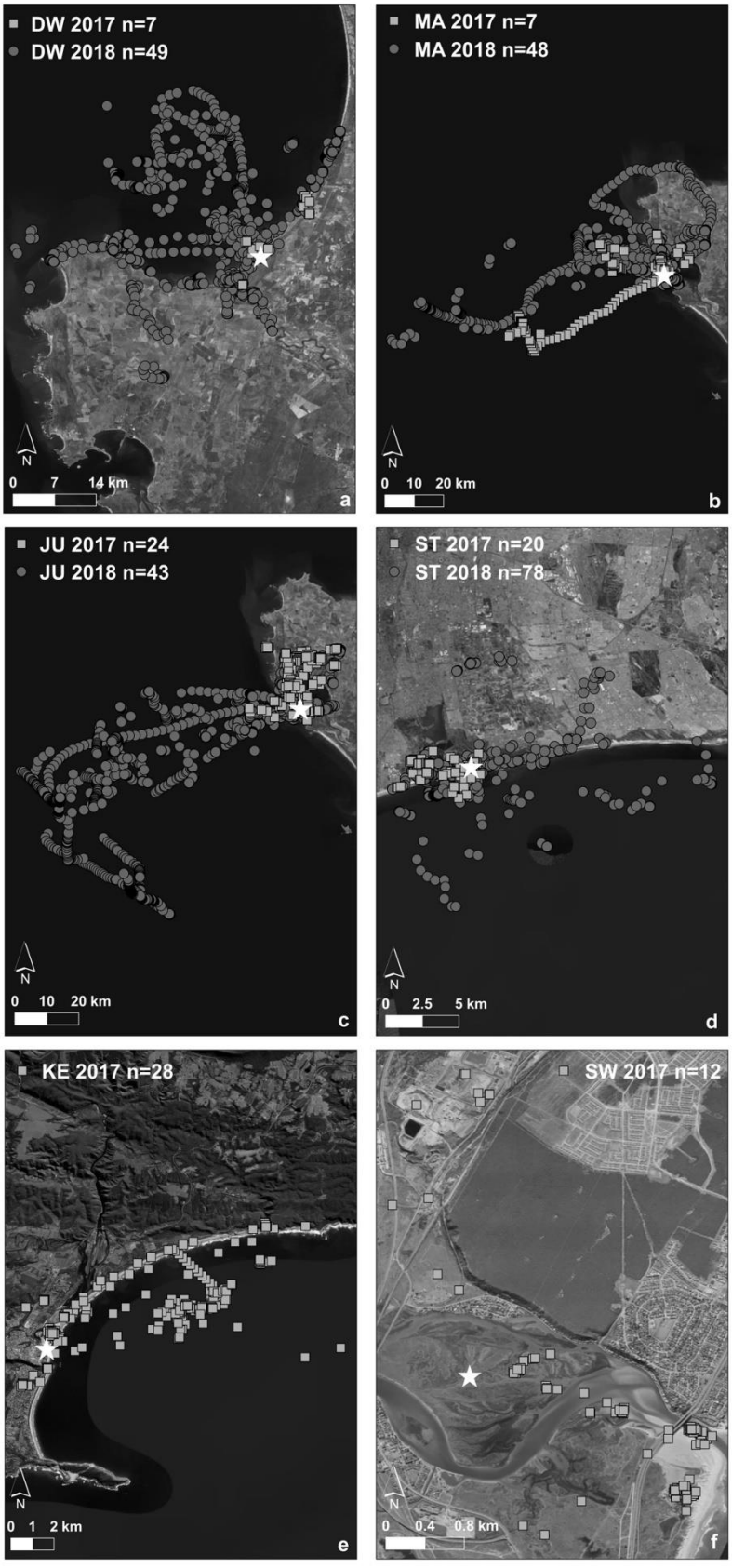

Figure 2.5: a-f) Foraging locations of incubating Kelp Gulls for each of the six colonies (DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, KE

= Keurbooms, SW = Swartkops). The colony is represented by a white star, foraging locations from 2017 are shown in light grey squares and from 2018 in dark grey dots, respectively.

Results from the conditional inference tree showed that foraging habitat choice was significantly influenced by colony ($p < 0.001$; Figure 2.6) and maximum foraging distance ($p < 0.01$; Figure 2.6), which explained 47% of the variance in habitat choice. The first split (Node 1) showed a significant difference between birds from Swartkops and the other colonies, as the former foraged predominantly in terrestrial natural habitats. The next split showed that birds from all other five colonies were more likely foraging in the marine environment (A, Node 9) when trips were farther from their respective colonies (>26.51 km; Node 3). The following split revealed different foraging behaviours between colonies again, with Keurbooms colony foraging only in coastal areas (B, Node 7), when foraging ≤ 0.41 km from their colony, and in the marine environment when foraging further away (Node 8). Finally, birds from Dwarskersbos, Malgas, Jutten and Strandfontein were dividing their time more equally among the four habitats when foraging closer to the colony (Node 5).

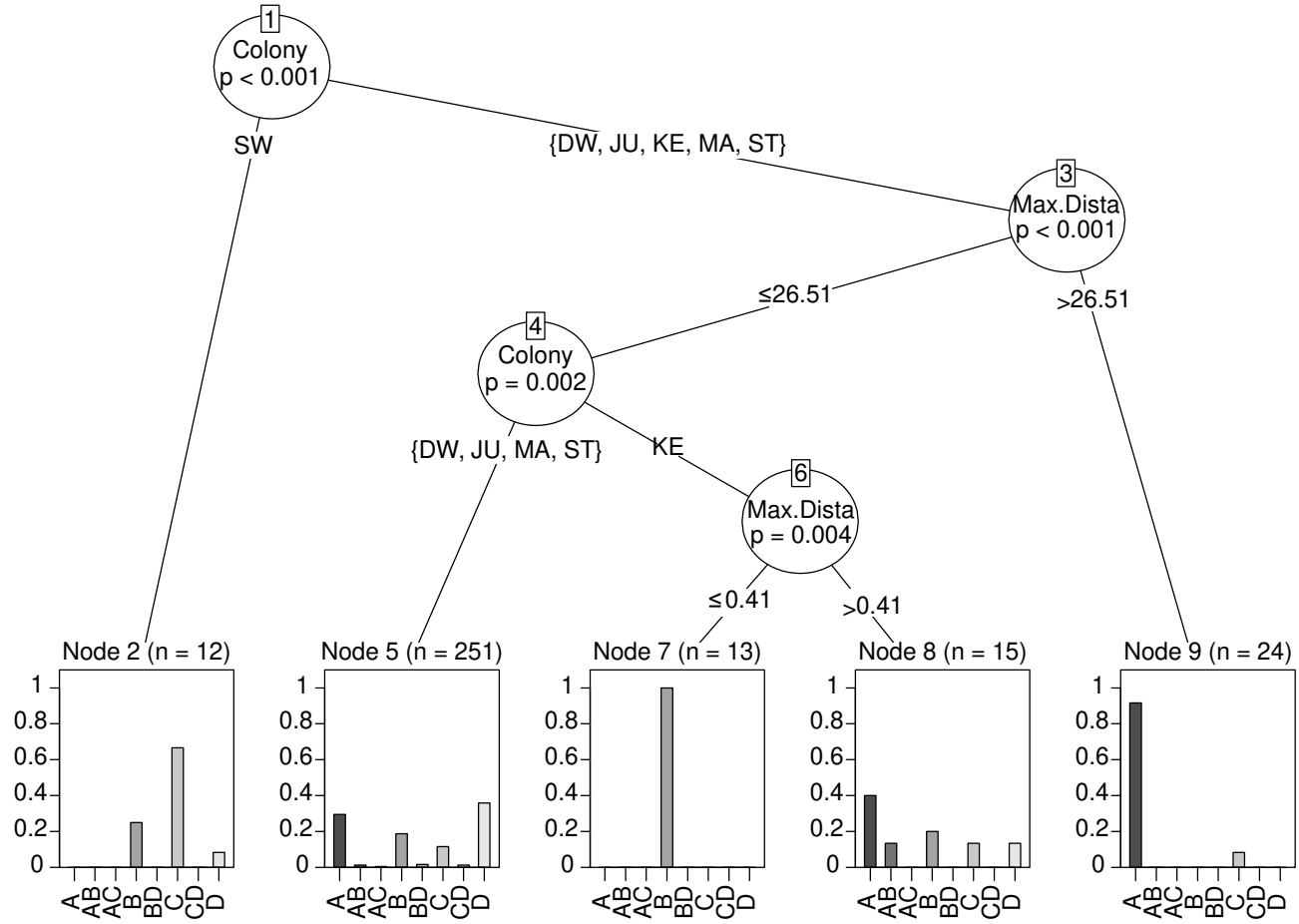

Figure 2.6: Conditional inference tree for the effect of colony and maximum distance on dominant habitat (A = Ocean, B = Coastal, C = Terrestrial natural, D = Terrestrial anthropogenic, AB, AC, BD, and CD are combinations of the major categories). Each oval contains one of the two explanatory variables, colony or maximum distance. Following the branches lead to the partitions of the variables based on a significance value of $p \leq 0.05$. The value above each leaf represents the total number of observations that fall within the node. Histograms show the probability of dominant habitat. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, KE = Keurbooms, SW = Swartkops.

Discussion

Our study showed high foraging flexibility of incubating Kelp Gulls in South Africa. Their foraging range varied from 30 m up to 80 km from the colonies, with colony means ranging between 1.7 ± 0.8 and 17.8 ± 21.7 km, which was generally shorter than other gull species. For example, incubating Ring-billed Gulls *Larus delawarensis* in Canada

had an average foraging range of 30.2 ± 23.8 km from their colony, even though they were also breeding close to urban areas (Patenaude-Monette et al. 2014). Similarly, incubating Kelp Gulls tracked in Argentina travelled on average 19.6 ± 24.4 km from their colony, while their breeding site was located within 4.5 km of a landfill and birds feeding on the refuse dump made relatively shorter trips (< 7 km) (Kasinsky et al. 2018). Kelp Gulls from South Africa made on average shorter trips close to their respective colonies compared to other species, which suggest that they are able to exploit a variety of food sources closer to their breeding sites than other gulls.

In addition, most of their foraging time was spent in natural environments (ocean, coastal, or natural terrestrial), and Kelp Gulls from all South African colonies seemed to rely less on anthropogenic food than expected, even when their colony was located close to urban areas or landfills. These results are in contrast with the foraging ecology of Kelp Gulls in Argentina (Kasinsky et al. 2018) or Lesser Black-backed Gulls nesting in urban areas in Bristol, UK (Spelt et al. 2019). In Argentina gulls only spend 10% of their time in the marine environment and often foraged at a landfill site close to the colony (75%), mainly on fishery waste disposed there from recreational activities (Kasinsky et al. 2018), whereas Lesser Black-backed gulls spent most of their time in anthropogenic habitats and, even though located close to the coast, seldom foraged at sea (Spelt et al. 2019). The observed difference between urban nesting gulls might reflect differences in prey profitability or availability in their respective environments, with the marine and coastal environments in South Africa seemingly more profitable for gulls. Indeed, foraging profitability can influence foraging habitat choice (Patenaude-Monette et al. 2014), which in turn will influence foraging distance from the colony (Duhem et al. 2005, Patenaude-Monette et al. 2014).

When feeding in the marine environment, Kelp Gulls in South Africa travelled farther away from their colonies, suggesting that foraging at sea may require higher effort but might be balanced as the energetic gain from an oceanic diet is generally higher than food derived from e.g. intertidal areas (O'Hanlon et al. 2017, Van Donk et al. 2017). It is also possible that farther trips offshore might represent scavenging on fishery discard from trawlers, which Kelp Gulls are known to take advantage of (Steele 1992, Kasinsky et al. 2018). A higher calorific diet during breeding can lead to a better body condition, which is important for an increased breeding success (Bukacinska et al. 1996). By contrast, gulls might chose to forage in more natural areas close to the colony, reducing

the energy costs associated with moving to the feeding area (Van Donk et al. 2019), which in turn might allow higher nest attendance (Bukacinska et al. 1996). As our birds were incubating, i.e. with low energy demands (Pierotti & Annett 1991), they might choose a “risk averse” feeding strategy (Annett & Pierotti 1989) as anthropogenic areas such as landfills can be highly competitive (Monaghan 1980).

We must bear in mind that our model on habitat choice explained only 47% of the variance using distance travelled and colonies as explanatory variables. The remaining variance might be explained by variables not measured in this study such as weather or energy expenditure (Isaksson et al. 2016, Van Donk et al. 2019). Nevertheless, the results obtained in this study show the high trophic plasticity and opportunism of this species as has been described for other species of gulls (e.g. Duhem et al. 2003a, Shaffer et al. 2017). Studying Kelp Gull foraging strategies during other breeding stages might give a better overview of the range of foraging habitats used and the spatial requirements of this species in South Africa.

According to our prediction, colonies located further away from urban areas would feed more in natural habitats, but our results showed that some colonies located relatively far from urban centres (i.e. Malgas), spent more time in terrestrial anthropogenic areas (42%), than some colonies located within cities (i.e. Strandfontein in Cape Town). However, terrestrial anthropogenic habitats where birds from Malgas fed were mainly agricultural fields and artificial water bodies, whereas gulls from Strandfontein spent their time in highly degraded habitats such as the landfill or sewage plant both close to the colony. Even though gulls might use artificial water bodies and sewage plants for bathing or roosting, these habitats can potentially provide food in the forms of small fish or insects (Vernon 1972), while agricultural fields can offer food in the form of e.g. insects (Coulson & Coulson 2008), annelids during ploughing (Patenaude-Monette et al. 2014), termite alates (Haarhoff 1982), or snails *Theba pisana* (Whittington et al. 2016). Therefore, Kelp Gulls in our study could feed to some extend on natural prey while foraging in anthropogenic habitats. It may be worth noting that gulls from the neighbouring colony, Jutten Island, located 3,7 km from Malgas, spent more time in the ocean and coastal areas, possibly to reduce intra-specific competition through spatial segregation (Corman et al. 2016, Shaffer et al. 2017).

Finally, gulls from all our studied colonies spent a significant amount of time on the colony while incubating (75-87% of the tracking time), which was comparable to Ring-

billed Gulls time budget (86.7% on colony; Caron-Beaudoin et al. 2013), or Lesser Black-backed Gulls (75-80% on colony; Spelt et al. 2019). The high colony attendance by Kelp Gulls might represent resting or feeding on the colony e.g. on insects as well as predating on other seabird eggs, or eggs and chicks from conspecifics (pers. obs.; Pichegru 2019), or kleptoparasiting other breeding seabirds (García et al. 2010). It is likely that during food shortages, predation on conspecifics and other seabirds will increase with colony attendance, as foraging on or close to the colony can be beneficial for breeding success (Bukacinska et al. 1996). However, this situation will present a problem in mixed seabird colonies, such as Malgas and Jutten Island. Indeed, gulls from these colonies fed extensively in the marine environment and on terrestrial anthropogenic areas during our study and changes in the availability of these food sources could result in increased predation on other seabird eggs and chicks. For example, during the 2018 breeding season Kelp Gulls on Malgas predated on 8000 endangered Cape Gannet eggs (Pichegru 2019), i.e. some 50% of the total gannet colony, which for a species that does not lay repeat clutches, will have serious population-level effects over the long term. The resolution of our GPS did not allow us to discriminate between time spend resting/ foraging on the colony or nest attendance, and it is possible that data from accelerometers may allow gain that insight by identifying behaviours such as standing, sitting or walking.

Conclusions

This is the first comprehensive study using GPS loggers to investigate the foraging ecology of incubating Kelp Gulls in South Africa. We showed that like other *Larus* gulls, this opportunistic seabird is capable of foraging in various habitats, regardless of the proximity of their colony to urban areas or landfills. Additional information on Kelp Gull diet from stomach and pellet samples would be necessary to understand the energetic consequence of feeding in different habitats. Similarly, this study should be repeated during the chick-rearing stage to gain a more complete picture of the foraging ecology and energetics of South African Kelp Gulls. Such information is important to understand and predict the future population trajectory of Kelp Gulls in South Africa, with potential consequences on their environment and other species breeding in their vicinity.

As incubating Kelp Gulls in South Africa did not seem to depend highly on food made available from landfills, it is possible that changes in the availability of scraps due to improved landfill management (e.g. closing, covering, or diverting organic waste to composting facilities) might have little impact on South African Kelp Gull populations. The ability of Kelp Gulls in South Africa to exploit different foraging habitats allows this opportunistic forager to be highly adaptable and can thus be considered ‘winners’ of global change.

Supplementary information

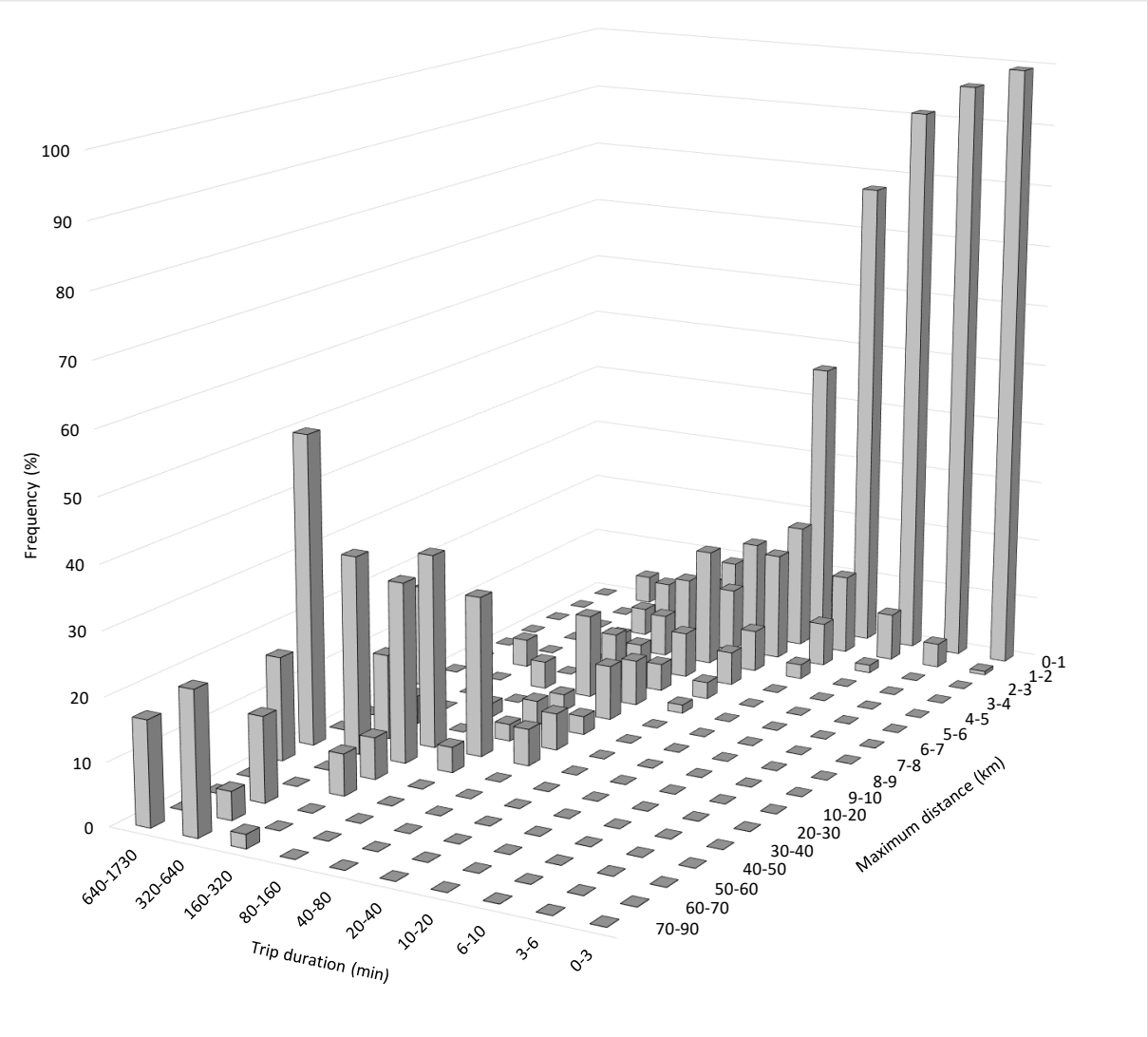

Figure S2.1: 3D graph showing trip duration (min) and maximum distance (km) of foraging trips (%) between 0 and 1730 min and 0 and 90 km from colony in intervals.

Table S2.1: Overview of timing of data collection and number of adult Kelp Gulls deployed and recaptured per colony in South Africa in 2017 and 2018 with number of complete foraging trips performed.

Colony	Year tracked	Dates	Captured	Recaptured	Trips
Dwarskersbos	2017	23/10-24/10	8	6 (75%)	7
Dwarskersbos	2018	18/10-23/10	10	9 (90%)	49
Malgas Island	2017	20/10-22/10	6	6 (100%)	7
Malgas Island	2018	8/10-12/10	10	8 (80%)	48
Jutten Island	2017	17/10-19/10	10	10 (100%)	24
Jutten Island	2018	13/10-17/10	10	10 (100%)	43
Strandfontein	2017	26/10-28/10	8	7 (87.5%)	20
Strandfontein	2018	2/10-7/10	10	9 (90%)	78
Keurbooms	2017	6/11-8/11	8	7 (87.5%)	28
Swartkops River	2017	12/10-14/10	5	3 (60%)	12
Total			**85**	**75**	**316**

Table S2.2: Time spent (%) in each of the foraging habitats in detail (Ocean, shore, natural, natural-transformed, urban, agriculture, landfill) for each of the six colonies.

Colony	Habitat						
	Ocean	Coastal	Natural	Natural-transf	Urban	Agriculture	Landfill
Dwarskersbos	36.8%	30.3%	16.0%	11.2%	3.2%	2.2%	0.3%
Jutten Island	51.7%	12.8%	11.7%	11.6%	2.8%	3.5%	5.8%
Malgas Island	42.5%	6.1%	9.9%	19.0%	5.6%	15.5%	1.4%
Strandfontein	20.6%	21.6%	24.3%	14.7%	3.4%	0.3%	15.0%
Keurbooms	30.3%	56.6%	9.2%	1.0%	2.8%	0%	0%
Swartkops	0%	29.6%	64.8%	1.5%	0.5%	0%	3.5%

Chapter 3: Spatio-temporal differences in the diet and trophic ecology of Kelp Gulls in South Africa

Chapter 3: Spatio-temporal differences in the diet and trophic ecology of Kelp Gulls in South Africa

Katharina Reusch, Maëlle Connan, Peter G. Ryan, Mike Butler, Lorien Pichegru

Abstract

The Kelp Gull *Larus dominicanus* is an opportunistic foraging species that preys on a wide variety of resources. Urbanisation is increasing the amount of anthropogenic food resources, often resulting in increasing numbers of Kelp Gulls. Knowledge of the level of exploitation of anthropogenic resources is important to understand how changes in food availability might affect gull populations or in turn other seabirds through potentially increased predation by gulls. We investigated the diet and trophic ecology of incubating Kelp Gulls and Kelp Gull chicks from seven colonies with varying proximity to landfills over two consecutive years in South Africa. We used a combination of conventional diet sampling (stomach contents, regurgitated pellets), and stable isotope analysis of blood plasma. Even though distance to landfill did not seem to affect the diet and trophic ecology of Kelp Gulls overall, differences were evident between colonies. Kelp Gulls preyed upon a variety of items, from fish, land snails, and mussels to refuse, bird remains, and crustaceans. Diet differed at most colonies between incubating adults and chicks, with chicks mostly being fed more natural and higher trophic level resources. Our results confirm that South African Kelp Gulls exploit a wide range of resources during the breeding season. It seems likely that their broad feeding ecology will allow them to switch to alternative food resources, buffering any changes in prey availability.

Keywords: *Larus dominicanus*; Stomach content; Pellets; Stable isotopes; Anthropogenic impact; Incubation; Chick-rearing; Urbanisation; Landfills

Introduction

During the breeding season, seabirds are central place foragers, limiting their possible foraging range to habitats and resources within the vicinity of their breeding site (Orians & Pearson 1979). Specialist species are often sensitive to changes in resource availability in their foraging range due to their specific dietary adaptations (Crawford

1998, Trivelpiece et al. 2011). Generalist species on the other hand are able to buffer against changes of preferred food availability by switching to alternative resources, making them more resilient towards changes (Votier et al. 2004a, Polito et al. 2015). Substantial additional foraging opportunities such as fishery discards, landfills, or agricultural areas, are increasingly being made available through human-induced global changes, often benefiting generalist seabirds (Mitchell et al. 2004, Cotter et al. 2012).

Many large gulls (*Larus* spp.) are opportunistic foragers able to exploit anthropogenic as well as natural food resources, showing a high plasticity in foraging behaviour and resilience towards changes (Schwemmer & Garthe 2008, Yoda et al. 2012). This ability has often been attributed as the reason for population increases among many gull populations (Cotter et al. 2012). Even though foraging on anthropogenic resources can be highly competitive (Monaghan 1980, Camphuysen et al. 2015), areas such as landfills offer predictable and easily accessible food (Horton et al. 1983) and can thus contribute substantially to the diet of some gull species (Belant et al. 1998, Duhem et al. 2003b). For gulls relying heavily on anthropogenic resources, changes in landfill management or fishery discard policies could potentially have negative population level effects, making it necessary to understand to what extent these species rely on human-derived food (Duhem et al. 2003b, Calado et al. 2018).

