Investigating the foraging ecology and energy requirements of a seabird population increasing in an intensely exploited marine environment

Davide Gaglio

Investigating the foraging ecology and energy requirements of a seabird population increasing in an intensely exploited marine environment

Davide Gaglio

March 2017

Supervisor:

Prof. Peter G. Ryan

Co-supervisors:

Dr. Timothée R. Cook

Dr. Richard B. Sherley

FitzPatrick Institute of African Ornithology

Department of Biological Sciences

University of Cape Town

Thesis presented for the degree of Doctor of Philosophy

March 2017

I, Davide Gaglio, hereby declare that the work on which this thesis is based is my original work (except where acknowledgements indicate otherwise) and that neither the whole work nor any part of it has been, is being, or is to be submitted for another degree in this or any other university. I authorise the University to reproduce for the purpose of research either the whole or any portion of the contents in any manner whatsoever.

In accordance with the guidelines outlined by the Doctoral Degrees Board, this thesis does not exceed 80,000 words.

Signature: Signed

Date: 12/03/2017

This thesis should be cited as:

Gaglio D. (Submitted for examination) Investigating the foraging ecology and energy requirements of a seabird population increasing in an intensely exploited marine environment. PhD thesis. University of Cape Town, South Africa.

Signed by candidate

Signature: signature removed

Date: 12/03/2017

Plagiarism Declaration

"This thesis/dissertation has been submitted to the Turnitin module (or equivalent similarity and originality checking software) and I confirm that my supervisor has seen my report and any concerns revealed by such have been resolved with my supervisor."

Name: Davide Gaglio

Student number: GGLDAV001

Signature:

Signed

Date: 12/03/2017

KREE-ECK…KREEEEEE-ECK

The Greater Crested Tern

TABLE OF CONTENTS

ACKNOWLEDGEMENTS

I am extremely grateful to my three supervisors for taking me in on this adventure first as a MSc and then allowing me to continue as a PhD student. Thank you, Peter Ryan, for supporting my project and giving me the opportunity to develop my research skills under your supervision. I feel privileged to be part of your research at the FitzPatrick Institute and I really enjoyed our conversations about bird photography.

Thank you to Timothée Cook for thinking up this project and for the many discussions, often over a glass of wine or two. For all your confidence in me and your support, especially with the field work.

Thank you, Richard Sherley, for introducing me to the mysterious world of R, for your patience and understanding during my analysis, and for your continued encouragement and support during my 'imprisonment' in Robben Island.

I would also like to extend my thanks to Tom Flower, for all your support and invaluable feedback. Your enthusiasm in behavioural ecology allowed me to discover a new discipline and your supervision was crucial for the writing of Chapter 5 (I can't thank you enough!). A big thanks to Maelle Connan for your assistance in the identification of prey from regurgitations and writing of Chapter 2 of this thesis, and for your enthusiastic support and continuous encouragement for my project. I owe much thanks to Alistair McInnes and Chevonne Reynolds for their constant presence, when any problem arose, especially when 'R' analyses were making my life miserable!

I would also like to thank the funders of my research which was supported by a Department of Science and Technology-Centre of Excellence grant of the FitzPatrick Institute of African Ornithology. Thanks to the Department of Environmental Affairs (DEA) and South African National Parks, who provided permits for this research and access to the tern colonies. Thanks to Leshia Visagie and DEA for use of the house on Robben Island. Thanks to staff of Robben Island Museum for providing logistical support and access to the tern colonies on Robben Island and all the penguin people for their entertainment during my stay on the island. I would also like to thank Pierre Pistorius, for supporting the research on Seal Island. Thanks to Carl van der Lingen and Cecile Reed for providing me with samples of anchovy and the length-mass anchovy regression, used in Chapter 4. To Janet Coetzee, thank you for providing annual hydro-acoustic surveys conducted by DAFF, used in Chapter 3. Thanks to Robert Crawford and Bruce Dyer for providing historical bird counts and sharing crucial thoughts on tern's ecology and their population dynamics. Thanks to the South African Weather Service for providing me with weather data from Robben Island.

I am really grateful to the late Barrie Rose and Bruce Dyer, Carl van der Lingen, Rob Leslie, Bryan Maritz, Charles Griffiths, Mike Picker, Jean-Paul Roux and Malcolm Smale for their assistance with prey identification. Thanks to Carl van der Lingen and Kate Watermayer for important inputs on pelagic fish ecology, and to Stephen Votier for constructive comments on an earlier version of Chapter 2. Thanks to the numerous volunteers who helped in the field and Alistair McInnes and Dominic Rollinson for taking photo-sampling on the 18th and 19th April 2015 in Robben Island.

I can't thank enough my Fitz family, for the many informal meetings (especially at the UCT pub), which drove my intellectual curiosity and inspired me immensely during my PhD. Both past and present students and post-docs (Alistair, Chevonne, DomRoll, Ralph, Ben, Ross, DomH, Leo, Sophie, Hayley, Kate, Tanja, Margaux, Antje, Tim Reid, Andrew, Ditiro, Laurie, Kim, Otto, Dayo, Lisa, Rowen, Gareth, Meg, Petra and Diana). Thanks to all lecturers (Susie, Claire, Arjun and Robert) and staff members of the Fitz (Hilary, Margaret, Anthea, Tanja, Denise, Susan, Phelisa, Rob, Chris and Gonzalo), who became my family away from home; thank you all!

Thanks to Nicola Okes for sharing the wisdom that 'one does not simply write a PhD thesis' and for introducing me to this project and to my wife. To Gabriele, Miriam and Nico in Australia and all my friends in Sicily: il Grillo e famiglia, Ric, Rudy, Rosy, Gabriellina, Panza, Zassa, Mastrilli, Eleoninni, Seregna, Pilvia, Mathia, Stefano e il Filippone.

Thanks to Michelle's family for welcoming and hosting me in the first weeks in South Africa, and then still allowing me to marry your daughter.

Thanks to my family: mamma, papá, Riccardo, Sara e il piccolo Flavio *per aver da sempre creduto in me, nelle mie potenzialita' di ricercatore, di fotografo e di persona…grazie!!* Mum and Dad, thanks for your unconditional and constant love from across the miles.

To my lovely (and pretty) wife, Michelle, I could never have finished this without you! Not only for your help with English gr'u'mmar, or for sharing long interesting thoughts 'out of the box', but especially for your enthusiasm and interest for this project that helped me to survive until the end. Thanks for falling in love with my terns and with me! I love you too! Let the new adventure begin!

Last but not least, thanks to my terns for making my job so magic!!! Yes…you are way better than penguins!

ABSTRACT

Their high energetic demands make seabirds sensitive to changes in prey availability, which is often reflected in their diet and energetic expenditure during breeding. Populations of the three seabirds endemic to southern Africa's Benguela upwelling ecosystem that rely on small pelagic fish have decreased dramatically over the last decade. In contrast, the population of the greater crested tern *Thalasseus bergii* has increased. To understand these conflicting trends, I investigated the foraging ecology and energy requirements of the greater crested tern breeding in the Western Cape, South Africa. Diet was assessed by a novel non-invasive methodology developed in this study, using digital photography. More than 24,000 prey items from at least 51 different prey taxa were identified, with 34 new prey species recorded, revealing a high degree of foraging plasticity for this seabird. Greater crested terns rely mainly on anchovy *Engraulis encrasicolus* (65%), which averaged 84 mm long. Prey composition differed significantly between breeding stages, with anchovy especially dominant at the onset of the breeding period and the diet becoming more variable as the season progressed. Time-energy models for breeding terns were built based on activity budgets collected from non-invasive video-recordings and focal observations. Foraging trips were significantly longer during incubation than the chick provisioning stages, and feeding rates doubled from early to late chick provisioning. This study illustrated a steady increase in energy needs of adults throughout the breeding season, due to their increased foraging effort to meet chick energy needs. In comparison to other Benguela endemic seabirds that also rely on small pelagic fish, terns displayed substantially lower energy requirements at both individual and population levels. Their low energy requirements are due to their small body size, reduced flight costs and efficient foraging strategies, which together allow this population to cope with recent changes in the distribution and abundance of their main prey, and likely drive their recent population increase, in contrast with decreases in other seabirds relying on the same prey base also exploited by human fisheries. I also explored the costs underlying interactions within mixed-species aggregations by investigating the costs induced by kleptoparasitism between mixed colonies of greater crested terns and Hartlaub's gulls *Chroicocephalus hartlaubii* and colonies with greater crested terns alone. Video-recordings coupled with focal observations showed that terns suffer direct costs to chick provisioning rates and indirect costs through energy expenditure in a mixed-species colony, suggesting that these breeding assemblages may be a form of parasitism rather than a mutualistic association. Despite the detrimental effects of interspecific kleptoparasitism, the marked foraging plasticity and low energetic requirements of greater crested terns, described in this study, coupled with specific life history traits such as low fidelity to breeding sites and extended post-fledging care, are key factors that allow this species to cope with changes in the availability and abundance of their main prey. Understanding species-specific behavioural responses to ecosystem variations in the Benguela

upwelling system is vital for assessing the impact of commercial fisheries on seabird populations and fish stocks. Finally, the implementation of the method developed in this study, in long-term monitoring programmes, may provide crucial knowledge for conservation plans and key input to realising an ecosystem approach to fisheries management.