Kelp Gulls *Larus dominicanus* are distributed largely throughout the southern Hemisphere (BirdLife International 2018a), with breeding pairs in South Africa distributed in colonies along the coast and on islands (Crawford et al. 1982). In South Africa, their population size was estimated at 8 906 breeding pairs between 1976-1981 (Crawford et al. 1982). Population numbers increased drastically to 21 000 pairs between 2000-2005 due to protection from control and the availability of anthropogenic resources from fishery discards and landfills (Whittington et al. 2016). Between 2009 and 2014 the number of breeding pairs decreased to an estimated 17 500 mostly due to predation of Kelp Gull chicks by Great White Pelicans *Pelecanus onocrotalus* (Whittington et al. 2016).

The last comprehensive study on Kelp Gull diet in South Africa was conducted some 30 years ago and focused on the southwestern Cape of South Africa (Steele 1992). That study showed that their diet comprised a wide variety of resources, ranging from natural to anthropogenic and marine to terrestrial items (Brooke & Cooper 1979, Steele

1992). Their preferred foraging areas seemed to be rocky shores and sandy beaches, where they prey on mussels (Steele 1992), such as the invasive Mediterranean Mussel *Mytilus galloprovincialis* (Hockey et al. 2005) or the sand mussel *Donax serra* (Steele 1992), but they also fed on insects, small mammals, invertebrates, fish, seabird eggs and chicks (e.g. Cape Gannet *Morus capensis*), and were able to exploit anthropogenically modified areas such as landfills, fishing harbours or croplands (Hockey et al. 2005). There has been an increase in urbanization in South Africa since the 1990s (World Bank 2021), thus this study provides an excellent opportunity to determine whether gulls have changed their foraging behaviour by feeding more on anthropogenic resources. In this study we combined conventional diet analysis (i.e. stomach content samples and regurgitated pellets) with stable isotope analysis of blood plasma. Stomach content samples and pellets offer data on diet composition (Barrett et al. 2007), with pellets often containing mostly large and indigestible prey items in comparison to stomach content samples (Duffy & Jackson 1986). Stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provides information on the source of carbon at the base of the food web (foraging habitat) and trophic level, respectively (Hobson et al. 1994). Here we investigated the diet and trophic ecology of incubating Kelp Gulls and chicks during two consecutive breeding seasons in seven colonies across South Africa with varying proximity to landfills. We expected 1) spatial differences in resource use and trophic ecology, with gulls feeding more on anthropogenic resources with increasing proximity of colonies to landfills; 2) temporal differences in diet and trophic ecology between years; and 3) a distinct diet between incubating adults and chicks, with chicks being fed a more natural energy-rich diet on a higher trophic level. Our results will help to understand the foraging ecology of Kelp Gulls in South Africa and their dependence on anthropogenic resources throughout the breeding season, and ultimately allow an assessment as to how changes in food availability might affect Kelp Gull population levels and potentially other seabird species through direct predation.

Methods

Field sites

The diet and trophic ecology of Kelp Gulls were investigated during incubation and chick-rearing in seven colonies in the Eastern and Western Cape of South Africa (Figure 3.1).

The Steenbras Dam colony (SD; 34°10'S, 18°54'E) is located 35 km east of Strandfontein in a nature reserve not open to the public near Gordons Bay in the Western Cape of South Africa. The colony is situated on a small island covered densely with pine trees and is 26 km from the closest landfill. It had ca. 300 breeding pairs in 2017 (pers. obs. 2017).

A detailed description of the six remaining colonies can be found in Chapter 2.

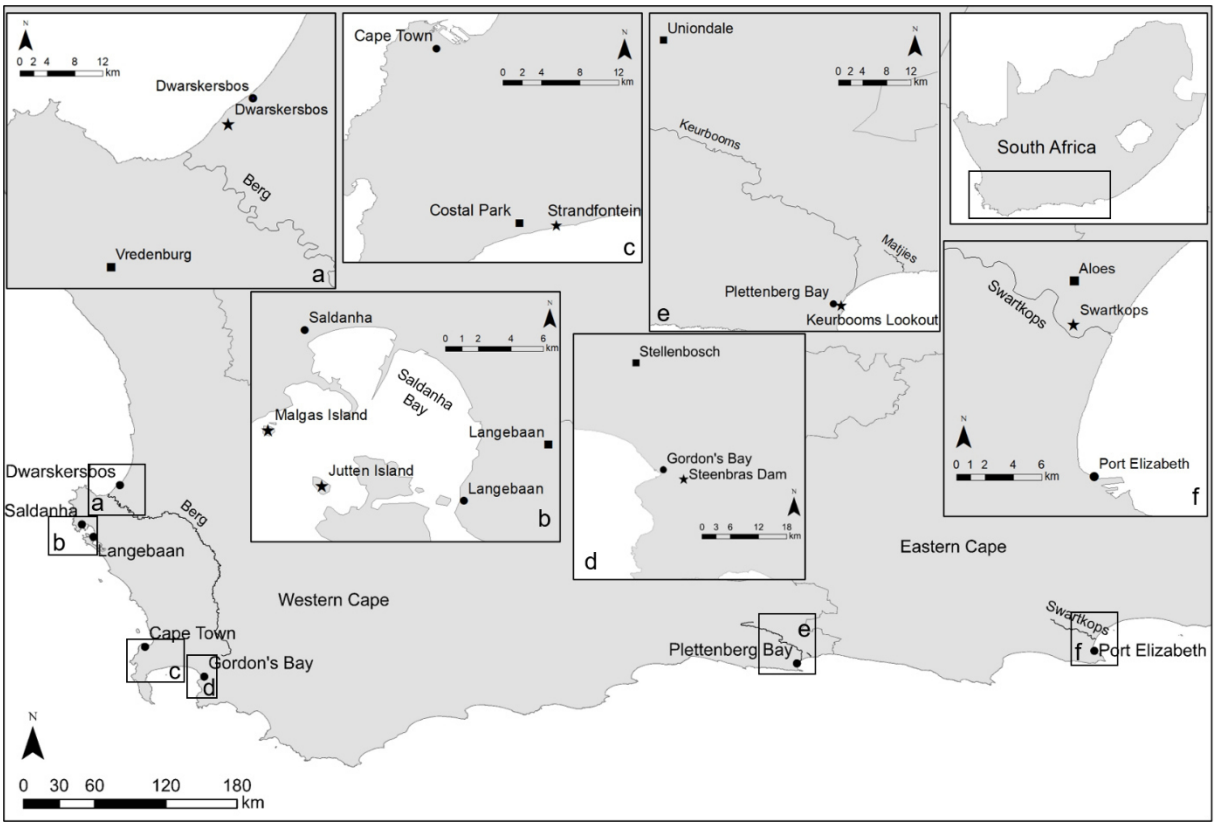

Figure 3.1: Map of the study areas showing the locations of the seven Kelp Gull colonies in South Africa (stars), closest urban areas (circles), and closest landfills (squares).

Sample collection

The diet and trophic ecology of incubating Kelp Gulls were investigated at seven colonies in October-November 2017 and at four colonies in October 2018, where incubating adults were captured with a noose placed over their nest. The diet of chicks was assessed in November-December 2017 at five colonies, with chicks, at least two weeks old, being captured by hand. Blood sample collection (1 ml) was attempted from all individuals either from the tarsal or brachial vein for stable isotope analysis using a slightly heparinized 2 ml syringe with a 25 gauge needle. Approximately 0.2 ml of whole blood was stored immediately in 70% ethanol. The rest of the blood, where available, was centrifuged for 10 minutes within 8 hours of collection, and plasma and red blood cells were stored in 70% ethanol and frozen upon return from fieldwork until sample preparation for stable isotope analysis. In addition, spontaneous regurgitates were systematically collected to assess the most recent diet of sampled Kelp Gull adults and chicks. When birds did not regurgitate spontaneously, standard stomach-pumping methods were applied by using a catheter to flush individuals with seawater (Martin & Hockey 1993). Samples were drained through a 0.5 mm sieve and stored in 70% ethanol until analysis in the lab. Due to additional samples collected for another part of this study (Chapters 2 and 4), handling time was ~ 10-12 minutes for each bird. Finally, regurgitated pellets were collected at all colonies during both incubation and chick-rearing stages in 2017 (except at SW during incubation in 2017 due to logistical issues) and during incubation in 2018. All pellets were stored individually in plastic bags and frozen until further analysis upon return from the field.

Diet sampling of seabirds can be challenging, and all methods used to collect information on the diet and trophic ecology have their limitations (Barrett et al. 2007). Stomach content samples can be collected through direct regurgitations or stomach-pumping, which are both causing disturbance to the animals, and samples can show differential digestion (Barrett et al. 2007). Collecting regurgitated pellets is less invasive, but they contain mostly large and indigestible prey items and can thus overestimate hard parts in the diet; like shells of coastal molluscs (Duffy & Jackson 1986). In addition, bones from smaller fish species can be digested (González-Solís et al. 1997), potentially resulting in underestimating marine items in pellets. Stable isotope analysis of carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$ provides information on the foraging habitat and trophic level, but can lack detail (Barrett et al. 2007). To overcome some of the limitations inherent to diet sampling we used a multifaceted approach.

Stomach content sample and pellet analysis

Both stomach contents and pellets were analysed in the lab using a stereo microscope where necessary to identify food remains. Food items were identified and assigned to five broad categories: “marine”, “coastal“, “terrestrial”, “anthropogenic”, and “unknown” (Table 3.1). Marine items were defined as any item from offshore environments, whereas coastal items originated from rocky shores, shallow coastal areas, and beaches. Terrestrial items of natural origin, such as remains from birds, mammals or land snails were classified as terrestrial. In addition, grass and vegetation were included as indicators for terrestrial foraging, as they might have been consumed while feeding on e.g. insects (O’Hanlon et al. 2017). Anthropogenic items included all non-natural debris such as plastic or glass mostly from terrestrial origin, as well as anthropogenic food remains, such as chicken bones. The frequency of occurrence was calculated for each of these five broad categories as the number of pellets or stomach content samples containing the respective food item, divided by the total number of pellets, or by the number of stomach content samples collected containing food items. Frequency of occurrence was calculated separately for each colony (DW, MA, JU, ST, SD, KE, SW), year (2017, 2018), and age group (adult or chick) and breeding stage (incubation or chick-rearing). For easier graphical representation, results are displayed as a percentage of 100%. The distinction between age group and breeding stage was necessary to clarify sample origin. Stomach content samples came directly from sampled individuals, and thus were known as to age group, as were pellets from incubating adults prior to the first chicks hatching. However, pellets collected after the first chicks hatched might have been from adults or chicks (Spaans 1971), thus reflecting breeding stage rather than age group, i.e. incubation vs chick-rearing.

Table 3.1: Broad diet categories of different food types from Kelp Gull *Larus dominicanus* stomach content and pellet samples collected during the breeding seasons 2017 and 2018.

Broad category	Food type
Marine	Fish remains Cephalopoda Cnidaria (*Vellela velella*) Violet sea snail *Janthina janthina* Red bait Marine anthropogenic (offal)
Coastal	Rocky shore mussel shells Other coastal molluscs

	Crustaceans (e.g. crayfish) Marine worms (mussle worm, wonder worm)
Terrestrial	Small mammals (e.g. hair and/ or small bone remains) Terrestrial arthropod pieces (e.g. insects) Terrestrial snails Bird remains (e.g. feathers, egg remains) Animal parts natural origin Grass and vegetation
Anthropogenic	Plastic Paper Glass and other hard materials Urban food remains (e.g. rice, chips, bread, dog pellets) Animal parts with terrestrial anthropogenic origin (e.g. chicken or pork bones) Remains of unidentified anthropogenic origin
Unknown	Meat and bone remains from unidentifiable origin (anthropogenic or natural) Arthropod remains from unidentifiable origin (terrestrial or coastal) Unidentifiable items

Stable isotope analysis

Blood plasma was used for stable isotope analysis as it integrates information from a few days to a week (Vander Zanden et al. 2015), thus represents the trophic ecology shortly before stomach sampling of incubating adults and chicks. Prior to analysis, plasma samples were oven dried at 50°C for 24-48 hours. The dried samples were subsequently ground to a fine powder. As plasma contains high lipid contents which can lower $\delta^{13}C$ values (Cherel et al. 2005), lipids were subsequently removed from a subsample where possible by using a 2:1 chloroform: methanol solution. Samples were then vortexed every 10 minutes for 1 hour, then centrifuged and the liquid fraction containing the lipids discarded. A subsample of 0.50 to 0.55 mg of both raw and delipidated plasma was weighed into a tin capsule and analysed to obtain $\delta^{15}N$ and $\delta^{13}C$ values. As all the plasma samples still had a C:N ratio above 3.5, even after delipidation, all samples were normalised using an equation for aquatic animals (Post et al. 2007):

$$\delta^{13}C_{\text{lipid corrected}} = \delta^{13}C_{\text{raw}} - 3.32 + 0.99 \times C{:}N$$

as has been done previously for gull blood plasma samples (Mendes et al. 2018). Relative isotopic abundances of carbon and nitrogen were determined with a Flash HT Plus elemental analyser coupled to a Delta V Advantage isotope ratio mass spectrometer by a ConFloIV interface (Environmental Isotope Laboratory, iThemba

Labs, Gauteng, Johannesburg, South Africa). Two in-house standards (Merck gel, $\delta^{13}C$ = -20.57 ‰, $\delta^{15}N$ = 6.80 ‰; urea IVA Analysentechnik e.K., $\delta^{13}C$ = -39.73 ‰, $\delta^{15}N$ = -0.73 ‰) were used to correct carbon and nitrogen isotope values for potential instrument drift. Laboratory standards and blanks were run after every 24 samples. Instrument drift was invariably less than 0.28 ‰ for $\delta^{13}C$ and 0.18 ‰ for $\delta^{15}N$ for Merck gel and 0.24 ‰ $\delta^{13}C$ and 0.12 ‰ $\delta^{15}N$ for urea.

Statistical analysis

All statistical analyses were carried out in R (version 4.0.2, R Core Team 2020). To check whether there were any possible differences in diet among colonies, years, and age group (stomach contents) or breeding stages (pellets), an ADONIS test (permutational multivariate analysis of variance using distance matrices) was implemented on the composition of stomach contents and pellets separately using the vegan package (Oksanen et al. 2019). A Jaccard dissimilarity matrix, suitable for presence-absence data, was used as the response variable, whereas the factors colony, year, and age group or breeding stage as well as the interactions colony and year, and colony and age group or breeding stage were used as explanatory variables. We performed post hoc pairwise Adonis tests on the significant explanatory variables using Benjamini and Hochberg corrections for multiple comparisons to allow pair-wise comparisons (package pairwiseAdonis, Martinez Arbizu 2020).

To further identify the effects of the factors colony, year, and age group/breeding stage on each of the four main broad diet categories in stomach content and pellet samples (presence-absence data), logistic regression models were fitted using the GLM function with a binomial family from the stats package (R Core Team 2020). Colony effect was tested by comparing all colonies sampled in 2017 during the incubation period only (stomach content samples: DW, MA, JU, ST, SD, KE, SW; pellet samples: DW, MA, JU, ST, SD, KE). For differences between years, only colonies sampled in both 2017 and 2018 were compared, i.e. DW, MA, JU, ST. Age group/ breeding stage effect was tested by comparing colonies sampled during both incubation and chick-rearing stages in 2017 only (stomach content samples – adults vs chicks: DW, ST, SD, KE, SW; pellet samples – incubation vs chick-rearing: DW, ST, SD, KE).

A correlation matrix was used to assess whether distance to landfill from each colony was related to the frequency of occurrence of anthropogenic diet items found in stomach content and pellet samples by using the cor.test function with the “Pearson”

method from the stats package (R Core Team 2020). For this we compared all colonies sampled in 2017 during the incubation period (DW, MA, JU, ST, SD, KE, SD).

Plasma $\delta^{13}C$ and $\delta^{15}N$ were analysed for differences between the factors colony, year, and age group by fitting general linear models (GLMs), after checking for normality of residuals. As before, differences between colonies were tested only during the 2017 incubation period, whereas differences between years were tested only between DW, MA, JU, and ST. Finally, age group differences were tested in 2017 only by comparing incubating adults with chicks sampled at five colonies (DW, ST, SD, KE, SW).

The MuMIn package (Barton 2019) was used for both the logistic regression models and the GLMs for averaging the different models and selecting the best fit model based on Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson 2002). Models were considered to be better than the null model when AIC_c differences were at least > 2 (Burnham & Anderson 2002). We performed post hoc Dunn's test on each significant explanatory variable of each model with Benjamini and Hochberg correction for multiple comparisons using the FSA package (Ogle et al. 2020).

Isotopic niche width of plasma stable isotope data was analysed using stable isotope Bayesian ellipses in R (SIBER), by calculating the standard ellipse areas corrected for small sample size (SEA_c) containing 40% of the data to measure and compare isotopic niches between colonies, years and age groups (Jackson et al. 2011). Posterior Bayesian standard ellipse areas (SEA_B) were calculated (Jackson et al. 2011) and used to test whether one group's SEA_B (colony, year, age group) was smaller than the other group's SEA_B in a probalistic manner. One group's SEA_B was almost always smaller than the other group's SEA_B with a probability of close to 1, and almost always bigger with a probability close to 0. Overlap in isotopic niche areas was used to identify overlap in resource use among groups (colony, year, age group). Therefore, the overlap between two ellipses was calculated based on the maximum likelihood fitted ellipses, and expressed as the proportion of area of overlap between two ellipses divided by the area of each ellipse, respectively (Jackson & Parnell 2020).

Results

Of the 373 birds sampled, 76 had empty stomachs, resulting in a total of 297 stomach content samples with food items. In addition, 1163 pellets and 345 plasma blood samples were collected at all seven colonies (Table 3.2).

Table 3.2: Number (N) of stomach content and plasma samples collected from incubating adult Kelp Gulls and Kelp Gull chicks, as well as number (N) of regurgitated pellets collected in each colony during either incubation or chick-rearing at seven colonies in South Africa in 2017 and 2018.

Colony	Year	Age group	N of stomach content samples	N of blood plasma samples	Breeding stage	N of pellet samples
Dwarskersbos	2017	Adult	16	21	Incubation	76
		Chick	26	19	Chick-rearing	66
	2018	Adult	16	23	Incubation	66
Malgas Island	2017	Adult	16	17	Incubation	68
	2018	Adult	21	22	Incubation	68
Jutten Island	2017	Adult	15	20	Incubation	62
	2018	Adult	21	26	Incubation	81
Strandfontein	2017	Adult	13	22	Incubation	90
		Chick	21	21	Chick-rearing	91
	2018	Adult	21	25	Incubation	71
Steenbras Dam	2017	Adult	15	22	Incubation	62
		Chick	21	22	Chick-rearing	88
Keurbooms	2017	Adult	17	21	Incubation	77
		Chick	21	20	Chick-rearing	91
Swartkops River	2017	Adult	12	22	Incubation	
		Chick	25	22	Chick-rearing	106
Total			**297**	**345**		**1163**

Results from the ADONIS test on the presence/absence data of stomach content and pellet samples showed that colony, year, age group/breeding stage, and the interactions colony and year and colony and age group/breeding stage all had a

significant effect on the diet (Table 3.3). Post-hoc pairwise Adonis tests on all the factors revealed that most comparisons were significant (Table S3.1-Table S3.6). Overall, marine items and mainly fish had the highest frequency of occurrence in all stomach content samples across colonies, years, and age groups (Table S3.7). In pellet samples, rocky shore mussel shells were the most frequent (coastal category; Table S3.8).

Spatial differences

Logistic regression results of stomach content samples showed significant differences between colonies across all broad diet categories (Table 3.3; Table S3.9). While anthropogenic food items were found in the diet of gulls from all colonies, birds from Strandfontein and Steenbras Dam had the highest amount in their diet (53-57%; Figure 3.2a), consisting mostly of animal parts (Table S3.7). Birds breeding at Swartkops, Jutten Island, and Keurbooms fed on terrestrial prey at a similar frequency (35-43%), while no terrestrial items were recorded in stomach contents of Dwarskersbos birds. These birds fed significantly more on coastal items (rocky shore mussels and other molluscs; 42%), compared to birds from Malgas Island, Strandfontein, Steenbras Dam, or Keurbooms (0-5%). Most marine items were found in stomach content samples at Malgas Island (63%), which differed significantly from Jutten, Strandfontein, Steenbras Dam and Keurbooms birds i.e. 11-24%, and was mostly fish and cephalopods.

Similarly, logistic regression results of pellets also showed significant differences in all broad diet categories apart from marine (Table 3.3; Table S3.10). Strandfontein, Steenbras Dam and Keurbooms all had more anthropogenic items in the pellets than Dwarskersbos, Malgas and Jutten Island (46-57% vs 0-17%), with a high contribution of plastic (Table S3.8). Pairwise comparisons showed significant differences between the two groups, as well as between Malgas and Jutten Island i.e. 5% and 17% (Figure 3.2b). Terrestrial items were present in over one quarter of the pellets from all colonies (Jutten, Malgas, Steenbras Dam, and Keurbooms), except Dwarskersbos, where the majority of pellets had coastal items, mainly rocky shore mussels. Coastal remains were also more frequent in the two island colonies (39-49%) compared to Strandfontein, Steenbras Dam, and Keurbooms (6-19%).

Table 3.3: Overview of significant effects (colony, year, age group/ breeding stage) on broad diet categories in stomach content and pellet samples from logistic regression models, and on $\delta^{13}C$ and $\delta^{15}N$ plasma stable isotope samples from general linear models (s: significant, ns: not significant).

Effect	Colony	Year	Age group/ Breeding stage	Colony*Year	Colony*Age group/ Breeding stage
Stomach content samples					
Marine	s	s	s	s	s
Coastal	s	s	ns	ns	ns
Terrestrial	s	ns	s	s	s
Anthropogenic	s	ns	ns	ns	ns
Unknown	ns	ns	ns	ns	ns
Pellets					
Marine	ns	ns	s	ns	s
Coastal	s	ns	s	ns	s
Terrestrial	s	s	s	s	ns
Anthropogenic	s	s	s	ns	s
Unknown	s	s	ns	ns	ns
Plasma stable isotopes					
$\delta^{13}C$	s	s	s	ns	s
$\delta^{15}N$	s	ns	ns	s	s

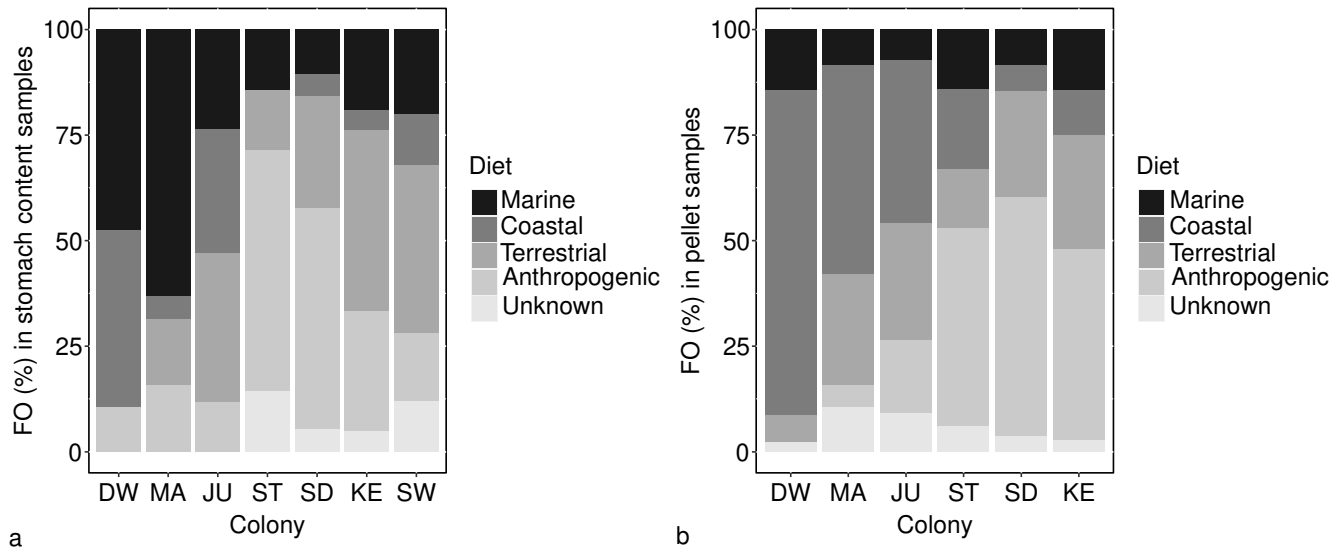

Figure 3.2: Frequency of occurrence (FO (%)) of each broad diet category (Marine, coastal, terrestrial, anthropogenic, unknown) at each colony during incubation in 2017 for **a)** stomach content samples and **b)** pellet samples. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops.

Plasma stable isotope data differed significantly among colonies for both $\delta^{13}C$ and $\delta^{15}N$ values (Table 3.3; Table S3.11). Both Dwarskersbos and Swartkops showed trends of higher $\delta^{13}C$ values in comparison to Malgas, Jutten, Strandfontein, and Steenbras Dam (Figure 3.3, Table S3.12). In addition, $\delta^{13}C$ values of Keurbooms were higher than Jutten and Strandfontein. Both Strandfontein and Swartkops had significantly lower $\delta^{15}N$ values than Dwarskersbos, Malgas, Jutten, and Keurbooms. Furthermore, $\delta^{15}N$ values from Jutten were lower than from Dwarskersbos, and $\delta^{15}N$ values from Steenbras Dam were lower than Dwarskerbos and Malgas. SEA_c differed between colonies (Figure 3.4; Table S3.13). SEA_B of Jutten was bigger than the SEA_B of all other colonies (Table S3.14). In addition, SEA_B of both Dwarskersbos and Keurbooms were smaller than Malgas, Steenbras Dam and Swartkops. Niche overlap was high with > 50% between most colonies (Table S3.15), except for Swartkops, which did not overlap with any of the other colonies.

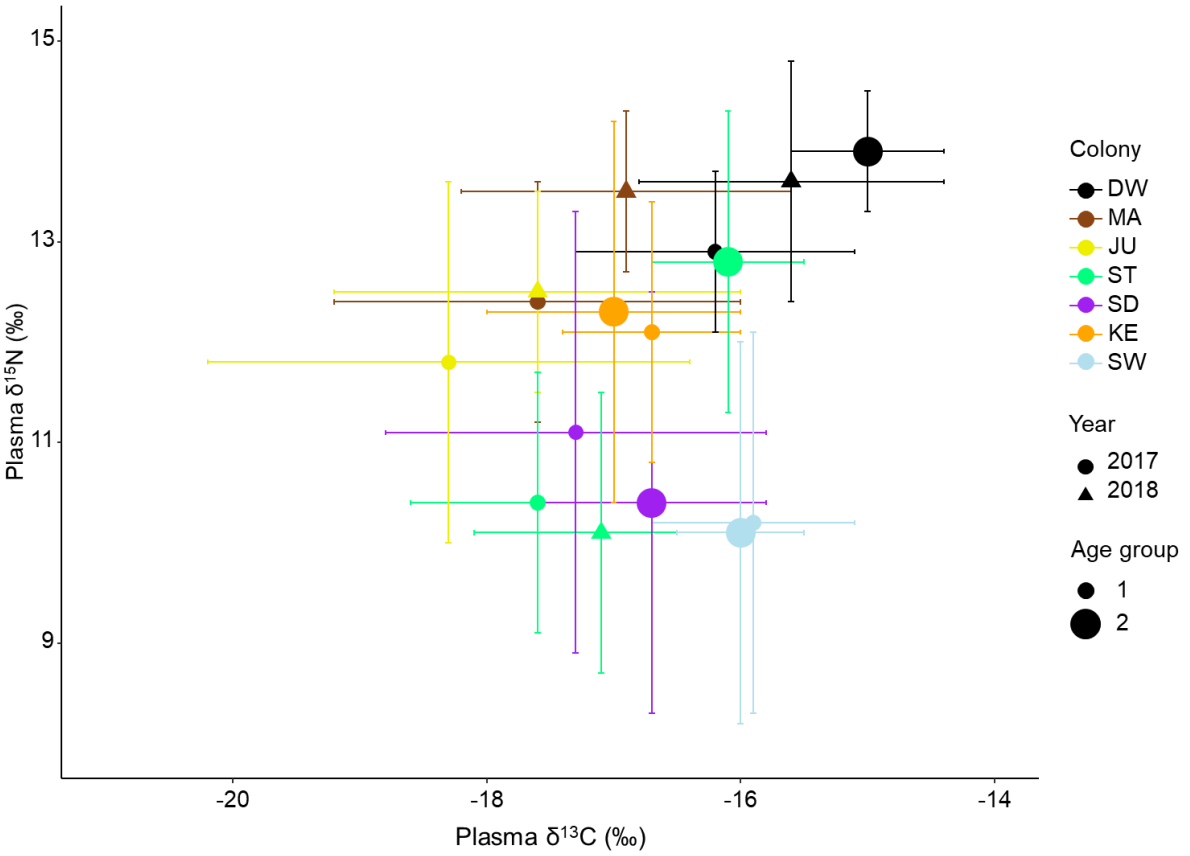

Figure 3.3: Mean ± SD stable carbon and nitrogen isotope ratios (‰) of blood plasma at seven different Kelp Gull colonies in South Africa sampled in 2017 (●) and 2018 (▲) of incubating adults (1) and chicks (2).

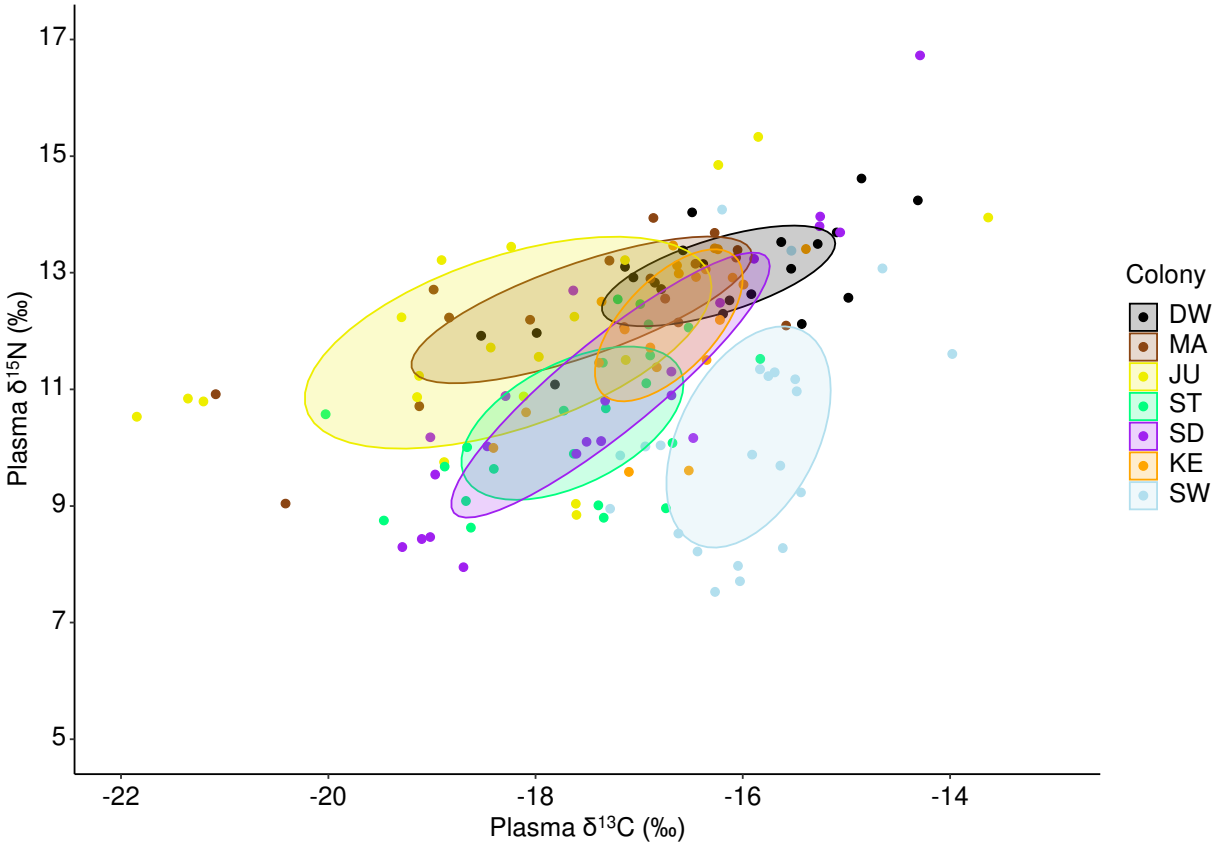

Figure 3.4: Biplot showing blood plasma stable isotope ratio values (points) of incubating adults at seven different colonies in 2017. Ellipses show the standard ellipse areas corrected for small sample size containing 40% of the data for each group. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops.

Results from the correlation tests showed no link between distance to landfill from each colony and frequency of occurrence of anthropogenic diet items found in either stomach contents (r value: -0.01, n = 7, p value > 0.05) or pellet samples (r value: 0.2, n = 6, p value > 0.05).

Annual differences

Stomach content samples did not vary significantly between years in frequency of occurrence of either anthropogenic or terrestrial diet items (Table 3.3; Table S3.9). However, birds fed overall more frequently on coastal remains in 2018. In addition, birds on Malgas Island had more marine remains in their diet in 2017, i.e. 63% in 2017

vs 8% in 2018. Even though samples did not vary in the frequency of terrestrial items, birds on Malgas had more bird remains in their diet in 2018 than 2017 (Table S3.7).

However, logistic regression results from pellet samples revealed the opposite, showing significant differences in anthropogenic and terrestrial items between years, but not in coastal and marine (Table 3.3; Table S3.10). Overall anthropogenic and terrestrial items were more frequent in 2017 among colonies, especially on Jutten Island where terrestrial items occurred almost twice as much in pellet samples in 2017.

Stable isotope samples revealed a difference between years, with $\delta^{13}C$ values being lower in 2017. $\delta^{15}N$ values were higher on Malgas in 2018 than 2017 (Table 3.3; Figure 3.3; Table S3.11; Table S3.12). SEA_c differed between years at some colonies (Figure 3.5; Table S3.13). SEA_B size of Jutten 2018 was smaller than the SEA_B of Jutten in 2017 (Table S3.16). In addition, the SEA_B of Dwarskersbos was smaller in 2017 than 2018. Niche overlap between Dwarskersbos in 2017 and 2018, Jutten 2018 and 2017, and Strandfontein 2018 and 2017 was high with more than 50%, whereas overlap between the remaining year and colony pairs was < 50% (Table S3.17).

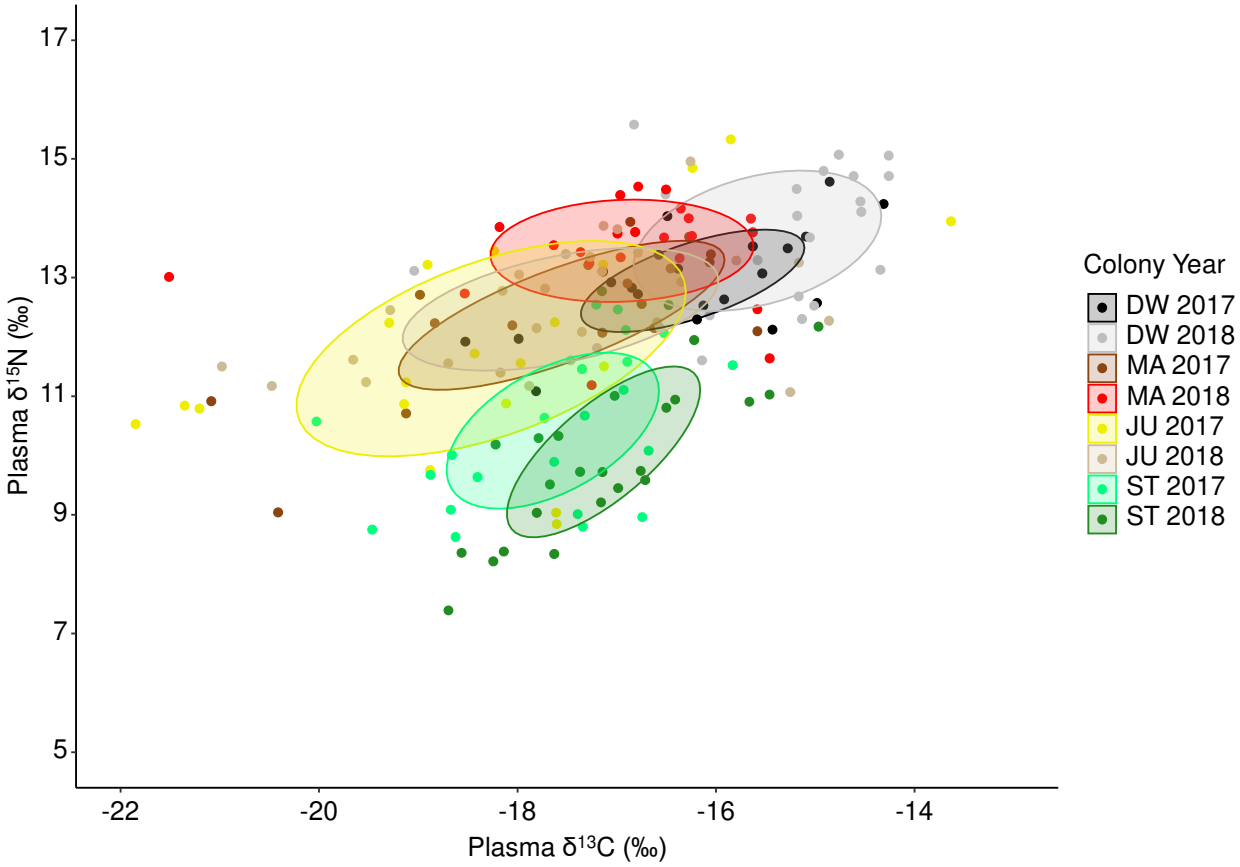

Figure 3.5: Biplot showing blood plasma stable isotope ratio values (points) of incubating adults at four different colonies in 2017 and 2018. Ellipses show the standard ellipse areas corrected for small sample size containing 40% of the data for each group. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein.

Age group/ breeding stage differences

Logistic regression results of stomach content samples showed a similar occurrence of anthropogenic and coastal items between age groups (Table 3.3; Table S3.9), but higher occurrence of terrestrial items in the stomachs of incubating adults than in chicks, especially in the south and east coast colonies, Keurbooms and Swartkops i.e. 40-43% in adults vs 10-18% in chicks. By contrast, there were significantly more marine items in chick stomachs than in incubating adults (mainly fish, Table S3.7), especially at Keurbooms and Strandfontein 14-19% in adults vs 58-65% in chicks.

In pellets, logistic regression results showed significant differences in all broad diet categories between breeding stages (Table 3.3; Table S3.10). Both anthropogenic and

marine items were more frequently found during chick-rearing, especially marine prey at Dwarskersbos, (i.e. 14% incubation vs 45% chick-rearing) representing fish (Table S3.8). Terrestrial and coastal items were represented more during incubation.

GLM results showed a significant effect of age group on $\delta^{13}C$, showing generally lower values in incubating adults than chicks (Table 3.3; Figure 3.3; Table S3.11; Table S3.12). The interaction between age group and colony also showed significant differences between incubating adults at Dwarskersbos and Strandfontein with significantly lower values for adults than for chicks at these two colonies. The interaction between age group and colony was also significant for $\delta^{15}N$ values, showing higher $\delta^{15}N$ values for chicks at Strandfontein compared to adults. SEA_c differed between age groups at some colonies (Figure 3.6; Table S3.13). SEA_B size of chicks at Dwarskersbos was smaller than SEA_B of all other colonies of both incubating adults and chicks (Table S3.18). Adults at Keurbooms had smaller SEA_B than their chicks, but this pattern was reversed at Strandfontein. Niche overlap between age groups varied between colonies (Table S3.19). High overlap of more than 50% was observed for both adults and chicks at Swartkops and Keurbooms.

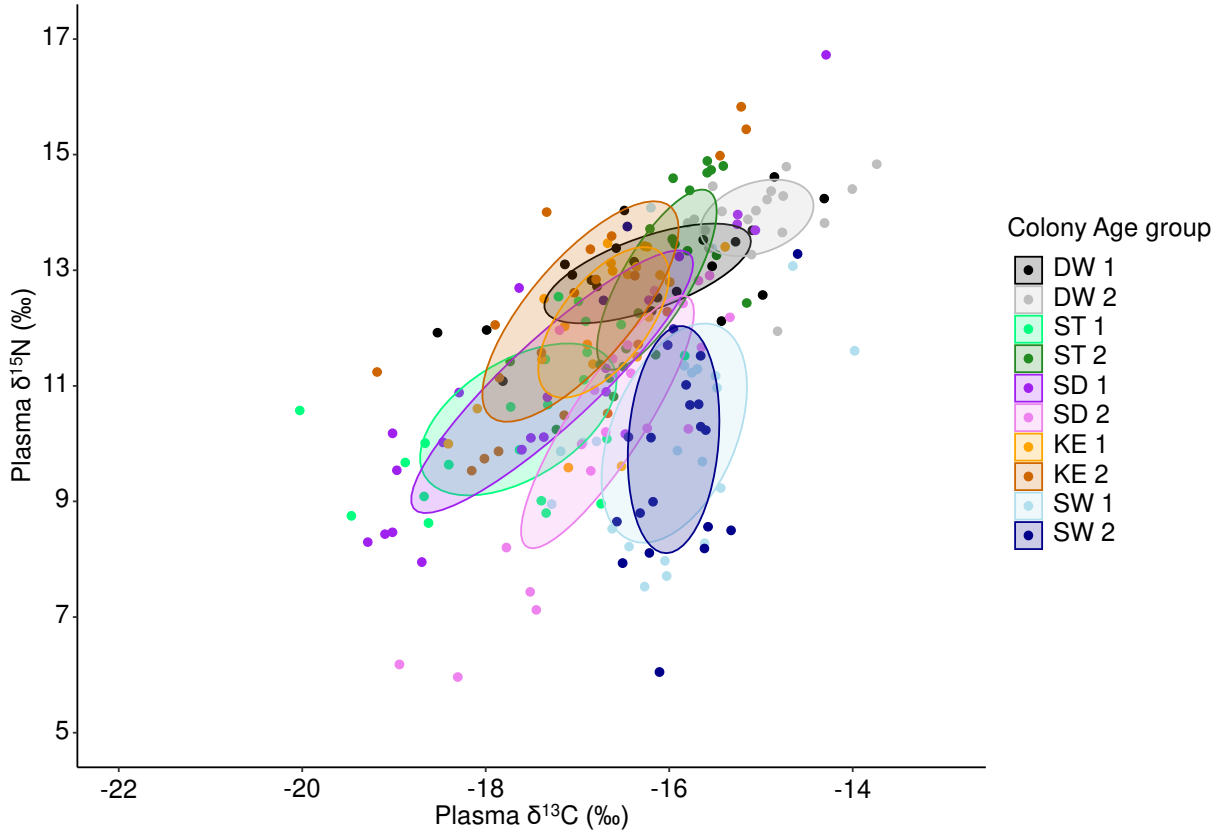

Figure 3.6: Biplot showing blood plasma stable isotope ratio values (points) of incubating adults and chicks at five different colonies in 2017 (1 = Incubating adult; 2 = Chick). Ellipses show the standard ellipse areas coorected for small sample size containing 40% of the data for each group. Colonies DW = Dwarskersbos, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops.

Discussion

Our study showed that breeding Kelp Gulls in South Africa were able to exploit a wide variety of resources, ranging from terrestrial to coastal and marine items, and from anthropogenic to natural food. These results, in addition to their wide isotopic spectrum, confirmed their opportunistic foraging behaviour as has been previously described in South Africa (e.g. Steele 1992, Hockey et al. 2005) and elsewhere (e.g. Bertellotti & Yorio 1999, Ludynia et al. 2005). However, despite this generalist behaviour, clear dietary and trophic differences were detected across spatial and annual scales, as well as between age groups and breeding stages.

Spatial differences

Only one of our colonies located close to a landfill, Strandfontein, had a high frequency of anthropogenic items in the diet. Thus, our hypothesis that anthropogenic items would be higher in the diet of birds breeding closer to landfills was only partly confirmed. Steenbras Dam and Keurbooms birds, located relatively far from landfills (26 and 51 km, respectively), also fed to a high extend on anthropogenic items, but as incubating Kelp Gulls can forage up to 80 km from their colonies (Chapter 2), those landfills are within their foraging range. In addition, both colonies are located close to relatively large cities (Gordon's Bay for Steenbras Dam, Plettenberg Bay for Keurbooms), so urban food could have been scavenged there, as has been shown for other opportunistic gulls (e.g. Shaffer et al. 2017, Van Donk et al. 2017, Spelt et al. 2019). Indeed, Keurbooms birds have been shown to forage relatively close to their colony, also within the urban area (Chapter 2). We expected birds from Swartkops to also feed on anthropogenic prey, given that the colony is close to a landfill and to the large urban area of Port Elizabeth. Previous work also showed a high contribution of anthropogenic items (65%) to their diet (Martin 1991). Interestingly, the contribution of anthropogenic items was low and might be related to better landfill management (P. Martin 2021, pers. comm.). Importantly, the Swartkops colony is located on a saltmarsh in an estuary close to the coast, and gulls may have chosen to forage in more natural areas readily available close to the colony, as landfills can also be areas of a highly competitive nature (Monaghan 1980). Therefore, the choice of South African Kelp Gulls to feed on anthropogenic food may have also depended on the availability of natural prey in the vicinity of their colony.

The two island colonies on the west coast, Malgas and Jutten, showed slight differences in diet composition despite being close neighbours. Jutten birds fed on a broader spectrum of resources and had the broadest isotopic niche, whereas gulls from Malgas exploited more marine (stomach contents) and coastal items (pellets). In fact, gulls on Malgas had the highest percentage of marine items compared to all other colonies, which could possibly originate from fishery discards (Steele 1992, Kasinsky et al. 2018), kleptoparasiting from other seabirds (García et al. 2010), or foraging at sea (Duffy 1989). As both colonies should have access to the same foraging habitats outside their breeding colonies due to their close geographical proximity, spatial segregation or differences in diet might be a strategy to reduce intra-specific competition (Corman et al. 2016, Shaffer et al. 2017, Bolton et al. 2019).

Gulls from Dwarskersbos fed almost exclusively on coastal and marine prey, mainly on rocky shore mussels and fish, reflected also in their narrower isotopic spectrum. Foraging habitat choice of Dwarskersbos gulls were also marine and coastal areas, with trips being farther when foraging at sea (Chapter 2). It seems like birds took advantage of rocky shore mussels closer to the colony, and even though mussels can have a comparably lower energy value, than e.g. fish, they can be an important food source for gulls, especially when located near the colony (O'Hanlon et al. 2017, Enners et al. 2018).

As a consequence, isotopic niches of gulls from Dwarskersbos and Keurbooms were narrower than niches from most colonies, suggesting some kind of specialisation or a smaller range of available resources. In particular, the plasma $\delta^{13}C$ and $\delta^{15}N$ values of gulls from Dwarskersbos were both enriched in comparison to some of the other colonies, revealing different foraging habitats and prey at a higher trophic level. Kohler et al. (2011) observed decreasing trends in $\delta^{15}N$ from west to east and increasing trends for $\delta^{13}C$ between the south and east coast and a relatively stable trend from Tsitsikamma to Namibia in African Black Oystercatcher *Haematopus moquini* tissues. The values in Kelp Gulls do not mirror these trends entirely, suggesting that those differences are indeed prey and habitat related rather than reflecting baseline changes.

Therefore, despite their generalist feeding behaviour, Kelp Gulls in South Africa show some tendency of specialisation at different colonies. Spatial differences in diet and trophic ecology between colonies might result from differences in resource availability within the foraging range (O'Hanlon et al. 2017, Yorio et al. 2020, Kasinsky et al. 2021), or local adaptations (Méndez et al. 2020, Ouled-Cheikh et al. 2021).

Annual differences

As expected, diet and trophic ecology of Kelp Gulls differed between years during the incubation period, especially in the amount of coastal and marine remains. In particular, birds from Malgas Island fed predominantly on marine items in 2017, but the higher $\delta^{15}N$ values in 2018 suggested that they were feeding at a higher trophic level that year. It is worth noting that in 2018, Kelp Gull predation on Cape Gannet eggs increased substantially in comparison to 2017, with Kelp Gulls taking roughly 8000 eggs from incubating birds (Pichegru 2019), possibly explaining enriched $\delta^{15}N$ values. This trend was also evident from stomach content samples, where terrestrial diet items

(especially bird remains) increased to more than double in frequency in 2018 than in 2017. Like many other large gull species (e.g. Spear 1993, Veitch et al. 2016, Maynard & Davoren 2020), Kelp Gulls in South Africa are known to predate on other seabird eggs and chicks (e.g. Cooper 1974, Du Toit et al. 2003). In mixed-seabird colonies there are usually some individual gulls that specialise on seabird predation (Pierotti & Annett 1991, Spear 1993), but opportunistic predation might increase as a result of a decrease in the frequency of other food sources, such as marine prey (Stenhouse & Montevecchi 1999), or even due to declining gannet population numbers, allowing easier predation (Gilchrist 1999). Furthermore, birds at Dwarskersbos had a wider isotopic niche in 2018 than 2017, and on Jutten in 2017 than 2018, which might indicate utilization of more diverse foraging habitats and trophic levels, potentially reflecting less resource availability in the environment, with birds foraging on a broader spectrum when preferred resources are not available (O'Hanlon et al. 2017). Nevertheless, niche overlap between years among colonies was high, apart from birds on Malgas, suggesting a somewhat general consistency in the broad spectrum of foraging habitat and trophic level choices for incubating Kelp Gulls in South Africa.

Interestingly, comparing Kelp Gull diet from pellet samples in this study to that from the southwestern Cape of South Africa from almost thirty years ago (Steele 1992) revealed similar patterns. Kelp Gulls in both studies foraged on a wide variety of prey, and showed comparable trends in their respective diet between gulls from more undisturbed and natural foraging areas and from anthropogenically modified areas (Steele 1992). Gulls foraging in natural areas fed mostly on coastal items, predominantly the sand mussel *Donax serra* (Steele 1992). Likewise, gulls from Dwarskersbos also extensively feed in coastal areas, mostly on rocky shore mussels. Urban foraging was mostly on fishery discards and refuse (Steele 1992), which, in part, is comparable to our Strandfontein colony with birds having the highest frequency of anthropogenic resources, mainly terrestrial anthropogenic animal parts (stomach contents) and plastic (pellets), in their diet. Even though the study by Steele (1992) did not discriminate between the breeding and non-breeding season, it still allowed a comparison of overall trends over time with regards to foraging habitat choice. It would be valuable for future studies to analyse foraging behaviour of non-breeding birds to identify whether individuals specialise on certain foraging areas or resources throughout their annual cycle, especially when they are not confined to areas around their breeding colony.