Paper arising from this thesis

The following manuscript was published prior to submission of this thesis. D.G. undertook all fieldwork, laboratory work, analysis and the writing of the manuscripts. P.G.R., T.R.C. and R.B.S, acting in a supervisory capacity aided in the study design and oversaw the writing of the manuscripts. M.C. contributed to the ID of prey from regurgitations and the writing of the paper.

Gaglio, D., Cook, T. R., Connan, M., Ryan, P. G., & Sherley, R. B. (2016) Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. *Methods in Ecology and Evolution*, **8**, 214–222.

Chapter 1

General Introduction

Introduction

Identifying factors causing variation in species abundance and understanding sources of fluctuations in population dynamics are important questions in applied ecology (Begon *et al.* 1996). The biotic (e.g. food abundance, competition) and abiotic (e.g. climate) conditions of an ecosystem have a large influence on population growth and shape the life history traits of animal species (Stearns 1992, Begon *et al.* 1996). Environmental constraints and regulatory processes, such as prey availability, habitat quality, competition, predation, human activities and population density can explain demographic variations (Sæther 1997). Generally, long-lived species allocate resources to maximise their own survival and future reproduction, whereas short-lived species tend to allocate resources favouring current reproduction (Williams 1966, Stearns 1992). Different life history strategies govern reproductive output, influences constrains the ability of individual species to respond to environmental variation (Fischer *et al.* 2011).

The ocean is a good example of a highly variable ecosystem, where top predators must respond to seasonal and inter-annual changes in food availability (Furness & Camphuysen 1997, Péron *et al.* 2010). Several marine top predators, such as seabirds, have evolved a common set of life history characteristics (e.g. delayed sexual maturity, high annual survival, great longevity) to buffer environmental stochasticity (Furness & Ratcliffe 2004, Berg *et al.* 2010). However, their capacity to buffer changing conditions is limited and some species may respond differently (e.g. foraging ecology, breeding strategies) to changes in the environment depending on their life history traits (e.g. Davis *et al.* 2005). The response of marine top predators, , to ecosystem modifications, especially when theiy are linked to human activities, can often be measured and as such enhance the value of such species as indicators of ecosystem health (Piatt *et al*. 2007; Parsons *et al.* 2008, Einoder 2009).

Seabirds as indicators of marine change and ecosystem health

Amongst marine top predators, knowledge of life history characteristics and population trends of seabirds have been studied extensively and their value as indicators of marine change and ecosystem health is widely acknowledged (Schreiber & Burger 2002, Piatt *et al.* 2007, Parsons *et al.* 2008, Vié *et al*. 2009). Due to their position as top predators, investigations of population dynamics of seabirds in complex and highly variable environments are crucial, because the outcomes of these studies are likely to reflect the health of coastal and oceanic systems (Furness & Camphuysen 1997, Einoder 2009). In addition, behavioural and reproductive parameters of seabirds have been found to be highly responsive to physical changes in the marine environment (e.g. Baird 1990, Boyd & Murray 2001, Inchausti *et al.* 2003). The availability and distribution of different prey resources, combined with foraging energetic costs and provisioning rates, influences the foraging strategies of breeding seabirds (Weimerskirch *et al.*

1994). Therefore, food availability has a major impact on seabird biology, affecting their distribution, energetic allocations, breeding success and survival (e.g., Montevecchi *et al.* 1988; Garthe *et al.* 1999). Environmental changes, result from human activities are considered to be the main drivers responsible for the sharp decline of the global populations of many seabirds over recent decades (Croxall *et al.* 2012). In particular, the cascade effects of industrial fishing on marine food-webs is a major concern among the most important commercial fisheries in this regard are those targeting small pelagic fish from the order Clupeiformes, which are key links in many marine wasp-waist structural controlled ecosystems, where an intermediate trophic level is dominated by one or a few species (Botsford *et al.* 1997, Cury *et al.* 2000, Hobday *et al.* 2015). Populations of these small pelagic fish undergo large inter-annual fluctuations in abundance, due to variations in biophysical processes that influence primary and secondary production, as well as the transport of fish eggs and larvae. As a result, these fish species are susceptible to overfishing (Cury *et al.* 2011, Croxall *et al.* 2012). The loss of low trophic level species has dire consequences on food webs and for the marine community relying on this resource, largely impacting top predators, including marine mammals and seabirds (Furness 2003, Frederiksen *et al.* 2004, Britten e*t al.* 2014). The extent to which seabirds cope with anthropogenicly driven decline in food resources plays an important role in seabird population trends and distribution shifts (e.g. Weimerskirch 2003, Frederiksen *et al.* 2004). The vital link between seabirds and food resources is reflected by seabird diet, time activity budgets or through changes in their life history parameters (e.g. breeding success) (Litzow & Piatt 2003, Anderson *et al.* 2014).