Age group and breeding stage

Differences between age groups were evident in diet and trophic ecology among colonies, although temporal variation in resource availability at the time of sampling might potentially be responsible for these differences. Chicks, at least at some colonies, were being fed a different and higher trophic level diet than incubating adults. As this trend was not evident at all colonies, it seems likely that results reflect a higher trophic level diet, rather than effects of growth and nutritional stress on $\delta^{15}N$ values (Sears et al. 2009). A change in the frequency of anthropogenic resources was especially evident between age groups at one of the urban colonies, Strandfontein. Chicks were being fed more marine resources, mostly fish, suggesting that habitat quality is more important than habitat location when provisioning chicks (Schwemmer & Garthe 2008). These results are in accordance with findings on Kelp Gull diet 30 years ago, where chicks from urban colonies were also provisioned with mainly marine prey, even though anthropogenic items seemed to be an important resource for incubating adults (Steele 1992).

Other opportunistic gull species also switch diets during chick rearing (e.g. Annett & Pierotti 1989, Smith & Carlile 1993, Bertellotti & Yorio 1999, Isaksson et al. 2016), and can demonstrate local differences between breeding sites (Arizaga et al. 2013, Pais de Faria et al. 2021). A diet comprising of energy-rich food (i.e. domestic refuse and fishery discards) can result in a higher breeding success than feeding on low-energy items such as bivalves (Van Donk et al. 2017), although close proximity to lower energy resources might also benefit breeding success (O'Hanlon et al. 2017). However, especially food from the marine environment, i.e. fish, has a high nutritional value and can easily be handled by chicks (Annett & Pierotti 1989), thus making it a valuable food resource for chick growth (Annett & Pierotti 1999). Fish quality might also be an important factor for chick development and subsequently breeding success (Wanless et al. 2005, Kitaysky et al. 2006). Low-lipid fish or fisheries discard can be considered "junk food", as they might not be sufficient for chick growth and survival (Grémillet et al. 2008), but adequate for adult gulls (Furness 2003).

Pellet samples also showed differences between breeding stages, but as pellets during chick-rearing can potentially be from both chick-rearing adults and chicks (Spaans 1971), we were not able to discern their origin. Adult gulls might feed their chicks a different diet than what they consume themselves (Schmutz & Hobson 1998,

Steenweg et al. 2011), thus making it difficult to interpret results from pellet samples between age groups.

While marine prey, especially fish, is often regarded as a high energy source for chicks (e.g. Annett & Pierotti 1989), a change in the trophic ecology between age groups was not systematic (e.g. Steenbras Dam or Swartkops). This has previously also been shown in other opportunistic gulls (O'Hanlon et al. 2017, Zorrozua et al. 2020). This result might be explained by differences in foraging areas and resources around the breeding areas (O'Hanlon et al. 2017), the lack of ability to switch to a higher-energy prey source (Zorrozua et al. 2020), or even the often more energetically demanding (Van Donk et al. 2019) and competitive nature of foraging in anthropogenic areas such as landfills (Monaghan 1980) or at sea on i.e. fishery discard (Camphuysen et al. 2015).

Conclusions

This is the first study on Kelp Gulls in South Africa to combine conventional diet analysis from stomach content and pellet samples with blood plasma stable isotope data to identify spatio-temporal and age group differences in diet and trophic ecology. We confirmed the flexibility of Kelp Gulls in their diet, which are able to take advantage of various resources around their breeding colonies. Observed differences in diet between colonies likely reflected local natural resource availability rather than proximity to landfills. Additional information on Kelp Gull diet outside the breeding season would be necessary to fully understand foraging patterns of Kelp Gulls in South Africa, as birds are then not confined to foraging close to their breeding colonies (Chapter 2). To see whether differences in diet and trophic ecology result in increased or decreased reproductive success, as has been shown in other studies (O'Hanlon et al. 2017), (Van Donk et al. 2017), it would be valuable to incorporate a measure of breeding success and colony health status in the future (Chapter 4). Such information will help to identify drivers for population dynamics and can subsequently be used for management purposes.

Overall, their ability to exploit various resources has allowed the Kelp Gull to be an abundant species in South Africa. In case of food scarcity, switching to different foraging habitats makes them less prone to population declines, but could potentially

increase predation on other seabird eggs and chicks, especially in mixed breeding colonies.

Supplementary information

Table S3.1: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether stomach content samples differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops). Cells in grey show significant results.

	DW	MA	JU	ST	SD	KE
MA	F=4.90 R^2=0.05 p.adj.=0.013					
JU	F=2.61 R^2=0.03 p.adj.=0.095	F=0.44 R^2=0.01 p.adj.=0.716				
ST	F=13.99 R^2=0.11 p.adj.=0.004	F=7.15 R^2=0.07 p.adj.=0.004	F=8.52 R^2=0.09 p.adj.=0.004			
SD	F=14.06 R^2=0.13 p.adj.=0.004	F=4.23 R^2=0.06 p.adj.=0.014	F=5.83 R^2=0.08 p.adj.=0.004	F=2.09 R^2=0.02 p.adj.=0.128		
KE	F=7.64 R^2=0.08 p.adj.=0.006	F=2.62 R^2=0.03 p.adj.=0.083	F=3.94 R^2=0.05 p.adj.=0.015	F=5.42 R^2=0.06 p.adj.=0.009	F=5.41 R^2=0.07 p.adj.=0.009	
SW	F=11.57 R^2=0.11 p.adj.=0.004	F=2.27 R^2=0.03 p.adj.=0.095	F=3.85 R^2=0.05 p.adj.=0.018	F=5.03 R^2=0.05 p.adj.=0.013	F=1.78 R^2=0.02 p.adj.=0.175	F=2.30 R^2=0.03 p.adj.=0.105

Table S3.2: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether stomach content samples differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops) and sampling years (2017,2018). Cells in grey show significant results.

	DW_2017	DW_2018	MA_2017	MA_2018	JU_2017	JU_2018	ST_2017	ST_2018	SD_2017	KE_2017
DW_2018	F=4.17 R^2=0.07 p.adj.=0.036									
MA_2017	F=2.66 R^2=0.05 p.adj.=0.083	F=7.07 R^2=0.19 p.adj.=0.007								
MA_2018	F=11.74 R^2=0.16 p.adj.=0.003	F=2.93 R^2=0.08 p.adj.=0.059	F=8.95 R^2=0.20 p.adj.=0.003							
JU_2017	F=5.17 R^2=0.09 p.adj.=0.011	F=2.05 R^2=0.07 p.adj.=0.136	F=4.14 R^2=0.12 p.adj.=0.031	F=0.51 R^2=0.01 p.adj.=0.678						
JU_2018	F=1.25 R^2=0.02 p.adj.=0.300	F=1.11 R^2=0.03 p.adj.=0.363	F=2.69 R^2=0.07 p.adj.=0.072	F=3.22 R^2=0.07 p.adj.=0.041	F=1.14 R^2=0.03 p.adj.=0.323					
ST_2017	F=5.80 R^2=0.07 p.adj.=0.008	F=6.72 R^2=0.12 p.adj.=0.003	F=1.69 R^2=0.03 p.adj.=0.224	F=9.60 R^2=0.15 p.adj.=0.003	F=4.60 R^2=0.09 p.adj.=0.011	F=3.35 R^2=0.06 p.adj.=0.041				
ST_2018	F=20.08 R^2=0.25 p.adj.=0.003	F=9.87 R^2=0.22 p.adj.=0.003	F=12.40 R^2=0.26 p.adj.=0.003	F=10.60 R^2=0.21 p.adj.=0.003	F=8.40 R^2=0.20 p.adj.=0.005	F=9.80 R^2=0.20 p.adj.=0.003	F=6.59 R^2=0.11 p.adj.=0.010			
SD_2017	F=14.60 R^2=0.16 p.adj.=0.003	F=6.73 R^2=0.12 p.adj.=0.003	F=6.77 R^2=0.12 p.adj.=0.003	F=5.36 R^2=0.09 p.adj.=0.008	F=3.41 R^2=0.07 p.adj.=0.038	F=5.34 R^2=0.09 p.adj.=0.005	F=3.56 R^2=0.05 p.adj.=0.036	F=2.98 R^2=0.05 p.adj.=0.059		

KE_2017	F=5.82 R^2=0.07 p.adj.=0.003	F=7.72 R^2=0.13 p.adj.=0.003	F=0.79 R^2=0.01 p.adj.=0.460	F=8.39 R^2=0.13 p.adj.=0.003	F=3.26 R^2=0.06 p.adj.=0.045	F=3.06 R^2=0.05 p.adj.=0.045	F=1.46 R^2=0.02 p.adj.=0.259	F=11.73 R^2=0.17 p.adj.=0.003	F=5.41 R^2=0.07 p.adj.=0.007	
SW_2017	F=11.20 R^2=0.13 p.adj.=0.003	F=6.93 R^2=0.12 p.adj.=0.003	F=4.22 R^2=0.08 p.adj.=0.011	F=4.79 R^2=0.08 p.adj.=0.007	F=2.13 R^2=0.04 p.adj.=0.094	F=3.87 R^2=0.06 p.adj.=0.011	F=3.24 R^2=0.04 p.adj.=0.041	F=8.41 R^2=0.13 p.adj.=0.003	F=1.78 R^2=0.02 p.adj.=0.171	F=2.30 R^2=0.03 p.adj.=0.083

Table S3.3: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether stomach content samples differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops) and age groups (1 Incubating adults, 2 Chicks). Cells in grey show significant results.

	DW_1	DW_2	MA_1	JU_1	ST_1	ST_2	SD_1	SD_2	KE_1	KE_2	SW_1
DW_2	F=4.65 R^2=0.08 p.adj.=0.023										
MA_1	F=4.08 R^2=0.06; p.adj.=0.014	F=4.99 R^2=0.08 p.adj.=0.012									
JU_1	F=1.99 R^2=0.03 p.adj.=0.152	F=3.96 R^2=0.06 p.adj.=0.023	F=0.44 R^2=0.01 p.adj.=0.718								
ST_1	F=17.18 R^2=0.21 p.adj.=0.002	F=21.70 R^2=0.27 p.adj.=0.002	F=11.56 R^2=0.14 p.adj.=0.002	F=13.36 R^2=0.16 p.adj.=0.002							
ST_2	F=8.49 R^2=0.14 p.adj.=0.002	F=1.29 R^2=0.03 p.adj.=0.267	F=6.26 R^2=0.10 p.adj.=0.002	F=6.28 R^2=0.10 p.adj.=0.006	F=17.54 R^2=0.25 p.adj.=0.002						
SD_1	F=11.12 R^2=0.20 p.adj.=0.002	F=15.10 R^2=0.28 p.adj.=0.002	F=4.85 R^2=0.09 p.adj.=0.012	F=6.46 R^2=0.12 p.adj.=0.002	F=1.31 R^2=0.03 p.adj.=0.288	F=13.72 R^2=0.29 p.adj.=0.002					

SD_2	F=5.27 R^2=0.09 p.adj.=0.008	F=6.25 R^2=0.12 p.adj.=0.002	F=2.07 R^2=0.04 p.adj.=0.155	F=2.63 R^2=0.05 p.adj.=0.063	F=3.66 R^2=0.06 p.adj.=0.023	F=5.63 R^2=0.12 p.adj.=0.006	F=2.12 R^2=0.06 p.adj.=0.106				
KE_1	F=9.29 R^2=0.17 p.adj.=0.002	F=10.62 R^2=0.21 p.adj.=0.002	F=2.07 R^2=0.04 p.adj.=0.136	F=3.66 R^2=0.07 p.adj.=0.023	F=5.63 R^2=0.10 p.adj.=0.006	F=9.99 R^2=0.22 p.adj.=0.002	F=1.38 R^2=0.04 p.adj.=0.261	F=1.95 R^2=0.05 p.adj.=0.152			
KE_2	F=11.31 R^2=0.18 p.adj.=0.002	F=1.87 R^2=0.04 p.adj.=0.145	F=7.83 R^2=0.12 p.adj.=0.004	F=7.94 R^2=0.13 p.adj.=0.002	F=23.34 R^2=0.31 p.adj.=0.002	F=0.33 R^2=0.01 p.adj.=0.821	F=18.23 R^2=0.35 p.adj.=0.002	F=8.30 R^2=0.17 p.adj.=0.002	F=12.44 R^2=0.26 p.adj.=0.002		
SW_1	F=9.02 R^2=0.18 p.adj.=0.002	F=10.93 R^2=0.23 p.adj.=0.002	F=2.37 R^2=0.05 p.adj.=0.093	F=3.40 R^2=0.07 p.adj.=0.032	F=10.73 R^2=0.20 p.adj.=0.002	F=12.33 R^2=0.28 p.adj.=0.002	F=4.45 R^2=0.15 p.adj.=0.023	F=3.33 R^2=0.10 p.adj.=0.030	F=1.16 R^2=0.04 p.adj.=0.317	F=15.08 R^2=0.33 p.adj.=0.002	
SW_2	F=7.62 R^2=0.12 p.adj.=0.002	F=6.17 R^2=0.11 p.adj.=0.004	F=2.52 R^2=0.04 p.adj.=0.084	F=3.58 R^2=0.06 p.adj.=0.014	F=4.86 R^2=0.08 p.adj.=0.008	F=4.69 R^2=0.10 p.adj.=0.018	F=2.58 R^2=0.06 p.adj.=0.094	F=0.27 R^2=0.01 p.adj.=0.872	F=1.74 R^2=0.04 p.adj.=0.191	F=6.71 R^2=0.13 p.adj.=0.002	F=3.30 R^2=0.09 p.adj.=0.045

Table S3.4: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether pellets collected differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops). Cells in grey show significant results.

	DW	MA	JU	ST	SD	KE
MA	F=16.77 R^2=0.05 p.adj.=0.001					
JU	F=22.24 R^2=0.06 p.adj.=0.001	F=4.72 R^2=0.02 p.adj.=0.005				
ST	F=134.35 R^2=0.23	F=77.39 R^2=0.17	F=43.13 R^2=0.10			

	p.adj.=0.001	p.adj.=0.001	p.adj.=0.001			
SD	F=204.36 R^2=0.36 p.adj.=0.001	F=123.03 R^2=0.30 p.adj.=0.001	F=81.65 R^2=0.22 p.adj.=0.001	F=14.32 R^2=0.03 p.adj.=0.001		
KE	F=192.04 R^2=0.34 p.adj.=0.001	F=115.55 R^2=0.28 p.adj.=0.001	F=76.27 R^2=0.20 p.adj.=0.001	F=10.88 R^2=0.03 p.adj.=0.001	F=0.90 R^2=0.003 p.adj.=0.407	
SW	F=122.03 R^2=0.28 p.adj.=0.001	F=66.70 R^2=0.22 p.adj.=0.001	F=44.19 R^2=0.15 p.adj.=0.001	F=9.58 R^2=0.03 p.adj.=0.001	F=4.49 R^2=0.02 p.adj.=0.019	F=3.27 R^2=0.01 p.adj.=0.044

Table S3.5: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether pellets collected differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops) and sampling years (2017,2018). Cells in grey show significant results.

	DW_2017	DW_2018	MA_2017	MA_2018	JU_2017	JU_2018	ST_2017	ST_2018	SD_2017	KE_2017
DW_2018	F=0.33 R^2=0.002 p.adj.=0.729									
MA_2017	F=10.56 R^2=0.05 p.adj.=0.001	F=5.22 R^2=0.04 p.adj.=0.005								
MA_2018	F=10.92 R^2=0.05 p.adj.=0.001	F=5.46 R^2=0.04 p.adj.=0.003	F=0.53 R^2=0.004 p.adj.=0.660							
JU_2017	F=18.78 R^2=0.09 p.adj.=0.001	F=10.88 R^2=0.08 p.adj.=0.001	F=2.36 R^2=0.02 p.adj.=0.079	F=3.80 R^2=0.03 p.adj.=0.017						

JU_2018	F=11.92 R^2=0.05 p.adj.=0.001	F=6.58 R^2=0.04 p.adj.=0.003	F=3.74 R^2=0.02 p.adj.=0.021	F=3.96 R^2=0.03 p.adj.=0.016	F=3.82 R^2=0.03 p.adj.=0.016					
ST_2017	F=115.15 R^2=0.26 p.adj.=0.001	F=66.96 R^2=0.21 p.adj.=0.001	F=51.70 R^2=0.17 p.adj.=0.001	F=58.43 R^2=0.19 p.adj.=0.001	F=26.42 R^2=0.10 p.adj.=0.001	F=41.97 R^2=0.14 p.adj.=0.001				
ST_2018	F=36.37 R^2=0.15 p.adj.=0.001	F=23.38 R^2=0.15 p.adj.=0.001	F=15.06 R^2=0.10 p.adj.=0.001	F=18.04 R^2=0.12 p.adj.=0.001	F=5.78 R^2=0.04 p.adj.=0.003	F=10.33 R^2=0.06 p.adj.=0.001	F=5.06 R^2=0.02 p.adj.=0.003			
SD_2017	F=171.11 R^2=0.37 p.adj.=0.001	F=104.93 R^2=0.33 p.adj.=0.001	F=78.71 R^2=0.27 p.adj.=0.001	F=87.04 R^2=0.29 p.adj.=0.001	F=44.39 R^2=0.17 p.adj.=0.001	F=71.09 R^2=0.24 p.adj.=0.001	F=8.88 R^2=0.03 p.adj.=0.001	F=17.21 R^2=0.07 p.adj.=0.001		
KE_2017	F=158.10 R^2=0.34 p.adj.=0.001	F=94.01 R^2=0.29 p.adj.=0.001	F=71.42 R^2=0.23 p.adj.=0.001	F=79.77 R^2=0.25 p.adj.=0.001	F=39.43 R^2=0.15 p.adj.=0.001	F=65.44 R^2=0.21 p.adj.=0.001	F=6.17 R^2=0.02 p.adj.=0.001	F=14.08 R^2=0.06 p.adj.=0.001	F=0.90 R^2=0.003 p.adj.=0.422	
SW_2017	F=103.34 R^2=0.30 p.adj.=0.001	F=63.20 R^2=0.27 p.adj.=0.001	F=42.56 R^2=0.20 p.adj.=0.001	F=48.43 R^2=0.22 p.adj.=0.001	F=21.65 R^2=0.12 p.adj.=0.001	F=41.96 R^2=0.18 p.adj.=0.001	F=8.13 R^2=0.03 p.adj.=0.001	F=8.87 R^2=0.05 p.adj.=0.001	F=4.49 R^2=0.02 p.adj.=0.013	F=3.27 R^2=0.01 p.adj.=0.027

Table S3.6: Post-hoc pairwise Adonis test results with Benjamini and Hochberg corrections for multiple comparisons after Adonis test on a Jaccard distance matrix for presence absence data, showing whether pellets collected differed among Kelp Gull colonies sampled (DW Dwarskersbos, MA Malgas, JU Jutten, ST Strandfontein, SD Steenbras Dam, KE Keurbooms, SW Swartkops) and breeding stages (1 Incubation, 2 chick-rearing). Cells in grey show significant results.

	DW_1	DW_2	MA_1	JU_1	ST_1	ST_2	SD_1	SD_2	KE_1	KE_2
DW_2	F=21.71 R^2=0.10 p.adj.=0.001									
MA_1	F=13.47 R^2=0.05	F=21.45 R^2=0.10								

	p.adj.=0.001	p.adj.=0.001								
JU_1	F=19.88 R^2=0.07 p.adj.=0.001	F=21.24 R^2=0.09 p.adj.=0.001	F=4.72 R^2=0.02 p.adj.=0.008							
ST_1	F=97.81 R^2=0.25 p.adj.=0.001	F=40.32 R^2=0.15 p.adj.=0.001	F=55.76 R^2=0.16 p.adj.=0.001	F=29.19 R^2=0.09 p.adj.=0.001						
ST_2	F=112.53 R^2=0.33 p.adj.=0.001	F=48.47 R^2=0.24 p.adj.=0.001	F=61.71 R^2=0.22 p.adj.=0.001	F=35.61 R^2=0.13 p.adj.=0.001	F=2.00 R^2=0.01 p.adj.=0.120					
SD_1	F=123.41 R^2=0.38 p.adj.=0.001	F=53.74 R^2=0.30 p.adj.=0.001	F=63.44 R^2=0.24 p.adj.=0.001	F=40.70 R^2=0.17 p.adj.=0.001	F=7.29 R^2=0.03 p.adj.=0.001	F=2.46 R^2=0.02 p.adj.=0.081				
SD_2	F=176.57 R^2=0.44 p.adj.=0.001	F=76.98 R^2=0.34 p.adj.=0.001	F=98.31 R^2=0.31 p.adj.=0.001	F=64.40 R^2=0.22 p.adj.=0.001	F=13.41 R^2=0.05 p.adj.=0.001	F=4.80 R^2=0.03 p.adj.=0.009	F=0.93 R^2=0.01 p.adj.=0.406			
KE_1	F=106.50 R^2=0.33 p.adj.=0.001	F=41.28 R^2=0.23 p.adj.=0.001	F=53.81 R^2=0.20 p.adj.=0.001	F=34.54 R^2=0.14 p.adj.=0.001	F=5.78 R^2=0.02 p.adj.=0.001	F=2.91 R^2=0.02 p.adj.=0.056	F=1.46 R^2=0.01 p.adj.=0.232	F=5.31 R^2=0.03 p.adj.=0.008		
KE_2	F=197.62 R^2=0.46 p.adj.=0.001	F=85.41 R^2=0.36 p.adj.=0.001	F=112.13 R^2=0.33 p.adj.=0.001	F=73.50 R^2=0.24 p.adj.=0.001	F=15.14 R^2=0.06 p.adj.=0.001	F=5.86 R^2=0.03 p.adj.=0.004	F=2.08 R^2=0.01 p.adj.=0.120	F=0.56 R^2=0.003 p.adj.=0.588	F=7.31 R^2=0.04 p.adj.=0.003	
SW_2	F=130.58 R^2=0.35 p.adj.=0.001	F=53.07 R^2=0.24 p.adj.=0.001	F=66.70 R^2=0.22 p.adj.=0.001	F=44.19 R^2=0.15 p.adj.=0.001	F=9.68 R^2=0.04 p.adj.=0.001	F=4.96 R^2=0.02 p.adj.=0.016	F=1.17 R^2=0.01 p.adj.=0.294	F=5.17 R^2=0.03 p.adj.=0.013	F=0.79 R^2=0.004 p.adj.=0.461	F=7.63 R^2=0.04 p.adj.=0.003

Table S3.7: Frequency of occurrence of detailed food type categories from stomach content samples of adults and chicks at seven colonies in 2017 and 2018.

	Colony	Dwarskerbos			Malgas		Jutten		Strandfontein			Steenbras Dam		Keurbooms		Swartkops		Total
	Year	2017		2018	2017	2018	2017	2018	2017		2018	2017		2017		2017		
	Age group	Adult	Chick	Adult	Adult	Adult	Adult	Adult	Adult	Chick	Adult	Adult	Chick	Adult	Chick	Adult	Chick	
Foraging habitat	Food type	Frequency of occurrence (%)																
Marine	Fish	50.0	80.8	31.3	50.0	9.5	26.7	14.3	15.4	81.0	14.3	13.3	47.6	17.6	90.5	16.7	36.0	595.0
	Cephalopoda	0	7.7	0	25.0	0	0	14.3	0	0	9.5	0	0	5.9	9.5	25.0	20.0	116.9
	Cnidaria	0	0	0	0	0	0	4.8	0	0	0	0	0	0	0	0	0	4.8
	Bubble raft shell	0	0	0	0	0	6.7	4.8	0	0	0	0	0	0	0	0	0	11.5
	Red bait	0	0	0	6.3	0	0	0	0	0	0	0	0	0	0	0	0	6.3
	Marine anthropogenic	6.3	0	0	0	0	0	14.3	0	4.8	0	0	0	5.9	4.8	0	0	36.1
Coastal	Rocky shore mussel shells	50.0	0	25.0	0	4.8	6.7	14.3	0	0	0	0	0	5.9	0	0	0	106.7
	Other coastal molluscs	12.5	19.2	31.3	0	23.8	6.7	23.8	0	14.3	0	0	9.5	0	9.5	0	4.0	154.6
	Crustaceans	0	11.5	0	6.3	0	20.0	4.8	0	0	0	6.7	0	0	0	25.0	4.0	78.3
	Marine worms	0	0	18.8	0	4.8	0	4.8	0	0	0	0	14.3	0	0	0	0	42.7

	Crayfish	0	3.8	0	0	14.3	20.0	4.8	0	0	9.5	0	0	0	0	0	0	52.4
Terrestrial	Small mammals	0	0	0	0	0	0	0	0	0	0	0	9.5	17.6	0	0	0	27.1
	Terrestrial arthropods	0	0	0	0	6.3	26.7	0	0	4.8	0	0	14.3	29.4	9.5	16.7	8.0	115.7
	Terrestrial snails	0	0	0	6.3	4.8	20.0	9.5	0	0	0	6.7	0	5.9	0	0	0	53.2
	Bird remains	0	3.8	0	6.3	38.1	6.7	4.8	7.7	9.5	0	6.7	4.8	0	0	41.7	12.0	142.1
	Animal parts natural origin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.3	8.0	16.3
	Grass and vegetation	0	3.8	0	6.3	0	0	0	7.7	0	0	26.7	4.8	11.8	4.8	16.7	0	82.6
Anthro-pogenic	Plastic	0	7.7	0	0	4.80	0	0	23.1	19.0	0	20.0	42.9	5.9	4.8	16.7	36.0	180.9
	Paper	0	0	0	6.3	0	0	0	15.4	4.8	4.8	0	0	0	0	0	0	31.3
	Glass and other hard materials	6.3	0	0	6.3	0	0	0	0	4.8	0	13.3	4.8	0.0	4.8	16.7	0	57.0
	Urban food remains	6.3	0	0	0	4.8	13.3	4.8	15.4	0	19.0	40.0	9.5	11.8	9.5	8.3	16.0	158.7
	Animal parts terrestrial anthropogenic origin	0	3.8	18.8	6.3	9.5	13.3	4.8	46.2	4.8	47.6	53.3	9.5	23.5	4.8	0	8.0	254.2
	Anthropogenic unidentified	6.25	0	0	6.25	0	0	0	0	0	0	0	0	0	0	0	0	12.5

Table S3.8: Frequency of occurrence of detailed food type categories from regurgitated pellet samples during incubation (incu) and chick-rearing (chick) at seven colonies in 2017 and 2018.

	Colony	Dwarskerbos			Malgas		Jutten		Strandfontein			Steenbras Dam		Keurbooms		Swartkops	Total
	Year	2017		2018	2017	2018	2017	2018	2017		2018	2017		2017		2017	
	Age group	Incu	Chick	Incu	Incu	Incu	Incu	Incu	Incu	Chick	Incu	Incu	Chick	Incu	Chick	Chick	
Foraging habitat	Food type	Frequency of occurence (%)															
Marine	Fish	17.1	56.1	33.3	8.8	7.4	11.3	7.4	20.0	18.7	18.3	11.3	8.0	18.2	12.1	10.4	258.4
	Cephalopoda	0	0	0	2.9	1.5	0	1.2	3.3	0	0	1.6	0	2.6	0	1.9	15.0
Coastal	Rocky shore mussel shells	84.2	21.2	54.5	32.4	58.8	35.5	54.3	24.4	13.2	38.0	3.2	0	1.3	1.1	0	422.1
	Other coastal molluscs	2.6	4.5	10.6	0	19.1	17.7	9.9	6.7	14.3	11.3	1.6	3.4	13.0	0	0.9	115.6
	Crustaceans	0	7.6	1.5	0	1.5	1.6	0	1.1	0	1.4	0	0	0	2.2	7.5	24.4
	Crayfish	6.6	24.2	22.7	38.2	8.8	9.7	16.0	2.2	1.1	1.4	3.2	0	1.3	0	0	135.4
Terrestrial	Small mammals	2.6	1.5	0	7.4	1.5	14.5	6.2	7.8	2.2	11.3	0	2.3	2.6	4.4	5.7	70.0
	Terrestrial arthropods	5.3	0	1.5	0	1.5	6.5	0	1.1	2.2	0	4.8	0	9.1	5.5	4.7	42.2
	Terrestrial snails	0	1.5	1.5	2.9	0	3.2	0	0	0	0	0	2.3	0	0	0	11.4

	Bird remains	1.3	4.5	12.9	27.9	27.9	12.9	6.2	7.8	16.5	12.7	22.6	15.9	7.8	4.4	30.2	211.5
	Animal parts natural origin	0	1.5	0	0	0	0	0	0	0	0	0	0	1.3	0	0	2.8
	Grass and vegetation	0	0	1.5	2.9	0	11.3	6.2	8.9	9.9	8.5	11.3	1.1	27.3	12.1	2.8	103.8
Anthro-pogenic	Plastic	0	0	3.8	7.4	2.9	25.8	18.5	44.4	57.1	39.4	48.4	54.5	22.1	36.3	32.1	392.7
	Paper	0	1.5	0	0	0	4.8	2.5	35.6	24.2	18.3	14.5	14.8	19.5	46.2	12.3	194.2
	Glass and other hard materials	0	1.5	0	1.5	1.5	8.1	2.5	18.9	20.9	12.7	16.1	4.5	15.6	5.5	9.4	118.7
	Urban food remains	0	0	0	0	0	3.2	1.2	3.3	6.6	1.4	11.3	3.4	20.8	3.3	0.9	55.4
	Animal parts terrestrial anthropogenic origin	0	1.5	0	1.5	0	1.6	1.2	18.9	17.6	14.1	16.1	9.1	16.9	9.9	6.6	115.0

Table S3.9: Results of logistic regression models of the effects of the factors colony, year, and breeding stage on each of the broad diet categories in stomach content samples (presence/ absence data) and results from post-hoc Dunn's test with significantly different pairwise comparisons. Only best fit models and null models are shown with significant results in bold. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. Age group: 1 = Incubating adult, 2 = Chick.

Model	Fixed factors	Model estimates ± SE	p	AIC_c	DF	R^2	Dunn's test	p
Colony effect								
Marine ~ Intercept				138.54	1			
Marine ~ Colony	Intercept MA	1.10 ± 0.58	0.06	129.12	7	0.20	JU:MA	0.03
	Colony DW	-0.85 ± 0.77	0.27				KE:MA	0.02
	Colony JU	**-2.11 ± 0.82**	**0.01**				MA:SD	0.008
	Colony KE	**-2.28 ± 0.81**	**0.005**				MA:ST	0.01
	Colony SD	**-2.97 ± 0.95**	**0.002**					
	Colony ST	**-2.80 ± 0.96**	**0.004**					
	Colony SW	-1.44 ± 0.82	0.08					
Coastal ~ Intercept				100.89	1			
Coastal ~ Colony	Intercept DW	1.92^{e-15} ± 0.5	1.00	91.21	7	0.20	DW:KE	0.01
	Colony KE	**-2.77 ± 1.15**	**0.02**				DW:MA	0.01
	Colony SW	-1.10 ± 0.83	0.19				DW:SD	0.01

	Colony ST	-18.57 ± 1809	0.99				DW:ST	0.01
	Colony SD	**-2.64 ± 1.15**	**0.02**					
	Colony JU	-0.69 ± 0.74	0.35					
	Colony MA	**-2.71 ± 1.15**	**0.02**					
Terr. natural ~ Intercept				134.85	1			
Terrestrial ~ Colony	Intercept KE	0.12 ± 0.49	0.81	114.21	7	0.27	DW:KE	0.007
	Colony ST	**-1.82 ± 0.91**	**0.045**				DW:SW	< 0.001
	Colony SD	-0.81 ± 0.73	0.27				MA:SW	0.003
	Colony DW	-18.68 ± 1630.66	0.99				SD:SW	0.03
	Colony JU	-0.52 ± 0.72	0.47				ST:SW	0.004
	Colony MA	**-1.58 ± 0.80**	**0.049**					
	Colony SW	1.49 ± 0.91	0.10					
Anthropogenic ~ Intercept				134.85	1			
Anthropogenic ~ Colony	Intercept ST	0.47 ± 0.57	0.41	127.05	7	0.19	DW:SD	0.03
	Colony DW	**-2.42 ± 0.95**	**0.01**				JU:SD	0.02
	Colony JU	**-2.34 ± 0.95**	**0.01**				MA:SD	0.03
	Colony KE	-1.08 ± 0.76	0.16				DW:ST	0.03
	Colony MA	**-1.94 ± 0.86**	**0.02**				JU:ST	0.03
	Colony SD	0.22 ± 0.79	0.78					
	Colony SW	-1.16 ± 0.84	0.16					

Colony and year effect

Marine ~ Intercept				181.20	1			
Marine ~ Colony*Year	Intercept MA Year 2017	1.10 ± 0.58	0.06	168.19	8	0.19	DW 2018:MA 2017	0.04
	Colony ST	**-2.80 ± 0.96**	**0.004**				JU 2017:MA 2017	0.03
	Colony DW	-0.85 ± 0.77	0.27				DW 2017:MA 2018	0.02
	Colony JU	**-2.11 ± 0.82**	**0.01**				JU 2018:MA 2018	0.04
	Year 2018	**-3.35 ± 0.94**	**< 0.001**				MA 2017:MA 2018	< 0.001
	Colony ST:Year 2018	**3.61 ± 1.34**	**0.01**				MA 2017:ST 2017	0.008
	Colony DW:Year 2018	2.31 ± 1.20	0.05				MA 2017:ST 2018	0.006
	Colony JU:Year 2018	**4.27 ± 1.19**	**< 0.001**					
Coastal ~ Intercept				173.99	1			
Coastal ~ Colony + Year	**Intercept MA Year 2017**	**-1.57 ± 0.47**	**< 0.001**	154.79	5	0.18	DW:MA	0.02
	Colony ST	**-1.86 ± 0.82**	**0.02**				DW:ST	< 0.001
	Colony DW	**1.37 ± 0.53**	**0.01**				JU:ST	0.02
	Colony JU	0.43 ± 0.52	0.41					
	Year 2018	**0.93 ± 0.43**	**0.03**					
Terrestrial ~ Intercept				129.93	1			
Terrestrial ~ Colony*Year	**Intercept MA Year 2017**	**-1.47 ± 0.64**	**0.02**	117.29	8	0.18	DW:JU	0.04
	Colony ST	-0.24 ± 1.00	0.81				DW:MA	0.008

	Colony DW	-18.10 ± 2688.50	0.99				MA:ST	0.01
	Colony JU	1.06 ± 0.83	0.20				DW 2017:JU 2017	0.02
	Year 2018	1.18 ± 0.78	0.13				DW 2017:MA 2018	0.01
	Colony ST : Year 2018	-19.04 ± 2346.72	0.99				DW 2018:MA 2018	0.02
	Colony DW : Year 2018	15.68 ± 2688.50	1.00				JU 2017:ST 2018	0.02
	Colony JU : Year 2018	**-2.56 ± 1.13**	**0.02**				MA 2018:ST 2018	0.007
Anthropogenic ~ Intercept				167.02	1			
Anthropogenic ~ Colony	**Intercept ST**	**0.74 ± 0.37**	**0.04**	139.85	4	0.26	DW:ST	< 0.001
	Colony DW	**-2.42 ± 0.61**	**< 0.001**				JU:ST	< 0.001
	Colony JU	**-2.82 ± 0.64**	**< 0.001**				MA:ST	< 0.001
	Colony MA	**-2.19 ± 0.56**	**< 0.001**					
Colony and age group effect								
Marine ~ Intercept				258.9	1			
Marine ~ Colony*Age group	**Intercept KE Age group 1**	**-1.18 ± 0.57**	**0.04**	215.38	10	0.30	DW:SD	0.008
	Colony DW	1.43 ± 0.76	0.06				DW2:KE1	0.001
	Colony ST	-0.53 ± 0.96	0.58				DW1:KE2	0.049
	Colony SW	0.84 ± 0.82	0.30				KE1:KE2	< 0.001
	Colony SD	-0.69 ± 0.95	0.47				DW1:SD1	0.049
	Age group 2	**4.17 ± 1.17**	**< 0.001**				DW2:SD1	< 0.001
	Colony DW:Age group 2	**-2.99 ± 1.37**	**0.03**				KE2:SD1	< 0.001

	Colony ST:Age group 2	-0.68 ± 1.54	0.66				KE2:SD2	0.009
	Colony SW:Age group 2	**-3.76 ± 1.37**	**0.006**				DW2:ST1	< 0.001
	Colony SD:Age group 2	-2.40 ± 1.46	0.10				KE2:ST1	< 0.001
							KE1:ST2	< 0.001
							SD1:ST2	< 0.001
							ST1:ST2	< 0.001
							KE2:SW1	0.01
							ST2:SW1	0.047
							KE2:SW2	0.01
							SD1:SW2	0.049
Coastal ~ Intercept				176.31	1			
Coastal ~ Colony	Intercept DW	-0.49 ± 0.32	0.13	169.18	5	0.09	DW:KE	0.004
	Colony SW	**-1.37 ± 0.58**	**0.02**				DW:SD	0.03
	Colony SD	**-1.12 ± 0.55**	**0.04**				DW:ST	0.005
	Colony KE	**-1.97 ± 0.68**	**0.004**				DW:SW	0.01
	Colony ST	**-1.85 ± 0.68**	**0.007**					
Terrestrial ~ Intercept				210.67	1			
Terrestrial ~ Colony*Age group	**Intercept SW Age group 1**	**1.61 ± 0.77**	**0.04**	185.14	10	0.24	DW:KE	0.02
	Colony KE	-1.49 ± 0.91	0.10				DW:SD	0.02
	Colony DW	-19.18 ± 989.05	0.98				DW:SW	< 0.001

	Colony SD	**-2.30 ± 0.95**	**0.02**				ST:SW	0.004
	Colony ST	**-3.31 ± 1.09**	**0.002**				DW1:KE1	0.003
	Age group 2	**-2.55 ± 0.89**	**0.004**				DW2:KE1	0.004
	Colony KE:Age group 2	0.64 ± 1.19	0.59				KE1:KE2	0.02
	Colony DW:Age group 2	17.64 ± 989.05	0.99				KE1:ST2	0.009
	Colony SD: Age group 2	**2.33 ± 1.15**	**0.04**				DW1:SW1	< 0.001
	Colony ST: Age group 2	2.01 ± 1.39	0.15				DW2:SW1	< 0.001
							KE2:SW1	< 0.001
							SD1:SW1	0.01
							SD2:SW1	0.003
							ST1:SW1	< 0.001
							ST2:SW1	< 0.001
							SW1:SW2	0.002
Anthropogenic ~ Intercept				246.03	1			
Anthropogenic ~ Colony	Intercept ST	-0.36 ± 0.35	0.31	229.59	5	0.12	DW:SD	< 0.001
	Colony SD	0.81 ± 0.49	0.10				KE:SD	0.01
	Colony DW	**-1.64 ± 0.59**	**0.005**				DW:ST	0.02
	Colony KE	-0.67 ± 0.51	0.18				DW:SW	0.01
	Colony SW	0.08 ± 0.48	0.86					

Table S3.40: Results of logistic regression models of the effects of the factors colony, year, and breeding stage on each of the broad diet categories in pellet samples (presence/ absence data) and results from post-hoc Dunn's test with significantly different pairwise comparisons. Only best fit models and null models are shown with significant results in bold. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms. Breeding stages: 1 = Incubation, 2 = Chick-rearing.

Model	Fixed factors	Model estimates ± SE	p	AIC_c	DF	R^2	Dunn's test	p
Colony effect								
Marine ~ Intercept				392.37	1			
Marine ~ Colony				394.72	6	0.02		
Coastal ~ Intercept				602.22	1			
Coastal ~ Colony	**Intercept DW**	**2.46 ± 0.43**	**< 0.001**	433.81	6	0.36	DW:JU	< 0.001
	Colony JU	**-2.00 ± 0.50**	**< 0.001**				DW:KE	< 0.001
	Colony SD	**-4.89 ± 0.63**	**< 0.001**				JU:KE	< 0.001
	Colony KE	**-4.15 ± 0.53**	**< 0.001**				DW:MA	0.007
	Colony MA	**-1.65 ± 0.50**	**< 0.001**				KE:MA	< 0.001
	Colony ST	**-3.25 ± 0.48**	**< 0.001**				DW:SD	< 0.001
							JU:SD	< 0.001
							MA:SD	< 0.001
							DW:ST	< 0.001

							JU:ST	< 0.001
							MA:ST	< 0.001
							SD:ST	0.007
Terrestrial ~ Intercept				532.60	1			
Terrestrial ~ Colony	Intercept JU	-0.26 ± 0.26	0.31	508.47	6	0.07	DW:JU	< 0.001
	Colony DW	**-2.20 ± 0.50**	**< 0.001**				DW:KE	< 0.001
	Colony SD	-0.41 ± 0.37	0.27				DW:MA	< 0.001
	Colony KE	-0.19 ± 0.35	0.58				DW:SD	0.003
	Colony MA	-0.28 ± 0.36	0.43				JU:ST	0.02
	Colony ST	**-0.93 ± 0.36**	**0.009**					
Anthropogenic ~ Intercept				598.07	1			
Anthropogenic ~ Colony	**Intercept SD**	**1.14 ± 0.30**	**< 0.001**	382.99	6	0.43	DW:JU	0.002
	Colony DW	-19.71 ± 748.20	0.98				DW:KE	< 0.001
	Colony JU	**-2.12 ± 0.41**	**< 0.001**				JU:KE	< 0.001
	Colony KE	-0.47 ± 0.38	0.22				JU:MA	0.03
	Colony MA	**-3.68 ± 0.55**	**< 0.001**				KE:MA	< 0.001
	Colony ST	0.11 ± 0.39	0.78				DW:SD	< 0.001
							JU:SD	< 0.001
							MA:SD	< 0.001
							DW:ST	< 0.001

							JU:ST	< 0.001
							MA:ST	< 0.001
Colony and year effect								
Marine ~ Intercept				526.46	1			
Marine ~ Colony	**Intercept DW**	**-1.12 ± 0.19**	**< 0.001**	514.48	4	0.03	DW:JU	0.005
	Colony JU	**-1.10 ± 0.34**	**0.001**				DW:MA	0.004
	Colony MA	**-1.05 ± 0.34**	**0.002**				JU:ST	0.02
	Colony ST	-0.20 ± 0.27	0.47				MA:ST	0.02
Coastal ~ Intercept				768.67	1			
Coastal ~ Colony	**Intercept JU**	**0.62 ± 0.18**	**< 0.001**	687.21	4	0.14	DW:JU	<0.001
	Colony MA	0.19 ± 0.26	0.47				DW:MA	0.005
	Colony ST	**-1.19 ± 0.24**	**< 0.001**				DW:ST	< 0.001
	Colony DW	**1.19 ± 0.30**	**< 0.001**				JU:ST	< 0.001
							MA:ST	< 0.001
Terrestrial ~ Intercept				648.76	1			
Terrestrial ~ Colony*Year	Intercept JU Year 2017	-0.26 ± 0.26	0.31	624.09	8	0.06	DW:JU	0.001
	Colony ST	**-0.93 ± 0.36**	**0.01**				DW:MA	< 0.001
	Colony DW	**-2.20 ± 0.50**	**< 0.001**				DW:ST	0.008
	Colony MA	-0.28 ± 0.36	0.43				DW 2017:JU 2017	< 0.001

	Year 2018	**-1.31 ± 0.39**	**< 0.001**				DW 2018:JU 2017	< 0.001
	Colony ST : Year 2018	**1.49 ± 0.53**	**0.01**				JU 2017:JU 2018	0.002
	Colony DW : Year 2018	**1.92 ± 0.68**	**< 0.001**				DW 2017:MA 2017	< 0.001
	Colony MA : Year 2018	1.04 ± 0.53	0.05				DW 2018:MA 2017	0.009
							JU 2018:MA 2017	0.02
							DW 2017:MA 2018	0.008
							JU 2017:ST 2017	0.02
							DW 2017:ST 2018	0.02
Anthropogenic ~ Intercept				682.62	1			
Anthropogenic ~ Colony*Year	**Intercept ST Year 2017**	**1.25 ± 0.25**	**< 0.001**	449.93	8	0.39	DW:JU	< 0.001
	ColonyJU	**-2.23 ± 0.38**	**< 0.001**				JU:MA	< 0.001
	ColonyDW	-19.82 ± 748.20	0.98				DW:ST	< 0.001
	ColonyMA	**-3.79 ± 0.53**	**< 0.001**				JU:ST	< 0.001
	Year2018	**-0.94 ± 0.35**	**0.007**				MA:ST	< 0.001
	ColonyJU:Year2018	0.80 ± 0.52	0.12					
	ColonyDW:Year2018	16.04 ± 748.20	0.98					
	ColonyMA:Year2018	0.40 ± 0.83	0.63					
Colony and breeding stage effect								
Marine ~ Intercept				645.73	1			
	Intercept DW Br. stage 1	**-1.58 ± 0.30**	**< 0.001**	600.11	8	0.11	DW:KE	< 0.001

Marine ~ Colony*Breeding stage (Br. stage)	Colony KE	0.24 ± 0.41	0.56				DW:SD	< 0.001
	Colony SD	-0.48 ± 0.50	0.34				DW:ST	0.003
	Colony ST	0.39 ± 0.39	0.32				SD:ST	0.01
	Br. stage 2	**1.82 ± 0.39**	**< 0.001**				DW1:DW2	< 0.001
	Colony KE:Br. stage 2	**-2.47 ± 0.58**	**< 0.001**				DW2:KE1	< 0.001
	Colony SD:Br. stage 2	**-2.21 ± 0.69**	**0.001**				DW2:KE2	< 0.001
	Colony ST:Br. stage 2	**-2.10 ± 0.54**	**< 0.001**				DW2:SD1	< 0.001
							DW2:SD2	< 0.001
							DW2:ST1	< 0.001
							SD2:ST1	0.04
							DW2:ST2	< 0.001
Coastal ~ Intercept				765.03	1			
Coastal ~ Colony*Breeding stage (Br. stage)	**Intercept DW Br stage 1**	**2.46 ± 0.43**	**< 0.001**	522	8	0.39	DW:KE	< 0.001
	Colony KE	**-4.15 ± 0.53**	**< 0.001**				DW:SD	< 0.001
	Colony SD	**-4.89 ± 0.63**	**< 0.001**				DW:ST	< 0.001
	Colony ST	**-3.25 ± 0.48**	**< 0.001**				KE:ST	< 0.001
	Br. stage 2	**-2.34 ± 0.49**	**< 0.001**				SD:ST	< 0.001
	Colony KE: Br. stage 2	0.65 ± 0.83	0.44				DW1:DW2	< 0.001
	Colony SD: Br. stage 2	1.42 ± 0.90	0.11				DW1:KE1	< 0.001

	Colony ST: Br. stage 2	**2.16 ± 0.59**	**< 0.001**				DW2:KE1	< 0.001
							DW1:KE2	< 0.001
							DW2:KE2	< 0.001
							DW1:SD1	< 0.001
							DW2:SD1	< 0.001
							DW1:SD2	< 0.001
							DW2:SD2	< 0.001
							DW1:ST1	< 0.001
							DW2:ST1	0.004
							KE1:ST1	0.04
							KE2:ST1	< 0.001
							SD1:ST1	0.003
							SD2:ST1	< 0.001
							DW1:ST2	< 0.001
							DW2:ST2	< 0.001
							KE2:ST2	< 0.001
							SD1:ST2	0.01
							SD2:ST2	< 0.001
Terrestrial ~ Intercept				689.88	1			
	Intercept KE Br. stage 1	**-0.69 ± 0.20**	**< 0.001**	668.29	5	0.04	DW:KE	< 0.001

Terrestrial ~ Colony+Breeding stage (Br. stage)	Colony SD	-0.11 ± 0.25	0.67				DW:SD	< 0.001
	Colony DW	**-1.53± 0.35**	**< 0.001**				DW:ST	< 0.001
	Colony ST	-0.24 ± 0.24	0.33					
	Br. stage 2	**-0.38 ± 0.19**	**0.049**					
Anthropogenic ~ Intercept				866.09	1			
Anthropogenic ~ Colony*Breeding stage (Br. stage)	**Intercept KE Br. stage 1**	**0.67 ± 0.24**	**0.005**	581.91	8	0.40	DW:KE	< 0.001
	Colony SD	0.47 ± 0.38	0.22				DW:SD	< 0.001
	Colony DW	-19.24 ± 748.2	0.98				DW:ST	< 0.001
	Colony ST	0.58± 0.35	0.10				DW1:KE1	< 0.001
	Age group 2	**0.95 ± 0.37**	**0.01**				DW2:KE1	< 0.001
	Colony SD:Br. stage 2	-0.93 ± 0.54	0.08				DW1:KE2	< 0.001
	Colony DW:Br. stage 2	14.57 ± 748.2	0.98				DW2:KE2	< 0.001
	Colony ST:Br. stage 2	**-1.06 ± 0.51**	**0.04**				KE1:KE2	0.049
							DW1:SD1	< 0.001
							DW2:SD1	< 0.001
							DW1:SD2	< 0.001
							DW2:SD2	< 0.001
							DW1:ST1	< 0.001
							DW2:ST1	< 0.001

							DW1:ST2	< 0.001
							DW2:ST2	< 0.001

Table S3.11: Results of general linear models of the effects of the factors colony, year, and age group on plasma stable isotope samples δ13C and δ15N and results from post-hoc Dunn's test with significantly different pairwise comparisons. Only best fit models and null models are shown with significant results in bold. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. Breeding stages: 1 = Incubating adult, 2 = Chick.

Model	Fixed factors	Model estimates ± SE	p	AIC_c	DF	R^2	Dunn's test	p
Colony effect								
$\delta^{13}C$ ~ Intercept				527.33	1			
$\delta^{13}C$ ~ Colony	**Intercept DW**	**-16.24 ± 0.28**	**< 0.001**	492.88	7	0.27	DW:JU	< 0.001
	Colony JU	**-2.03 ± 0.40**	**< 0.001**				JU:KE	0.005
	Colony KE	-0.48 ± 0.40	0.23				DW:MA	0.02
	Colony MA	**-1.32 ± 0.42**	**0.002**				DW:SD	0.02
	Colony SD	**-1.04 ± 0.39**	**0.009**				DW:ST	0.001
	Colony ST	**-1.41 ± 0.39**	**< 0.001**				KE:ST	0.03
	Colony SW	0.29 ± 0.39	0.46				JU:SW	< 0.001
							MA:SW	0.002

							SD:SW	0.002
							ST:SW	< 0.001
$\delta^{15}N$ ~ Intercept				587.45	1			
$\delta^{15}N$ ~ Colony	**Intercept DW**	**12.95 ± 0.34**	**< 0.001**	551.48	7	0.28	DW:JU	0.04
	Colony JU	**-1.14 ± 0.49**	**0.02**				DW:SD	0.002
	Colony KE	-0.85 ± 0.49	0.08				MA:SD	0.04
	Colony MA	-0.58 ± 0.51	0.26				DW:ST	< 0.001
	Colony SD	**-1.87 ± 0.48**	**< 0.001**				JU:ST	0.03
	Colony ST	**-2.53 ± 0.48**	**< 0.001**				KE:ST	0.004
	Colony SW	**-2.76 ± 0.48**	**< 0.001**				MA:ST	0.002
							DW:SW	< 0.001
							JU:SW	0.03
							KE:SW	0.003
							MA:SW	0.002
Colony and year effect								
$\delta^{13}C$ ~ Intercept				656.93	2			
$\delta^{13}C$ ~ Colony+Year	**Intercept DW Year 2017**	**-16.22 ± 0.23**	**< 0.001**	610.91	6	0.27	DW:JU	< 0.001
	Colony JU	**-2.00 ± 0.28**	**< 0.001**				DW:MA	< 0.001
	Colony MA	**-1.34 ± 0.30**	**< 0.001**				JU:MA	0.03
	Colony ST	**-1.48 ± 0.28**	**< 0.001**				DW:ST	< 0.001

	Year 2018	**0.62 ± 0.20**	**0.003**					
$\delta^{15}N$ ~ Intercept				697.97	2			
$\delta^{15}N$ ~ Colony*Year	**Intercept DW Year 2017**	**12.95 ± 0.27**	**< 0.001**	580.67	9	0.53	DW:JU	0.001
	Colony JU	**-1.14 ± 0.38**	**0.003**				JU:MA	0.01
	Colony MA	-0.58 ± 0.40	0.15				DW:ST	< 0.001
	Colony ST	**-2.53 ± 0.37**	**< 0.001**				JU:ST	< 0.001
	Year 2018	0.67 ± 0.37	0.07				MA:ST	< 0.001
	Colony JU:Year 2018	-0.01 ± 0.52	0.99				DW 2017:JU 2017	0.04
	Colony MA:Year 2018	0.41 ± 0.54	0.44				DW 2018:JU 2017	< 0.001
	Colony ST:Year 2018	**-1.03 ± 0.51**	**0.046**				DW 2018:JU 2018	0.02
							DW 2018:MA 2017	0.03
							JU 2017:MA 2018	< 0.001
							JU 2018:MA 2018	0.02
							MA 2017:MA 2018	0.03
							DW 2017:ST 2017	< 0.001
							DW 2018:ST 2017	< 0.001
							JU 2017:ST 2017	0.03
							JU 2018:ST 2017	< 0.001
							MA 2017:ST 2017	0.002
							MA 2018:ST 2017	< 0.001

							DW 2017:ST 2018	< 0.001
							DW 2018:ST 2018	< 0.001
							JU 2017:ST 2018	0.01
							JU 2018:ST 2018	< 0.001
							MA 2017:ST 2018	< 0.001
							MA 2018:ST 2018	< 0.001
Colony and age group effect								
$\delta^{13}C$ ~ Intercept				665.46	2			
$\delta^{13}C$ ~ Colony*Age group	**Intercept DW Age group 1**	**-16.24 ± 0.20**	**< 0.001**	584.47	11	0.38	DW:KE	< 0.001
	Colony KE	-0.48 ± 0.29	0.1				DW:SD	< 0.001
	Colony SD	**-1.04 ± 0.28**	**< 0.001**				DW:ST	< 0.001
	Colony ST	**-1.41 ± 0.28**	**< 0.001**				KE:SW	< 0.001
	Colony SW	0.29 ± 0.28	0.31				SD:SW	< 0.001
	Age group 2	**1.19 ± 0.29**	**< 0.001**				ST:SW	< 0.001
	Colony KE:Age group 2	**-1.44 ± 0.41**	**< 0.001**				DW 1:DW2	0.002
	Colony SD:Age group 2	-0.59 ± 0.41	0.15				DW 2:KE 1	< 0.001
	Colony ST:Age group 2	0.32 ± 0.41	0.44				DW 1:KE 2	0.046
	Colony SW:Age group 2	**-1.20 ± 0.41**	**0.004**				DW 2:KE2	< 0.001
							DW 1:SD 1	0.02
							DW 2:SD 1	< 0.001

DW 2:SD 2	< 0.001
DW 1:ST 1	< 0.001
DW 2:ST 1	< 0.001
KE 1:ST 1	0.045
SD 2:ST 1	0.02
KE 2:ST 2	0.02
SD 1:ST 2	0.01
ST 1:ST 2	< 0.001
DW 2:SW 1	0.02
KE 1:SW 1	0.02
KE 2:SW 1	0.007
SD 1:SW 1	0.002
SD 2:SW 1	0.04
ST 1:SW 1	< 0.001
DW 2:SW 2	0.02
KE 1:SW 2	0.02
KE 2:SW 2	0.006
SD 1:SW 2	0.002
SD 2:SW 2	0.04
ST 1:SW 2	< 0.001

$\delta^{15}N$ ~ Intercept				912.49	2			
$\delta^{15}N$ ~ Colony*Age group	**Intercept DW Age group 1**	**12.95 ± 0.36**	**< 0.001**	827.27	11	0.39	DW:KE	0.003
	Colony KE	-0.85 ± 0.51	0.1				DW:SD	< 0.001
	Colony SD	**-1.87 ± 0.50**	**< 0.001**				KE:SD	0.003
	Colony ST	**-2.53 ± 0.50**	**< 0.001**				DW:ST	< 0.001
	Colony SW	**-2.76 ± 0.50**	**< 0.001**				DW:SW	< 0.001
	Age group 2	0.96 ± 0.52	0.07				KE:SW	< 0.001
	Colony KE:Age group 2	-0.77 ± 0.73	0.29				ST:SW	0.003
	Colony SD:Age group 2	**-1.66 ± 0.72**	**0.02**				DW 2:KE 1	0.004
	Colony ST:Age group 2	**1.46 ± 0.73**	**0.046**				DW 2:KE 2	0.006
	Colony SW:Age group 2	-1.07 ± 0.72	0.14				DW 1:SD 1	0.003
							DW 2:SD 1	< 0.001
							DW 1:SD 2	< 0.001
							DW 2:SD 2	< 0.001
							KE 1:SD 2	0.03
							KE 2:SD 2	0.02
							DW 1:ST 1	< 0.001
							DW 2:ST 1	< 0.001
							KE 1:ST 1	0.008
							KE 2:ST 1	0.006

SD 1:ST 2	0.005
SD 2: ST 2	< 0.001
ST 1:ST 2	< 0.001
DW 1:SW 1	< 0.001
DW 2:SW 1	< 0.001
KE 1:SW 1	0.006
KE 2:SW 1	0.005
ST 2:SW 1	< 0.001
DW 1:SW 2	< 0.001
DW 2:SW 2	< 0.001
KE 1:SW 2	0.005
KE 2:SW 2	0.005
ST 2:SW 2	< 0.001

Table S3.52: Number of plasma samples collected and plasma stable isotope carbon $\delta^{13}C$ and nitrogen $\delta^{15}N$ values (mean ± SD, min/max) from incubating adult Kelp Gulls and Kelp Gull chicks in seven colonies in South Africa between 2017 and 2018.

Colony	Year	Age group	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Dwarskersbos	2017	Adult	21	-16.2±1.1 (-18.5/-14.3)	12.9±0.8 (11.1/14.6)
		Chick	19	-15.0±0.6 (-16.0/-13.7)	13.9±0.6 (11.9/14.8)

	2018	Adult	23	-15.6±1.2 (-19.0/-14.3)	13.6±1.2 (11.6/15.6)
Malgas Island	2017	Adult	17	-17.6±1.6 (-21.1/-15.6)	12.4±1.2 (9.0/13.9)
	2018	Adult	22	-16.9±1.3 (-21.5/-15.5)	13.5±0.8 (11.2/14.5)
Jutten Island	2017	Adult	20	-18.3±1.9 (-21.8/-13.6)	11.8±1.8 (8.8/15.3)
	2018	Adult	26	-17.6±1.6 (-21.0/-14.9)	12.5±1.0 (11.1/15.0)
Strandfontein	2017	Adult	22	-17.6±1.0 (-20.0/-15.8)	10.4±1.3 (8.6/12.5)
		Chick	21	-16.1±0.6 (-17.7/-15.2)	12.8±1.5 (10.2/14.9)
	2018	Adult	25	-17.1±1.0 (-18.7/-15.0)	10.1±1.4 (7.4/12.8)
Steenbras Dam	2017	Adult	22	-17.3±1.5 (-19.3/-14.3)	11.1±2.2 (7.9/16.7)
		Chick	22	-16.7±0.9 (-18.9/-15.3)	10.4±2.1 (6.0/12.9)
Keurbooms	2017	Adult	21	-16.7±0.7 (-18.4/-15.4)	12.1±1.3 (9.6/13.5)
		Chick	20	-17.0±1.0 (-19.2/-15.2)	12.3±1.9 (9.5/15.8)
Swartkops River	2017	Adult	22	-15.9±0.8 (-17.3/-14.0)	10.2±1.9 (7.5/14.1)
		Chick	22	-16.0±0.5 (-16.7/-14.6)	10.1±1.9 (6.0/13.8)

Table S3.63: Standard ellipse areas corrected for small sample sizes (SEAc) for incubating adults and chicks at all sampled colonies in South Africa between 2017 and 2018. Colonies DW = Dwarskersbos, MA = Malgas Island, JU = Jutten Island, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. Breeding stages: 1 = Incubating adult, 2 = Chick.

SEA_c	DW	MA	JU	ST	SD	KE	SW
2017/ Adult	2.344	4.370	9.584	3.828	4.853	2.301	4.303
2017/ Chick	1.227			2.095	3.246	4.266	3.054
2018/ Adult	4.352	3.594	4.559	3.026			

Table S3.14: Probability between 0 and 1 of Posterior Bayesian standard ellipse area (SEAB) of A being smaller than SEAB of B of colonies sampled in 2017. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. Cells in grey show that A is almost always smaller than B with a probability of close to 1.

		A						
		DW	MA	JU	ST	SD	KE	SW
B	DW		0.02	0.00	0.06	0.00	0.55	0.03
	MA	0.98		0.01	0.69	0.27	0.98	0.58
	JU	1.00	0.99		1.00	0.96	1.00	1.00
	ST	0.94	0.31	0.00		0.10	0.95	0.35
	SD	1.00	0.73	0.04	0.90		1.00	0.81
	KE	0.45	0.02	0.00	0.05	0.00		0.03

	SW	0.97	0.42	0.01	0.65	0.19	0.97	

Table S3.75: Proportion between 0 and 1 of niche area overlap between A and B based on the maximum likelihood fitted ellipses and calculated as the area of overlap between two ellipses divided by the area of each ellipse, respectively. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops.

		A						
		DW	MA	JU	ST	SD	KE	SW
B	DW		0.31	0.11	0.00	0.21	0.47	0.00
	MA	0.57		0.41	0.01	0.18	0.46	0.00
	JU	0.44	0.91		0.35	0.39	0.64	0.00
	ST	0.00	0.01	0.14		0.60	0.27	0.00
	SD	0.43	0.20	0.20	0.76		0.86	0.00
	KE	0.46	0.24	0.15	0.16	0.41		0.00
	SW	0.00	0.00	0.00	0.00	0.00	0.00	

Table S3.86: Probability between 0 and 1 of Posterior Bayesian standard ellipse area (SEAB) of A being smaller than SEAB of B of colonies sampled in 2017 and 2018. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein. Cells in grey show that A is almost always smaller than B with a probability of close to 1.

		A							
		DW 2017	MA 2017	JU 2017	ST 2017	DW 2018	MA 2018	JU 2018	ST 2018
B	DW 2017		0.02	0.00	0.06	0.03	0.11	0.01	0.18
	MA 2017	0.98		0.02	0.71	0.58	0.79	0.50	0.90
	JU 2017	1.00	0.98		1.00	0.99	1.00	0.99	1.00
	ST 2017	0.94	0.29	0.00		0.35	0.60	0.27	0.75
	DW 2018	0.97	0.42	0.01	0.65		0.74	0.41	0.87
	MA 2018	0.90	0.21	0.00	0.40	0.26		0.19	0.67
	JU 2018	0.99	0.50	0.01	0.73	0.59	0.81		0.91
	ST 2018	0.82	0.10	0.00	0.25	0.13	0.33	0.09	

Table S3.17: Proportion between 0 and 1 of niche area overlap between A and B based on the maximum likelihood fitted ellipses and calculated as the area of overlap between two ellipses divided by the area of each ellipse, respectively. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops.

		A							
		DW 2017	MA 2017	JU 2017	ST 2017	DW 2018	MA 2018	JU 2018	ST 2018
B	DW 2017		0.31	0.11	0.00	0.38	0.30	0.29	0.00
	MA 2017	0.57		0.41	0.01	0.19	0.42	0.82	0.00
	JU 2017	0.44	0.91		0.35	0.09	0.45	0.93	0.00
	ST 2017	0.00	0.01	0.14		0.00	0.00	0.01	0.52
	DW 2018	0.70	0.19	0.04	0.00		0.38	0.15	0.00
	MA 2018	0.46	0.34	0.17	0.00	0.32		0.33	0.00
	JU 2018	0.57	0.85	0.44	0.01	0.16	0.42		0.00
	ST 2018	0.00	0.00	0.00	0.41	0.00	0.00	0.00	

Table S3.98: Probability of Posterior Bayesian standard ellipse area (SEAB) of A being smaller than SEAB of B of colonies sampled in 2017. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. 1 = Incubating adult, 2 = Chick. Cells in grey show that A is almost always smaller than B with a probability of close to 1.

		A									
		DW 1	ST 1	SD 1	KE 1	SW 1	DW 2	ST 2	SD 2	KE 2	SW 2
B	DW 1		0.07	0.00	0.54	0.03	0.98	0.60	0.09	0.02	0.22
	ST 1	0.93		0.10	0.94	0.35	1.00	0.97	0.58	0.31	0.78
	SD 1	1.00	0.91		1.00	0.81	1.00	1.00	0.92	0.77	0.98
	KE 1	0.46	0.06	0.00		0.03	0.98	0.58	0.09	0.02	0.19
	SW 1	0.97	0.65	0.19	0.97		1.00	0.99	0.72	0.45	0.87
	DW 2	0.02	0.00	0.00	0.02	0.00		0.03	0.00	0.00	0.00
	ST 2	0.40	0.03	0.00	0.42	0.01	0.97		0.06	0.01	0.15
	SD 2	0.91	0.42	0.08	0.91	0.28	1.00	0.95		0.25	0.71
	KE 2	0.98	0.69	0.23	0.98	0.55	1.00	0.99	0.75		0.89
	SW 2	0.78	0.22	0.02	0.81	0.13	1.00	0.85	0.29	0.11	

Table S3.19: Proportion between 0 and 1 of niche area overlap between A and B based on the maximum likelihood fitted ellipses and calculated as the area of overlap between two ellipses divided by the area of each ellipse, respectively. Colonies: DW = Dwarskersbos, MA = Malgas, JU = Jutten, ST = Strandfontein, SD = Steenbras Dam, KE = Keurbooms, SW = Swartkops. 1 = Incubating adult, 2 = Chick.

		A									
		DW 1	ST 1	SD 1	KE 1	SW 1	DW 2	ST 2	SD 2	KE 2	SW 2
B	DW 1		0.00	0.21	0.47	0.00	0.21	0.57	0.01	0.34	0.00
	ST 1	0.00		0.60	0.27	0.00	0.00	0.02	0.19	0.29	0.00
	SD 1	0.43	0.76		0.86	0.00	0.00	0.62	0.17	0.55	0.00
	KE 1	0.46	0.15	0.41		0.00	0.00	0.50	0.09	0.45	0.00
	SW 1	0.00	0.00	0.00	0.00		0.00	0.00	0.30	0.00	0.94
	DW 2	0.11	0.00	0.00	0.00	0.00		0.05	0.00	0.00	0.00
	ST 2	0.51	0.01	0.27	0.46	0.00	0.08		0.12	0.24	0.00
	SD 2	0.01	0.16	0.12	0.12	0.23	0.00	0.19		0.00	0.21
	KE 2	0.62	0.32	0.48	0.84	0.00	0.00	0.48	0.00		0.00
	SW 2	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.20	0.00	

Chapter 4: Health status indices of Kelp Gull populations in South Africa

Chapter 4: Health status indices of Kelp Gull populations in South Africa

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Abstract

Kelp Gulls *Larus dominicanus* in South Africa exploit a wide variety of resources and foraging habitats both coastal areas and offshore. The increasing availability of anthropogenic diet items might potentially impact the health of gull populations. We investigated body condition and parasite loads of incubating adult Kelp Gulls and their chicks at seven colonies with varying proximity to landfills over two consecutive years. Adult body condition indices did not differ significantly among colonies during the incubation period, but were on average highest at one of the urban colonies, Strandfontein, which is next to a large landfill site. The only blood parasite identified was *Haemoproteus* spp., and even though prevalence was overall low, parasite presence in chicks was significantly lower than in adults. Yeast cells (*Candida* spp.) were identified in faecal smears and the presence of yeast cells coincided with higher body condition index values in incubating adults. Our results suggest that urban landscapes have little impact on these aspects of gull health. It seems likely that their opportunistic foraging nature allows Kelp Gulls in South Africa to maintain healthy populations.

Keywords: *Larus dominicanus*; Anthropogenic impact; Body condition index; Blood parasites; Faecal parasites

Introduction

Increasing human populations are affecting the environment in various ways through exploitation or land-use change such as urbanisation (Steffen et al. 2004). Most of these changes have negative impacts on biodiversity, but some species are able to adapt to human-modified environments (Hunter 2007). Among these are many species of gulls (*Larinae* spp.), which are often generalist foragers, able to exploit food from a variety of resources ranging from natural to anthropogenic (e.g. Duhem et al. 2003a, Pais de Faria et al. 2021). The success of many gull species and their subsequent

population increases have often been attributed to their broad diet (Oro et al. 2013) and ability to adapt to urban landscapes (Belant 1997), as well as protection from persecution (Kadlec & Drury 1968, Crawford et al. 2009a).

Human-derived food subsidies from e.g. landfills or fishery discards are often predictable and easily accessible (Horton et al. 1983). However, many anthropogenic resources, especially from landfills, have higher energy density, and greater fat and protein contents compared to natural food items (Pierotti & Annett 1991, O'Hanlon et al. 2017). Feeding on supplementary food sources can thus affect body condition, not only resulting in heavier birds having better condition (Auman et al. 2008), but also benefit smaller, less competitive individuals (Steigerwald et al. 2015). However, foraging on urban food resources can also significantly increase plasma cholesterol levels (Marteinson & Verreault 2020). Gull chicks on the other hand are often fed with more natural prey, especially fish (Annett & Pierotti 1989, Isaksson et al. 2016), most likely due to easier handling by chicks, than e.g. large anthropogenic items (Annett & Pierotti 1989), and provide nutrients necessary for chick growth (Spaans 1971), particularly digestible calcium (Annett & Pierotti 1989).

Foraging habitat choice might not only affect body condition, but also parasite load and diversity (Bosch et al. 2000, Diaz et al. 2011, Quillfeldt et al. 2011). The absence of suitable vectors in saline habitats might be one reason why seabirds tend to have fewer blood parasites than other birds (Martínez-Abraín et al. 2004). However, gulls also feed at coastal wetlands and inland on landfills where vector density might be higher, leading to potentially higher and more diverse blood parasite infections (Quillfeldt et al. 2011). In addition, foraging in anthropogenic areas might expose gulls to pathogens such as *Candida* (Al-Yasiri et al. 2016), *Campylobacter* (Ramos et al. 2010), or *Salmonella* (Moré et al. 2017), with gulls potentially acting as dispersal agents for those pathogens (Ramos et al. 2010). By comparison, the transmission of helminth parasites in seabirds is usually through invertebrate or fish intermediate hosts in marine environments (Esch et al. 2002, Galaktionov & Dobrovolskij 2003). This suggests that birds feeding more on terrestrial resources such as landfills might show less helminth diversity than individuals feeding on coastal or marine resources (Bosch et al. 2000, Diaz et al. 2011). Overall, high parasite loads or infections with certain parasite species might potentially lead to birds in poorer body condition (Bosch et al. 1997, Shutler et al. 1999, Bosch et al. 2000).

Kelp Gulls *Larus dominicanus* are abundant in South Africa with a breeding population of some 17 500 pairs (Whittington et al. 2016). They breed along the coast and on islands (Whittington et al. 2016) and are opportunistic feeders (Steele 1992). Their diet is very diverse and comprises terrestrial items such as insects or small mammals, coastal resources e.g. invertebrates, marine items such as fish, but also food from anthropogenic sources like landfills or fisheries in the form of fishery discards (Hockey et al. 2005). In addition, Kelp Gulls also predate on other seabird eggs and chicks and even conspecifics (Hockey et al. 2005). Knowledge on the health status of Kelp Gulls in South Africa is limited, with previous studies focusing mostly on general diet patterns (e.g. Steele 1992, Hockey et al. 2005), distribution (e.g. Steele & Hockey 1990, Whittington et al. 2006) and abundance (e.g. Crawford et al. 1997, Whittington et al. 2016).

In this study we investigated the health status of incubating adult Kelp Gulls and Kelp Gull chicks at seven colonies in South Africa with varying proximity to landfills during two consecutive breeding seasons. We assessed a body condition index as residuals of weight regressed on body size, which can give an indication of an individual's nutritional status (Jakob et al. 1996). We also assessed parasite load and diversity from blood and faecal samples. We expected 1) generally higher body condition in birds breeding in colonies closer to landfills; 2) higher blood parasite loads for birds in colonies closer to landfills; 3) lower helminth load and diversity for gulls breeding closer to landfill areas, reflecting increased use of anthropogenic resources; and 4) lower body condition values for gulls with high parasite loads. Results from this study will help to understand the possible effects of an urbanized landscape on the health of Kelp Gulls in South Africa, and allow an assessment of the pressures exerted through diet availability and parasite load and diversity on Kelp Gull populations.

Methods

Field sites

The body condition and presence of parasites of incubating adult Kelp Gulls and Kelp Gull chicks were investigated in seven colonies in the Eastern and Western Cape of South Africa (Figure 1). A detailed description of the seven colonies can be found in Chapters 2 and 3.

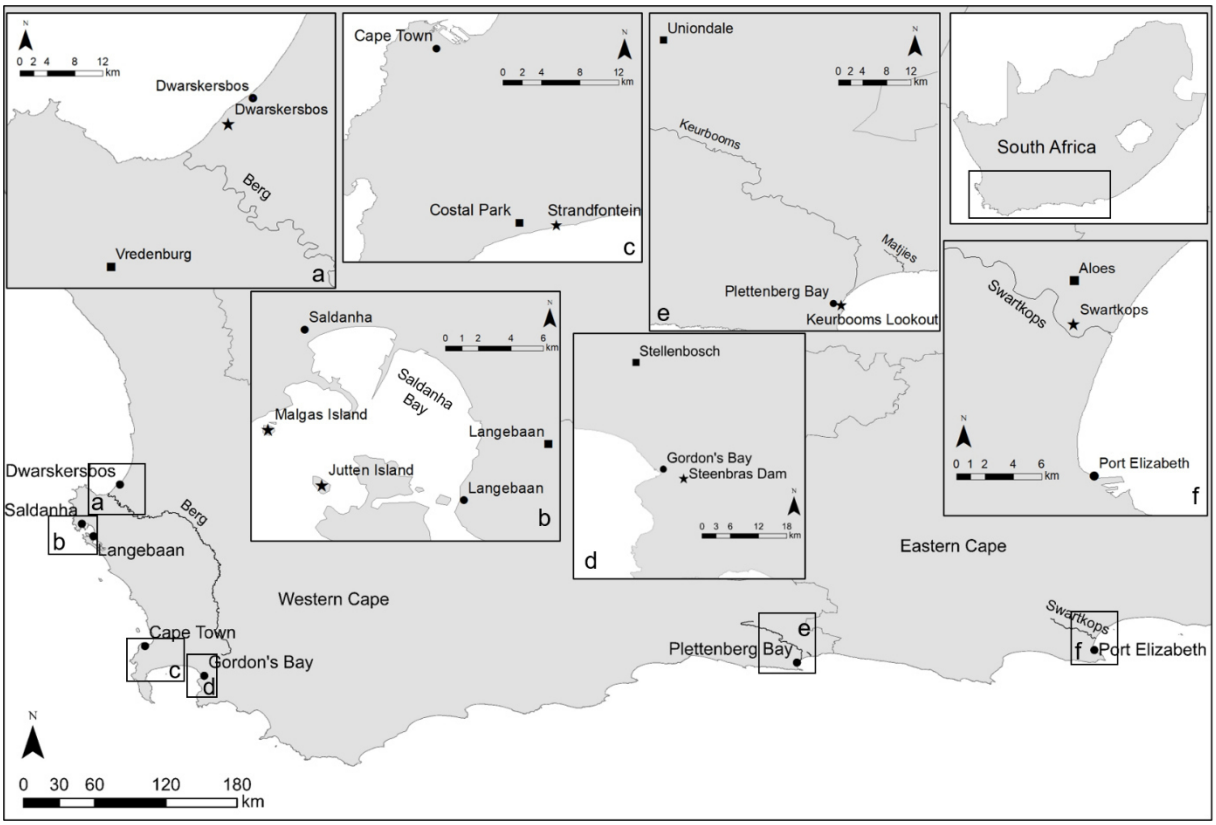

Figure 4.1: Map of the study areas showing the locations of the seven Kelp Gull colonies in South Africa (stars), closest cities (circles), and closest landfills (squares).

Sample collection

The health status of incubating Kelp Gulls was investigated at seven colonies in October-November 2017 and at four colonies in October 2018, and of chicks (at least two weeks old) at five colonies between November-December 2017. Adult birds incubating 2-3 eggs were captured with a noose placed over their nest, whereas chicks were captured by hand. Handling time after capture was ~ 10-12 minutes for each bird.

Body condition

Body condition was inferred by weighing all incubating adults and chicks upon capture using a hand-held spring balance to the nearest 10 g for adults and chicks. Head, tarsus, bill length, and bill depth in both adults and chicks were measured to the nearest 0.1 mm using Vernier callipers. Total head length was taken from the middle of the back of the head to the tip of the beak. Tarsus length was measured by holding the foot at a right angle to the tarsus and measuring the distance between those two bends. Bill length was taken from the base at the skull to the tip, whereas bill depth was

measured at a right angle at the deepest point of the gonys. The flattened wing chord of adult birds was measured to the nearest 1 mm using a stopped ruler.

Blood parasites

Blood sample collection (1 ml) was attempted from all individuals from either the tarsal or brachial vein using a slightly heparinized 2 ml syringe with a 25 gauge needle to prepare two thin blood smears per bird and for further stable isotope analysis (Chapter 3). Blood smears were air dried and then immediately fixed in absolute methanol in the field and stored frozen until stained with a modified Wright-Giemsa stain (Kyro-Quick stain set, Kyron Laboratories Pty Ltd, Benrose, South Africa) in the lab.

Faecal parasites

Cloacal swabs for intestinal parasites analysis were collected from each individual and stored in 10% formalin before analysis in the lab through faecal smears and faecal flotation. Faecal smears were prepared and after air drying, stained with a modified Wright-Giemsa stain (Kyro-Quick stain set, Kyron Laboratories Pty Ltd, Benrose, South Africa). In addition, an egg flotation fluid (sodium nitrate solution, S.G. 1.22; Kyron Laboratories (Pty) Ltd, South Africa) was used on samples with a reasonable amount of material (≥ 1.5 g) to perform faecal flotation.

Data analysis

A body condition index was estimated by linear regression of body mass on a structural body size measurement (Jakob et al. 1996, Schulte-Hostedde et al. 2005). A Pearson correlation matrix was used for adults and chicks separately to assess the level of correlation between weight and all body measurements (Alzola & Harrell 2006). For adults, wing and tarsus length both correlated best with weight ($N = 259$, $r = 0.68$, $p < 0.001$), but as wing length might decrease due to feather wear (Kitaysky et al. 1999), tarsus length was chosen. For chicks, head length best correlated with body mass ($N = 174$, $r = 0.86$, $p < 0.001$). The body condition index was not correlated with tarsus length of adults ($N = 259$, $r = 0$, $p > 0.05$) or head length of chicks ($N = 174$, $r = 0$, $p > 0.05$). Variations in body condition are likely not only reflecting variations in an individual's fat, but also in e.g. protein, water, or skeletal weight (Schulte-Hostedde et al. 2005), which we were unable to record as part of this study, as it involves euthanising the animal.

All blood and faecal smears were examined by experienced veterinary personnel under light microscopy. Blood smears were scanned for 10 minutes at x500

magnification (oil immersion) and approximately 80 high fields were examined with about 600 erythrocytes per high field (about 48,000 erythrocytes for intraerythrocytic parasites). Parasites were identified on morphology alone and parasite load was quantified as the number of parasites seen per high field or per smear when the level of parasitaemia was very low i.e. only up to five parasites seen on the blood smear during the examination time. Smear quality was categorized as good, medium, or poor based on thickness and spread of cells, and the staining quality. For further statistical analysis, only smears classified as good or medium were used (Valkiūnas et al. 2008).

Faecal smears were scanned for 10 minutes at x400 magnification and the parasite load estimated and categorised as “low” (1-3 parasites per slide), “medium” (5-10 parasites per slide), or “high” (> 1 parasite/high field). Smears with little faecal matter were discarded from the analysis.

For the faecal flotation analysis, only samples with enough faecal material (at least 1.5 g) were used, as lower quantities might reduce parasite detection rate (Herrin & Dryden 2017). The full sample was centrifuged for 5 minutes at 1500 rpm and the formalin subsequently decanted. The sedimented faecal sample was transferred into a faecal analysis kit (*Ovatector*®, Kyron Laboratories (Pty) Ltd, South Africa) and filled to the rim with the egg flotation fluid and covered with a 22 x 22 mm coverslip. The coverslip was removed after 10 minutes and placed on a microscope slide for further light microscope examination for parasite eggs and worms at x20 and x50 magnification. The whole cover slip was examined, and pictures of all potential parasite structures were taken with a Olympus SC 50 camera connected to the microscope and subsequently verified by a parasitologist. Due to the small number of samples for faecal flotation, as well as the low number of parasite eggs identified, results presented here are qualitative and not quantitative and no statistical analysis was performed. Furthermore, samples were stored up to two years in formalin until analysis was possible, and long storage time in formalin can affect the recovery of helminth eggs (e.g. Foreyt 1986, Crawley et al. 2016).

Statistical analysis

All statistical analyses were carried out in R (version 4.0.2; (R Core Team 2020). To identify the effects of the factors colony (on both adults and chicks) and year (on adults only) on the body condition, linear models were used, after checking for normality and homogeneity of variances. For differences between colonies, all colonies sampled in

2017 were compared: DW, MA, JU, ST, SD, KE, SW. For differences between years, comparisons were made between 2017 and 2018 in incubating adult Kelp Gulls sampled at four colonies (DW, MA, JU, ST). For differences in chick body condition, all colonies sampled with chicks in 2017 were compared: DW, ST, SD, KE, SW.

Presence/absence of blood and faecal parasites were compared between the factors year, colony, and age group by fitting logistic regression models with a binomial family (R Core Team 2020). Differences between years were tested by comparing the colonies DW, MA, JU, and ST sampled in 2017 and 2018, whereas DW, MA, JU, ST, SD, KE, and SW were used to compare colonies during the 2017 incubation period. Differences between age groups were tested by comparing incubating adults with chicks sampled at DW, ST, SD, KE, and SW in 2017.

To test for possible effects of the presence or absence of blood and faecal parasites on adult and chick body condition, linear models were fitted for each age group separately, after checking for normality and homogeneity of variances.

When necessary, the MuMIn package (Barton 2019) was used for averaging the different models and selecting the best fit model based on the Akaike Information Criterion corrected for small sample sizes (AIC_c; Burnham & Anderson 2002). Models were considered to be better than the null model when AIC_c differences were at least > 2 (Burnham & Anderson 2002). Post hoc Tukey tests were performed on the significant explanatory variables of each model to allow pair-wise comparisons using the multcomp package (Alzola & Harrell 2006).

Results

Body condition

Of the 436 incubating adult and chick gulls weighed and measured, 433 could be used for body condition index, as tarsus measurements were missing for the three remaining adults (Table 4.1; Table S4.1; Table S4.2).

Table 4.1: Number (N) of incubating adult Kelp Gulls and Kelp Gull chick samples for body condition index (g; mean ± SD), blood and faecal smears and number of positive samples from seven Kelp Gull colonies between 2017 and 2018.

Colony	Year	Body condition index Mean±SD (g) (Number of samples)		Blood parasites Number of positive samples (N total samples)		Faecal parasites Number of positive samples (N total samples)	
		Adult	Chick	Adult	Chick	Adult	Chick
Dwarskersbos	2017	10.1±107.4 (24)	-6.3±80.5 (26)	7 (23)	0 (23)	4 (8)	5 (7)
	2018	-22.0±79.8 (26)		11 (25)		3 (11)	
Malgas Island	2017	-23.7±88.7 (20)		2 (15)		4 (7)	
	2018	-47.7±88.6 (25)		6 (15)		3 (16)	
Jutten Island	2017	18.3±91.1 (21)		9 (16)		5 (13)	
	2018	-32.0±83.1 (27)		12 (27)		5 (10)	
Strandfontein	2017	59.7±99.9 (22)	12.2±79.9 (46)	11 (21)	1 (25)	5 (10)	12 (22)
	2018	-3.6±72.2 (25)		4 (13)		5 (14)	
Steenbras Dam	2017	10.3±78.4 (23)	-4.0±56.9 (25)	8 (21)	0 (25)	6 (6)	5 (15)
Keurbooms	2017	34.4±99.0 (24)	-2.4±51.6 (21)	8 (20)	1 (18)	2 (6)	13 (19)
Swartkops	2017	8.7±130.5 (22)	-4.5±80.2 (56)	5 (15)	0 (30)	1 (2)	7 (22)

Adult Kelp Gull body condition index ranged on average from -47.7 ± 88.6 g at Malgas Island to 59.7 ± 99.9 g at Strandfontein (Table 4.1). The body condition index did not differ between colonies, but between years with lower values in 2018 than 2017 (Figure 4.2, Table 4.2).

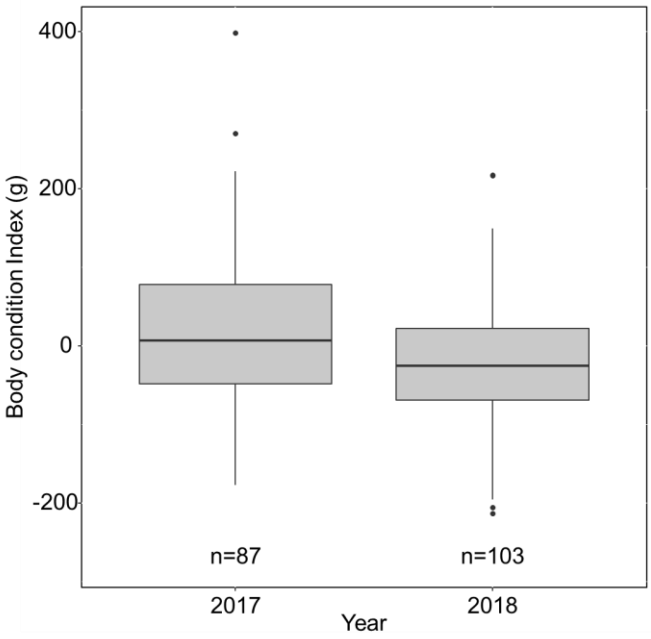

Figure 4.2: Boxplots representing adult Kelp Gull body condition in 2017 and 2018. The boxplots show the median values (band inside box), the 25th and 75th percentiles (box), the smallest and highest value within 1.5 times interquartile range (whiskers) and outliers (dots). N represents the number of birds per year.

Chick body condition index ranged on average from -6.3 ± 80.5 g at Dwarskersbos to 12.2 ± 79.9 g at Strandfontein (Table 4.1), but these differences between colonies were not significant ($p > 0.05$, Table 4.2).

Table 4.2: Summary statistics of linear model results of the factors colony and year on adult body condition, and colony on chick body condition. Best fit and significant models are shown in bold.

Model	Fixed factors	Model estimates ± SE	AIC_c	DF	R^2
BCI adult ~ Intercept			1886.83	1	
BCI adult ~ Colony	Intercept DW	10.11 ± 20.54	1891.25	6	0.01
	Colony JU	8.19 ± 30.06			
	Colony KE	24.27 ± 29.05			
	Colony MA	-33.86 ± 30.46			

	Colony SD	0.20 ± 29.36			
	Colony ST	49.57 ± 29.70			
	Colony SW	-1.45 ± 29.70			
BCI adult ~ Intercept			2264.22	1	
BCI adult ~ Colony			2259.41	5	
BCI adult ~ Year			2255.73	3	
BCI adult ~ Colony * Year			2255.84	9	
BCI adult ~ Year + Colony	Intercept 2017 DW	15.52 ± 14.22	**2250.73**	6	0.09
	Year 2018	-42.49 ± 12.91			
	Colony JU	-1.58 ± 17.92			
	Colony MA	-28.99 ± 18.22			
	Colony ST	33.11 ± 18.01			
BCI chick ~ Intercept			1994.10	1	
BCI chick ~ Colony	Intercept DW	-6.25 ± 14.59	2000.77	4	0.01
	Colony KE	3.88 ± 21.82			
	Colony SD	2.22 ± 20.83			
	Colony ST	18.48 ± 18.25			
	Colony SW	1.80 ± 17.65			

Blood parasites

A total of 364 blood smears were collected from the 394 birds caught for blood sampling, of which 332 were of good and medium quality and subsequently used for statistical analysis. The only parasite identified on blood smears was *Haemoproteus* spp. Overall, the presence of blood parasites was low, with only 25% of smears being positive, and with 58% of positive samples consisting of only one parasite being seen during the examination time. Logistic regressions showed no significant differences between years or colonies ($p > 0.05$; Table 4.3). However, age group had a significant effect on the presence and absence of *Haemoproteus* spp. (Table 4.3). Only 2% of chicks showed a presence of parasites, whereas the prevalence in adults was significantly higher (39%).

Table 4.3: Summary statistics of linear regression model result of the factors colony, year, and age on the presence/ absence of blood parasites. Best fit and significant models are shown in bold.

Model	Fixed factors	Model estimates ± SE	AIC_c	DF	R^2
Blood parasites adult ~ Intercept			284.84	1	
Blood parasites adult ~ Colony	Intercept DW	-0.51 ± 0.30	292.48	6	0.02
	Colony JU	0.46 ± 0.43			
	Colony KE	0.11 ± 0.55			
	Colony MA	-0.50 ± 0.51			
	Colony SD	0.03 ± 0.54			
	Colony ST	0.27 ± 0.46			
	Colony SW	-0.18 ± 0.62			
Blood parasites adult ~ Intercept			210.66	1	
Blood parasites adult ~ Year	Intercept 2017	-0.46 ± 0.24	212.60	2	0.00
	Year 2018	0.11 ± 0.33			
Blood parasites ~ Intercept			214.03	1	
Blood parasites ~ Age	Intercept Age 1	-0.45 ± 0.21	**158.18**	2	0.23
	Age 2	-3.64 ± 0.74			

Faecal parasites

Out of 213 faecal smears, 188 had enough material for microscope examination. No helminth eggs were identified, but yeast cells (*Candida* spp.) were noted on 45% of smears. Logistic regression results showed no significant effect of colony, year or age on the presence/absence of yeast cells ($p > 0.05$; Table 4.4). In addition, only 14 samples had “high” parasite loads.

Table 4.4: Summary statistics of linear regression model result of the factors colony, year, and age on the presence/ absence of faecal parasites.

Model	Fixed factors	Model estimates ± SE	AIC_c	DF	R^2
Faecal parasites adult ~ Intercept			141.97	1	
Faecal parasites adult ~ Colony	Intercept DW	-0.55 ± 0.48	141.78	6	0.1
	Colony JU	0.28 ± 0.63			
	Colony KE	-0.15 ± 0.99			
	Colony MA	-0.29 ± 0.66			
	Colony SD	18.11 ± 1615.10			
	Colony ST	0.20 ± 0.63			
	Colony SW	-0.54 ± 1.49			
Faecal parasites adult ~ Intercept			120.42	1	
Faecal parasites adult ~ Year	Intercept 2017	-0.11 ± 0.32	120.16	2	0.0
	Year 2018	0.68 ± 0.44			
Faecal parasites ~ Intercept			164.15	1	
Faecal parasites ~ Age	Intercept Age 1	0.25 ± 0.36	165.79	2	0.0
	Age 2	-0.27 ± 0.42			

The presence of helminth eggs was noted in nine of the 36 samples with enough material for faecal flotation, but the low detection rate for helminth parasite load should be considered with caution. The eggs identified were nematode eggs (one of the family Anisakidae and six *Capillaria* sp.), and two trematode eggs.

The presence of *Haeomoproteus* spp. did not affect chick or adult body condition ($p > 0.05$; Table 4.5). The presence of yeast cells was not correlated with chick body condition, but incubating adult Kelp Gulls with yeast cells in their faces had significantly higher body condition indices (Table 4.5, Figure 4.3).

Table 4.5: Summary statistics of linear model result of the factors presence/ absence of blood and faecal parasite on adult and chick body condition. Best fit and significant models are shown in bold.

Model	Fixed factors	Model estimates ± SE	AIC_c	DF	R^2
BCI adult ~ Intercept			1837.41	2	
BCI adult ~ Year + Colony			**1830.34**	6	0.1
BCI adult ~ Blood parasites * Colony * Year			1851.90	17	
BCI adult ~ Blood parasites + Colony + Year			1831.30	7	
BCI adult ~ Blood parasites + Colony			1835.13	6	
BCI adult ~ Blood parasites + Year			1832.26	4	
BCI adult ~ Blood parasites			1838.25	3	
BCI chick ~ Intercept			1372.43	2	
BCI chick ~ Blood parasites*Colony			1374.15	8	
BCI chick ~ Blood parasites + Colony			1379.51	7	
BCI chick ~ Blood parasites			1374.00	3	
BCI adult ~ Intercept			977.67	2	
BCI adult ~ Year + Faecal parasites	Intercept 2017 Absence Year 2018 Presence	90834.09 ± 36918.70 40.97 ± 18.40 -45.03 ± 18.30	**969.36**	4	0.12
BCI adult ~ Colony * Year * Faecal parasites			986.60	17	
BCI adult ~ Colony + Year + Faecal parasites			971.94	7	

BCI adult ~ Colony + Faecal parasites	975.05	6
BCI adult ~ Faecal parasites	973.21	3
BCI chick ~ Intercept	960.32	2
BCI chick ~ Colony * Faecal parasites	977.53	11
BCI chick ~ Colony + Faecal parasites	970.75	7
BCI chick ~ Faecal parasites	962.36	3

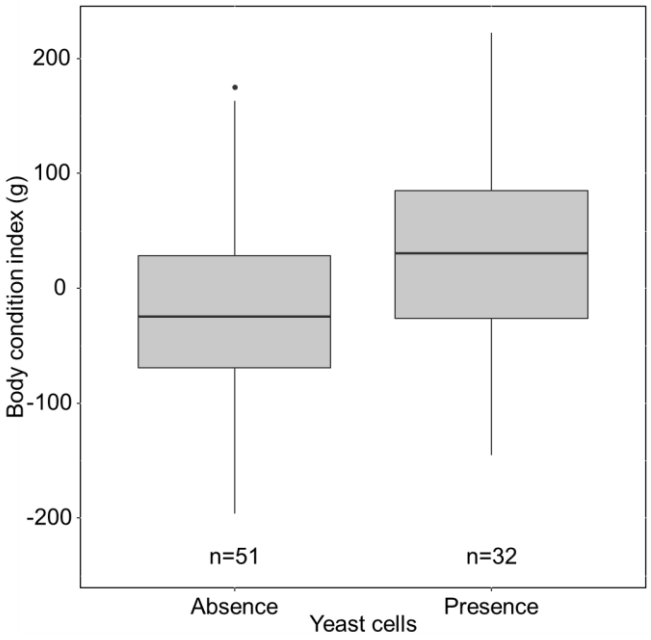

Figure 4.3: Boxplot of adult Kelp Gull body condition indices comparing birds with and without yeast cells in their faecal smears. The boxplots show the median values (band inside box), the 25th and 75th percentiles (box), the smallest and highest value within 1.5 times interquartile range (whiskers) and outliers (dots). N represents the number of faecal smears.

Discussion

In this study we failed to find any major differences in body condition or parasite loads among Kelp Gull colonies in South Africa, despite the various accessibility to landfills

and anthropogenic food. These results suggest that Kelp Gulls across South Africa seemed to be in a similar state during our study. Data collection was limited to incubating Kelp Gulls and their chicks, possibly biasing towards birds in sufficiently good condition to breed (Sorensen et al. 2009).

Body condition

We expected birds breeding in urban areas to have higher body condition values if they feed on more anthropogenic food of higher calorific value (Chapter 3). However, the body condition index of adults did not differ significantly between colonies, although birds at Strandfontein had the highest average values in 2017. This colony is very close to the large urban landfill of Cape Town, allowing easy access to anthropogenic diet items. Food derived from anthropogenic areas can have a higher energy density, protein, and fat content than natural prey (Pierotti & Annett 1991, O'Hanlon et al. 2017). The availability of human refuse in areas such as landfills allows gulls to access high lipid-content diet items such as pork, beef or chicken remains (O'Hanlon et al. 2017). It has previously been shown in e.g. Silver Gulls *Larus novaehollandiae* in Tasmania (Auman et al. 2008) or Yellow-legged Gulls *Larus michahellis* in Spain (Steigerwald et al. 2015) that diet choice can affect body condition. Male Silver Gulls breeding in an urbanized area were heavier and in better condition than males breeding at a remote site (Auman et al. 2008), whereas body condition decreased in both male and female Yellow-legged Gulls after landfill closure (Steigerwald et al. 2015). In 2017, breeding adult Kelp Gulls at Strandfontein had a high proportion of anthropogenic diet items in their stomach contents (Chapter 3), which might explain the higher body condition values for this colony.

Body condition values for adult Kelp Gulls varied between years and were higher in 2017 than 2018, and this difference in condition might be linked to the diet as well. Even though we did not find any significant differences in anthropogenic resources in stomach content samples of incubating birds between years, individuals fed in general more on natural coastal diet items in 2018 than 2017 and more on marine remains in 2017 than 2018 (Chapter 3). Considering that marine diet items are usually richer in energy than coastal prey (O'Hanlon et al. 2017), a higher contribution of marine diet items in 2017 might possibly explain higher body condition values. Likewise, a study investigating body condition and breeding performance in three petrel species

breeding at Kerguelen Island also reported differences in body condition between years, most likely due to annual fluctuations in prey availability (Chastel et al. 1995).

Blood parasites

Parasitaemia of blood parasites in South African Kelp Gulls was generally low and no difference was apparent between colonies. The only blood parasite identified was *Haemoproteus* sp. which can be transmitted to gulls through biting midges and louse flies (Valkiūnas 2004). The low presence of blood parasites in South African Kelp Gulls is consistent with the apparent scarcity or even absence of blood parasites in certain seabird species (Quillfeldt et al. 2011). Several hypotheses have been proposed to explain this pattern, including a scarcity of vectors, specific host-parasite associations, good immunological capabilities of the host preventing infection, and exclusion of blood parasite vectors due to high ectoparasite loads (see review by Martínez-Abraín et al. 2004). As Kelp Gull chicks had a significantly lower prevalence of *Haemoproteus* sp. than adults, it seems likely that the scarcity of vectors at colonies might explain low parasite loads (Esparza et al. 2004). Adult Kelp Gulls might be infected when visiting other foraging areas away from their breeding sites (Esparza et al. 2004). An absence of vectors was also inferred to explain the absence of blood parasites in Kelp Gulls breeding in Patagonia, Argentina (Jovani et al. 2001). Interestingly, our samples did not show any signs of infection with *Babesia* sp. or *Plasmodium* sp., even though some Kelp Gulls (e.g. on Malgas and Jutten Island) were breeding alongside Cape Gannets *Morus capensis* and Cape Cormorants *Phalacrocorax capensis*, both of which often are infected with these parasites (Parsons et al. 2017). One explanation could be that specific associations between host and parasites result in infrequent host switching (Ricklefs & Fallon 2002). The low presence of blood parasites in Kelp Gulls could also indicate a good immune system, as has been suggested for Common *Larus canus* and Black-headed Gulls *Chroicocephalus ridibundus* breeding in Estonia and Latvia (Krams et al. 2012). Blood parasite prevalence in Black-headed Gulls was very low and Common Gulls did not have any blood parasites, even though vectors for *Haemoproteus*, *Leucocytozoon* and *Plasmodium* were found at one of the colonies (Krams et al. 2012). In our study, ectoparasites were very seldom seen on either Kelp Gull adults or chicks (pers. obs.), suggesting that heavy ectoparasite loads were not responsible for low blood parasite presence (Martínez-Abraín et al. 2004). It is not

surprising that the presence of *Haemoproteus* sp. did not have an effect on body condition, given the low parasitaemia, but even heavily infected Audouin' s Gulls *Larus audouinii* showed no effect of parasite load on body condition (Ruiz et al. 1995). Species of the genus *Haemoproteus* are rather benign in birds (Bennett 1993) and do not seem to be clinically important to individuals in good health (Parsons & Vanstreels 2016).

Faecal parasites

Birds breeding in human-modified areas were expected to contain fewer helminth parasites than birds breeding in more natural environments, but due to the long storage time of samples until analysis was possible, the recovery of helminth eggs was most likely substantially decreased (Foreyt 1986, Crawley et al. 2016). Thus, we were not able to address this hypothesis. Nevertheless, the presence of yeast cells was noted in faecal smears, which are not uncommon in gulls (e.g. van Uden & Branco 1963, Buck 1983, Chryssanthou et al. 2011, Al-Yasiri et al. 2016). The variety of yeast species recovered from gulls ranged from marine to terrestrial and even potentially pathogenic (e.g. Chryssanthou et al. 2011, Al-Yasiri et al. 2016). It is likely that transmission of yeasts to birds is through feeding in habitats or on diet items contaminated with yeasts (Chryssanthou et al. 2011). Kelp Gulls in South Africa are generalists, feeding on a wide variety of diet items ranging from terrestrial to coastal and marine and from natural to anthropogenic (Chapter 2; Chapter 3), and use anthropogenic areas such as landfills or sewage works for feeding and roosting (Chapter 2), exposing birds to a wide variety of yeast species. Certain yeast species such as *Candida albicans* also occur in humans and can be pathogenic (Mayer et al. 2013). Transmission of these to birds is most likely through the ingestion of contaminated food or water (Friend et al. 1999) in areas polluted through e.g. wastewater (Chryssanthou et al. 2011).

Interestingly the presence of yeast cells in incubating adults coincided with higher values for body condition and might consequently be connected to Kelp Gull feeding habitats. Birds are likely to ingest yeast cells with their food by feeding in anthropogenic areas contaminated with human excrement (Al-Yasiri et al. 2016) and since anthropogenic food is often of higher caloric value (Pierotti & Annett 1991), this might explain higher body condition values with the presence of yeast cells.

Despite the scarcity of helminths in faecal smears, some helminth eggs were recovered from faecal flotation: two different nematode eggs (*Capillaria* sp., Anisakidae), two trematode eggs. Overall, helminth species diversity in gulls can vary (see review in Kennedy & Bakke 1989) and is thought to be linked to the gulls' feeding ecology (e.g. Bosch et al. 1994, Diaz et al. 2011, Labriola & Suriano 2001). For example, 18 helminth species were found in Kelp Gulls in Patagonia, Argentina, including 10 trematodes and four nematodes (Diaz et al. 2011), whereas Yellow-legged Gulls *Larus michahellis* breeding in Spain were parasitized by ten species (Bosch et al. 2000). Gulls in Patagonia fed on a more varied and natural diet, possibly explaining the high helminth species diversity (Diaz et al. 2011), whereas birds in Spain depended more on resources from landfills (Bosch et al. 1994), which usually does not include helminths (Bosch et al. 2000).

One of the nematode species found in South African Kelp Gulls was from the genus *Capillaria*, which is very widespread with over 300 different species being recognized and occurring in various species of wildlife such as fishes, mammals, and birds (Anderson 2000). Some *Capillaria* spp. can be transmitted to seabirds through earthworms (Anderson 2000) or in case of some marine species, intermediate hosts can include fish (Kleinertz et al. 2014). *Capillaria* has been recorded in Mediterranean Gulls *Ichthyaetus melanocephalus* in southern Italy (Santoro et al. 2011), in Herring Gulls *Larus argentatus* in northern Russia (Kuklin 2011), Red-billed Gulls in New Zealand (Fredensborg et al. 2004), and Kelp Gulls in Patagonia (Kreiter & Semenas 1997, Diaz et al. 2011).

The other nematode egg found in our samples was from the family Anisakidae. Infections of seabirds with Anisakidae can be through the consumption of marine invertebrates or fish (Anderson 2000) and have been recorded in Great Black-backed Gulls *Larus marinus* in Newfoundland (Threlfall 1968), Yellow-legged Gulls in north-west Spain (Sanmartín et al. 2005), Kelp Gulls in Argentina (Diaz et al. 2011), and Yellow-legged Gulls in the south-eastern Spain (Parejo et al. 2015).

The trematode eggs found in our samples may have been transmitted through molluscs, which play an important role in trematode transmission to seabirds (Galaktionov & Dobrovolskij 2003), but fish can also act as an intermediate host (Esch et al. 2002). Various trematode species have been recorded in different gull species, such as Great Black-backed Gulls in Newfoundland (Threlfall 1968), Yellow-legged

Gulls in Spain (Bosch et al. 2000), Red-billed Gulls in New Zealand (Fredensborg et al. 2004), Herring Gulls in Russia (Kuklin 2011), or Mediterranean Gulls in southern Italy (Santoro et al. 2011).

Overall, high helminth loads might negatively affect seabird condition and health (Khan et al. 2019) and high intensities of certain species negatively affected body condition of Yellow-legged Gulls breeding in Spain (Bosch et al. 2000). As body condition seems to have an influence on reproductive performance (Pons & Migot 1995, Steigerwald et al. 2015), reduced body condition could also negatively affect breeding success (Houston et al. 1983), through lower egg volume and clutch sizes (Pons & Migot 1995, Steigerwald et al. 2015).

Conclusions

This is the first study investigating the body condition and parasite load of adult Kelp Gulls and their chicks in South Africa. We showed that overall body condition was similar across our study sites, and blood parasite loads were generally low, as has been reported for many other seabird species. Faecal sampling should be repeated as the analysis of helminth in gulls offers valuable opportunities to identify the effects of a natural and urban diet on parasite load and diversity. In addition, repeated chick measurements and diet recordings, as well as breeding success should be recorded in future studies, to be able to link the effect of diet on body condition and subsequently breeding success in South African Kelp Gulls.

As Kelp Gulls in South Africa seem to have almost entirely similar body condition values and low blood parasite loads, it is possible that urban landscapes have little impact on the health status of Kelp Gulls. Their ability to feed opportunistically might thus allow them to successfully maintain the population.

Supplementary Information

Table S4.1: Weight and structural size measurements (mean ± SD) of incubating adult Kelp Gulls (N) from seven Kelp Gull colonies between 2017 and 2018.

Colony	Year	Weight (g) (N)	Tarsus (mm) (N)	Wing length (mm) (N)	Head length (mm) (N)	Bill length (mm) (N)	Bill depth (mm) (N)
Dwarskersbos	2017	988.8±133.3 (24)	80.5±4.4 (24)	420.8±14.8 (24)	119.7±5.7 (24)	54.7±3.4 (24)	21.4±1.4 (24)
	2018	993.8±127.3 (26)	82.3±4.4 (26)	423.2±14.9 (26)	122.2±6.7 (26)	55.2±3.6 (26)	21.3±1.2 (26)
Malgas Island	2017	948.5±123.3 (20)	80.1±4.9 (20)	414.7±15.6 (20)	118.2±6.5 (20)	53.0±3.1 (20)	20.6±1.0 (20)
	2018	923.2±136.0 (25)	80.1±3.8 (25)	414.8±13.6 (25)	120.2±8.2 (25)	53.8±3.2 (25)	21.4±1.4 (25)
Jutten Island	2017	995.2±124.5 (21)	80.4±4.0 (21)	422.9±14.0 (21)	122.3±8.6 (21)	53.8±3.4 (21)	21.9±1.3 (21)
	2018	948.1±123.5 (27)	80.5±4.3 (27)	416.7±14.2 (27)	120.2±5.6 (27)	55.2±3.6 (27)	22.0±1.6 (27)
Strandfontein	2017	1065.5±110.2 (22)	81.8±3.4 (22)	421.0±9.8 (22)	122.9±5.2 (22)	56.0±2.9 (22)	22.3±1.0 (22)
	2018	992.0±125.6 (25)	81.3±4.9 (25)	417.8±14.9 (25)	120.8±6.8 (25)	54.5±3.7 (25)	21.7±1.4 (25)
Steenbras Dam	2017	969.6±89.2 (23)	79.5±5.0 (23)	418.9±11.2 (22)	122.5±7.1 (23)	56.3±3.9 (23)	21.7±1.4 (23)
Keurbooms	2017	1002.5±137.2 (24)	79.9±4.2 (24)	412.3±15.9 (24)	117.4±6.3 (24)	53.1±3.2 (24)	21.1±1.3 (24)
Swartkops	2017	1055.0±150.2 (22)	83.9±4.3 (22)	423.0±14.5 (22)	121.2±6.0 (22)	54.7±3.5 (22)	22.1±1.6 (22)

Table S4.2: Weight and structural size measurements (mean ± SD) of Kelp Gull chicks (N) from five Kelp Gull colonies in 2017.

Colony	Weight (g) (N)	Tarsus (mm) (N)	Wing length (mm) (N)	Head length (mm) (N)	Bill length (mm) (N)	Bill depth (mm) (N)
Dwarskersbos	841.5±114.8 (26)	79.0±3.8 (26)	231.2±38.5 (26)	100.0±5.3 (26)	44.6±10.5 (26)	14.4±.0.9 (26)
Strandfontein	843.5±147.2 (46)	79.1±4.7 (46)	214.9±42.0 (46)	98.9±7.2 (46)	42.4±3.2 (46)	14.4±1.2 (46)
Steenbras Dam	876.8±133.8 (25)	80.7±4.5 (25)	238.4±39.2 (25)	102.1±7.0 (25)	44.3±4.4 (25)	14.1±1.3 (25)
Keurbooms	872.9±124.7 (21)	82.6±3.7 (21)	244.4±42.6 (21)	101.7±6.2 (21)	43.4±3.1 (21)	14.3±1.1 (21)

Swartkops	771.6±155.8 (56)	77.7±5.7 (56)	209.9±65.2 (56)	95.4±9.5 (56)	40.1±4.8 (56)	13.8±1.4 (56)

Chapter 5: General discussion

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Global changes are affecting terrestrial, freshwater, and marine ecosystems worldwide (Steffen et al. 2004). Increasing human population numbers are exerting pressure on natural resources (Smail 1997), are responsible for global climate change (Dunn et al. 2020), or cause alterations to the global land area (Winkler et al. 2021). Human-induced land use changes through urbanisation or agriculture cause habitat fragmentation, modification or loss (Foley et al. 2005, Pickett et al. 2011), but also create opportunities for species better adapted to anthropogenically modified areas (McKinney 2006). In general, a species ability to adapt or even thrive under these conditions largely depends on specific traits such as a high tolerance towards change, widespread distribution, generalist foraging nature, or even a high rate of innovation (Baskin 1998, McKinney & Lockwood 1999, Møller 2009). Seabirds are among the most threatened groups of birds (Croxall et al. 2012), being exposed to many threats both on land and at sea (Dias et al. 2019). They are often used as sentinels for ocean health as they integrate changes at lower levels of the food web (Piatt et al. 2007) and can be relatively easily accessed during the breeding season (Schreiber & Burger 2002). Seabirds can be broadly classified according to their diet and are either generalists or specialists (Le Bohec et al. 2013). Generalist species are able to exploit a wide variety of food resources and are thus generally less susceptible towards changes in resource availability (Votier et al. 2004a, Mendes et al. 2018). Many generalist species take advantage of anthropogenic food sources from e.g. fisheries discard or landfill sites (Oro et al. 2013), often leading to increased population numbers (Oro et al. 2013, Noreen & Sultan 2021).

Kelp Gulls are widespread in the southern hemisphere and are currently listed as ‘least concern’ (BirdLife International 2018a). They are generalists and feed on a wide variety of prey including terrestrial, coastal, marine, and anthropogenic resources (Steele 1992, Hockey et al. 2005). They are also predators of other seabirds’ eggs and chicks (Hockey et al. 2005). Population numbers in South Africa increased in the 1980s due to protection from persecution (Crawford et al. 2009a) and the availability of supplementary food resources from fisheries bycatch and landfills (Steele & Hockey 1990, Steele 1992). The overarching aim of this thesis was to assess to what extent South African Kelp Gulls depend on anthropogenic resources during the breeding season with implications for their foraging habitat choice, diet and health status.

Key findings

Firstly, I analysed the foraging movements of Kelp Gulls incubating at six different colonies in South Africa (Chapter 2). The study revealed a high foraging flexibility with foraging habitat areas ranging between 30 m up to 80 km from their respective colonies. Gulls from west coast colonies (Dwarskerbos, Malgas and Jutten Island), generally located further from urban areas or landfills, travelled farther than south and east coast colonies (Strandfontein, Keurbooms, and Swartkops), and all birds travelled farther when foraging at sea. Foraging in marine habitats might thus require higher effort than foraging in coastal or terrestrial environments but might be balanced by feeding on high energy resources at sea (O'Hanlon et al. 2017, Van Donk et al. 2017). Foraging habitats were varied and ranged from marine to coastal, and terrestrial natural to terrestrial anthropogenic areas, with birds generally foraging more in marine, coastal and natural terrestrial habitats. The variability in foraging habitat choice in South African Kelp Gulls shows their high plasticity in foraging behaviour, conforming to other gull species (Duhem et al. 2003a, Shaffer et al. 2017). Gulls spend most of their time on the colony, probably related to resting or even feeding on the colony. Many gull species often switch to a more natural diet when provisioning chicks (e.g. Annett & Pierotti 1989, Isaksson et al. 2016). Thus, to reveal possible differences in foraging habitat choice between incubation and chick-rearing, it would be vital to use GPS deployments over the entire breeding period. In addition, it would be valuable to explore the costs and benefits associated with each foraging habitat type with regard to energy expenditure and calorific gain of diet (Patenaude-Monette et al. 2014, Van Donk et al. 2019).

Secondly, I investigated the diet and trophic ecology of incubating Kelp Gulls and their chicks from stomach content, regurgitated pellet, and plasma blood samples. Results showed that gull diet and trophic ecology differed between colonies, years, and age groups/breeding stages. Distance to the nearest landfill seemed to only impact the diet of one of the urban colonies sampled, Strandfontein, showing a high contribution of anthropogenic items in their diet. The other two colonies with a high ratio of anthropogenic resources most likely scavenged these in the urban centres close to the colonies. As the other colony located close to a landfill (the Swartkops colony) did not feed highly on anthropogenic food, this behaviour might be linked to natural prey availability close to the colony. The two neighbouring island colonies (Jutten and

Malgas) showed differences in diet and trophic ecology, potentially to reduce intra-specific competition (Corman et al. 2016, Shaffer et al. 2017). Birds from one of the more remote colonies, Dwarskersbos, had a smaller isotopic niche and foraged mainly on rocky shore mussels and fish, suggesting some kind of specialisation. Spatial differences are most likely the result of different resource availability around the colonies (O'Hanlon et al. 2017, Yorio et al. 2020, Kasinsky et al. 2021), or local adaptations (Méndez et al. 2020, Ouled-Cheikh et al. 2021).

Differences between years were evident especially for birds breeding on Malgas Island, showing higher $\delta^{15}N$ values in 2018 than 2017, suggesting that they were feeding at a higher trophic level that year, which was confirmed by their stomach content samples with a higher contribution of bird remains that year. Kelp Gulls are natural predators of seabirds (e.g. Cooper 1974, Du Toit et al. 2003), and gull predation on Cape Gannet *Morus capensis* eggs increased substantially in 2018 (Pichegru 2019), possibly explaining the enriched $\delta^{15}N$ values observed here. Overall, however, niche overlap between colonies and years was high, suggesting a general consistency in diet and trophic ecology. Comparing trends in diet based on pellet analysis from this study and a study from thirty years ago (Steele 1992) showed similar patterns and a general overlap in overall diet. Incubating adults and chicks differed in their diet and trophic ecology at least at some of the studied colonies. Chicks were being fed a different and higher trophic level diet and changes in anthropogenic diet consumption was especially evident at one of the urban colonies, Strandfontein. Here, chicks were being fed mostly marine items, i.e. fish, indicating that habitat quality is important when provisioning chicks (Schwemmer & Garthe 2008). A diet with high energetic value is important for chick growth and subsequent survival (Annett & Pierotti 1999, van Donk et al. 2017). However, not all sampled colonies showed a change in trophic ecology, potentially linked to habitat and resource availability (O'Hanlon et al. 2017), the inability to switch prey (Zorrozua et al. 2020), or the demanding and competitive nature of feeding in anthropogenic areas (Monaghan 1980, Camphuysen et al. 2015, Van Donk et al. 2019). During the breeding period, Kelp Gulls are restricted to foraging habitats and resources in the vicinity of the breeding colony. Their diet outside the breeding season might differ, with supplementary food resources potentially becoming more important (Ramírez et al. 2020). To allow effective population management, it is thus vital to also assess their diet outside the breeding season. Furthermore, a measure of

breeding success would be valuable to discern effects of diet and trophic ecology on hatching survival and colony production.

Thirdly, I evaluated the effect of colony location and diet on Kelp Gull body condition and parasite load and diversity (Chapter 4). The study revealed that body condition indices of incubating adults and chicks were overall similar across colonies, although adults at one of the urban colonies, Strandfontein, tended to be in slightly better body condition. This colony is located very close to a landfill, thus allowing easy access to high-lipid diet items from anthropogenic resources (O'Hanlon et al. 2017). This is confirmed by findings from the previous chapter (Chapter 3), showing that gulls incubating at Strandfontein had a high percentage of refuse in their diet. Blood parasite prevalence was low, and the only parasite identified was *Haemoproteus* sp. In addition, chicks had a significantly lower prevalence of *Haemoproteus* sp. than adults. This suggests that adult Kelp Gulls might get infected with parasites outside their breeding colonies, in areas where vector density might be higher (Esparza et al. 2004). Yeast cells (*Candida* spp.) were identified from faecal samples and the presence of yeast cells was linked to higher values of body condition in adults. Both body condition and parasite load and diversity can be linked to foraging habitat choice and diet (Bosch et al. 2000, Auman et al. 2008, Quillfeldt et al. 2011). Yeast cells can be ingested by foraging in anthropogenic environments contaminated with human faeces (Al-Yasiri et al. 2016). Since urban food can be of higher calorific value (Pierotti & Annett 1991), this might explain the correlation between the presence of yeast cells and higher body condition indices. Unfortunately, the long storage time of faecal samples most likely affected the recovery of helminth eggs (Foreyt 1986, Crawley et al. 2016), but should be repeated in the future to identify effects of foraging habitat choice and diet on helminth diversity and load.

Kelp Gulls and global change

South African Kelp Gulls are undoubtedly exhibiting some of the specific traits characterising winners of global change (Baskin 1998, McKinney & Lockwood 1999, Møller 2009). As shown in this study, their generalist foraging nature allowed them to exploit a wide variety of different foraging habitats and resources, from marine to terrestrial and natural to anthropogenic. Thus, they are less likely to be sensitive towards changes in habitat or resource availability as they are able to switch to

alternative resources (Votier et al. 2004a, Mendes et al. 2018). They are widespread, as Kelp Gulls are distributed throughout the southern Hemisphere (BirdLife International 2018a). Furthermore, their ability to take advantage of various anthropogenic landscapes or resources, such as agricultural fields, urban areas, landfills, or fisheries discard shows some rate of innovation in their foraging behaviour, important for living in human-dominated landscapes (Møller 2009).

Kelp Gulls are usually found in coastal areas or on islands and are thus subjected to global changes both on land and at sea (BirdLife International 2018a). Changes in land use can create new foraging opportunities of anthropogenic nature, such as urban areas or landfills (Navarro et al. 2017). The emergence of these feeding opportunities may have caused a shift to a higher carrying capacity for generalist species due to high predictability of these new foraging sites (Oro et al. 2013). It has been hypothesized that the increase in South African Kelp Gull numbers might be linked to increased survival of juvenile gulls, as the availability of supplementary food resources from e.g. landfills allows exploitation of resources for less experienced foragers (Steele & Hockey 1990) or even handicapped individuals (Carmona et al. 2021). Changes in landfill management might thus affect Kelp Gull population numbers by reducing survival of juvenile gulls but probably not adults (Delgado et al. 2021). In addition, as observed for birds on Malgas Island, Kelp Gulls can take a large percentage of seabird eggs through direct predation (Pichegru 2019). Changes in the availability of anthropogenic resources might lead to increased predation on other seabirds (e.g. Regehr & Montevecchi 1997, Votier et al. 2004a), especially from colonies such as Strandfontein, that fed to a high extent on refuse during incubation. Some of our studied colonies had a high proportion of marine resources in their diet and especially chicks were fed a more natural (i.e. fish) and higher trophic level diet. Fish usually originates from scavenging fisheries discard (Steele 1992, Kasinsky et al. 2018) or foraging at sea (Duffy 1989). Overfishing, climate-induced changes in fish distributions or changes in fisheries discard policies might create shortages of marine prey items (Goñi 1998, Crawford et al. 2015, Calado et al. 2018). Changes in high quality marine resource availability could potentially have negative effects for chick physiology (Pais de Faria et al. 2021) or breeding success (Kitaysky et al. 2006, Foster et al. 2017).

Kelp Gulls in our study did not show a high prevalence of blood parasites, potentially related to e.g. scarcity of vectors or specific host-parasite associations (Martínez-

Abraín et al. 2004). Climate change related temperature changes might alter parasite transmission and subsequently the potential for host switching (Brooks & Hoberg 2007), potentially resulting in an increase in blood parasites in gulls. Furthermore, land use change and resource availability might also alter gull foraging behaviour leading to a higher susceptibility to parasites or pathogens from urban areas. As coastal areas are changed into urban environments, the potential for human-gull conflicts is increasing (Seto et al. 2011). Gulls are already often perceived as pests due to their aggressive behaviour, noise, and/or potential for pathogen dispersal (Belant 1997, Rock 2005). To properly manage gull populations, it is important to understand the underlying reasons behind the emergence of superabundant populations (Ramírez et al. 2020). Supplementary food resources are one of the reasons for high Kelp Gull populations numbers (Steele 1992) and thus identifying the main foraging habitats was vital to understand population dynamics and propose suitable management policies.

Future perspectives

This thesis explored the foraging ecology and health status of Kelp Gulls in South Africa in relation to the proximity of colonies to anthropogenic resources during the breeding season. Kelp Gulls are central place foragers during breeding and thus depend on foraging habitats in the vicinity of their breeding colony (Orians & Pearson 1979). Optimal foraging theory predicts, among others, that an individual will choose a foraging strategy that maximises energy intake from the diet by minimising energetic costs to obtain those resources (Sinervo 1997). To test optimal foraging theory for a generalist species foraging in a heterogenous environment, such as the Kelp Gull, accelerometer deployments will allow calculation of energy expenditure for each foraging trip, and, in combination with the calorific gain of the potential diet, can provide information on the costs and benefits linked to each foraging habitat (Van Donk et al. 2019). In addition, the diet and foraging habitat choice of Kelp Gulls outside the breeding season might differ, with individuals potentially exploiting other resources when birds are not restricted by colony location or energy requirements (Ramírez et al. 2020). Thus, supplementary food resources might play an important role during the non-breeding period, making it necessary to assess foraging movements and diet patterns outside the breeding season, to guarantee efficient population management. For that, it would be beneficial for future studies to deploy GPS loggers or transmitters

on birds for longer time periods by using e.g. a wing harness to ensure devices remain attached through moult (Thaxter et al. 2014). Furthermore, stable isotope analysis of feathers can also give an insight into the trophic ecology outside the breeding season as feathers integrate isotopic signatures on the diet during feather growth (Hobson & Clark 1992). Kelp Gulls undergo a complete post breeding moult (Hockey et al. 2005) and thus feathers sampled during the breeding season provide information on the diet before breeding.

Another important aspect to consider when trying to understand global change impacts on a species' population dynamics is individual specialisation. Individuals specialising on certain resources might respond differently to changes in resource availability or habitat, which could have implications for population dynamics (Phillips et al. 2017). Thus, assuming a populations ecological niche to be similar for all individuals might lead to inaccurate and insufficient management plans (Bolnick et al. 2003). Even though results from this study showed that Kelp Gulls are overall foraging on a wide variety of resources, typical for a generalist species, there might be individuals that specialise on specific resources. Individual specialisation has been reported for other species of gulls (e.g. Pierotti & Annett 1990, Spear 1993, Masello et al. 2013) and can be related to nutritional requirements (Pierotti & Annett 1990), resource availability (Spear 1993), learned behaviour (Masello et al. 2013), or individual size (Van Donk et al. 2020). Stable isotopes of different tissues can provide information on the trophic ecology for different time scales ranging from a few days (blood plasma; Vander Zanden et al. 2015) to several weeks (red blood cells; Hahn et al. 2012) and months (feathers; Hobson & Clark 1992). Combining stable isotope analysis with GPS deployments might allow to identify potential specialists within the South African Kelp Gull population, necessary to predict their ability to adapt to changes in resource availability for population dynamics.

Even though adult Kelp Gulls do not differ in plumage, males are overall larger than females (Hockey et al. 2005), which might lead to sex specific dietary differences. Differences in diet between males and females have been reported for Herring Gulls (Pons 1994) or Lesser Black-backed Gulls (Camphuysen et al. 2015), and are often associated with differences in size between males and females (Pons 1994, Camphuysen et al. 2015). Foraging on certain resources, such as fishery discard or anthropogenic diet items from landfill sites, can be highly competitive (Monaghan 1980,

Camphuysen et al. 2015) and might thus be more suitable for larger males (Camphuysen et al. 2015). Furthermore, females might have different dietary requirements during egg formation due to an increased need of calcium (Pierotti & Annett 1990), which might result in feeding more on calcium rich food, like mussels, possibly to recover calcium reserves (Niebuhr 1983). In addition, foraging habitat choice might also affect parasite load and diversity (Bosch et al. 2000, Diaz et al. 2011, Quillfeldt et al. 2011) as well as pathogen exposure (Ramos et al. 2010, Al-Yasiri et al. 2016, Moré et al. 2017). Therefore, different foraging strategies for males and females might lead to differences in parasite and pathogen prevalence. This might affect body condition (Bosch et al. 2000), which in turn could lead to lower clutch sizes or decreased egg quality and ultimately decreased breeding success (Houston et al. 1983, Steigerwald et al. 2015).

Finally, another important factor to incorporate in future studies would be a measure of breeding success. It has been shown in several studies that the diet of gulls can be linked to reproductive success (e.g. Pierotti & Annett 1987, O'Hanlon et al. 2017, van Donk et al. 2017), with conflicting results as to whether more natural (e.g. Pierotti & Annett 1987, O'Hanlon et al. 2017) or anthropogenic resources lead to higher breeding performance (e.g. Weiser & Powell 2010, Steigerwald et al. 2015). Furthermore, reproductive success might also be used as a proxy for adult fitness, with diet impacting egg quality and subsequently number of chicks hatched (Pierotti & Annett 1990). If diet choice affects Kelp Gull breeding success, changes in resource availability or land use might affect reproductive performance and could ultimately affect Kelp Gull population levels. Thus, it would be valuable to measure breeding success by monitoring marked nests from egg laying until fledgling and 1) measuring egg size and weight; 2) record hatching success; 3) calculate chick growth rate through repeated measurements; and 4) record fledging success.

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