Foraging ecology in seabirds

Predator-prey interactions are key to comprehend seabird behaviour and population dynamics (Crawford & Dyer 1995, Hedd *et al.* 2002, Davoren *et al*. 2003). Seabird foraging ecology (e.g. foraging habitat, behavior, and strategy) determines the amount of energy collected from an ecosystem and the allocation of energy for survival and reproduction. Diet is therefore an important determinant for breeding success, which is impacted by food accessibility and the predictability of prey distribution (Hedd *et al.* 2002, Crawford *et al.* 2006). Seabirds, are often generalists, as marine ecosystems are typically subject to variation in prey availability (Begon *et al.* 1996). However, the ability to switch to alternate prey when the availability of one prey decreases may result in the exploitation of lower quality prey (Grémillet *et al.* 2008, Ludynia *et al*. 2010). Consequently, changes in foraging strategies can reduce energy acquisition rates and increase energetic costs (e.g. Suryan *et al.* 2000, Ponchon *et al.* 2014). Thus, the combination of life history traits with marked behavioural flexibility may explain dynamics that compensate for low food abundance and allow successful rearing of chicks, despite a shortage of food (Wendeln & Becker 1999, Takahashi *et al.* 2003). Given the impacts of human activities and environmental changes on global marine resources, many seabird species struggle to cope with such variations (Crawford *et al.* 2014). Investigating variations in diet, time budgets and energy allocation for species that are able to buffer environmental variation is essential to infer species-specific responses to ecosystem change and assess which are the driving factors responsible for the contrasting population trends of seabirds breeding in the same system.

The Benguela upwelling System: a productive, but exploited ecosystem

The Benguela Upwelling Ecosystem is one of four major upwelling systems in the world, located off the south-western coast of Southern Africa, between southern Angola and Algoa Bay, South Africa. It is characterised by coastal wind-induced upwelling, which results in cold, nutrient rich-water being transported to the surface and generating high productivity (Shannon *et al.* 2006, van der Lingen *et al.* 2006, Kämpf & Chapman 2016). The Benguela upwelling system is one of the most productive and highly dynamic marine systems on the planet (Hutchings *et al.* 2009, Kämpf & Chapman 2016). Historically, this high productivity supported large populations of marine organisms, including those of many fish species (van der Lingen *et al.* 2006, Hutchings *et al.* 2009). However, the development of industrialised fishing resulted in large amounts of shoaling fish, especially sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* been caught in the region from the 1940s onwards (Crawford 1980, Griffiths *et al.* 2004, Roux *et al.* 2013). Within the first two decades of the purse-seine fishery, there was a rapid increase in annual catches of sardines, followed by the collapse of that fishery. Sardines have failed to recover in the northern Benguela off Namibia, and catches off South Africa remained low until the late 1980s, when the development of a fishery-independent programme to estimate pelagic fish abundance allowed fishing mortality of sardine and anchovy to be maintained at relatively low levels in the southern Benguela (Hampton 1987, van der Lingen *et al.* 2006, Coetzee *et al.* 2008). Consequently, sardine stocks in the early 2000s have reached levels in the southern Benguela similar to those estimated prior to the collapse of sardine in the 1960s (van der Lingen *et al.* 2006).

Small pelagic fish in the southern Benguela also show extensive temporal variability in spatial distribution. Sardines shifted from principally spawning off the west coast to off the south coast of South Africa on at least two occasions (van der Lingen *et al.* 2006). Since 1996, there was also an eastward shift in the distribution of anchovy spawners from the west to the central and eastern Agulhas Bank (van der Lingen *et al.* 2002, Blamey *et al.* 2015). The return of sardine spawning off the south coast since 2001 seems to have coincided with a general eastward shift in the sardine population, which may be linked to both changes in environmental conditions and fishing pressure on the west coast (Fairweather *et al.* 2006, Roy *et al.* 2007, Coetzee *et al.* 2008) (Figure 1.1). Other pelagic fish species (e.g. redeye round-herring *Etrumeus whiteheadi* and chub mackerel *Scomber japonicus*) also showed a similar increased biomass east of Agulhas Bank during this period, although not to the same extent as sardine and anchovy (Watermeyer 2014). This eastward shift in fish distributions has created a spatial mismatch between fishing pressure and fish abundance off the west coast of South Africa, where most catches still take place and most seabirds breed, causing a drastic reduction in the availability of pelagic fishes to endemic seabirds (Kemper *et al.* 2007, Crawford *et al.* 2014).

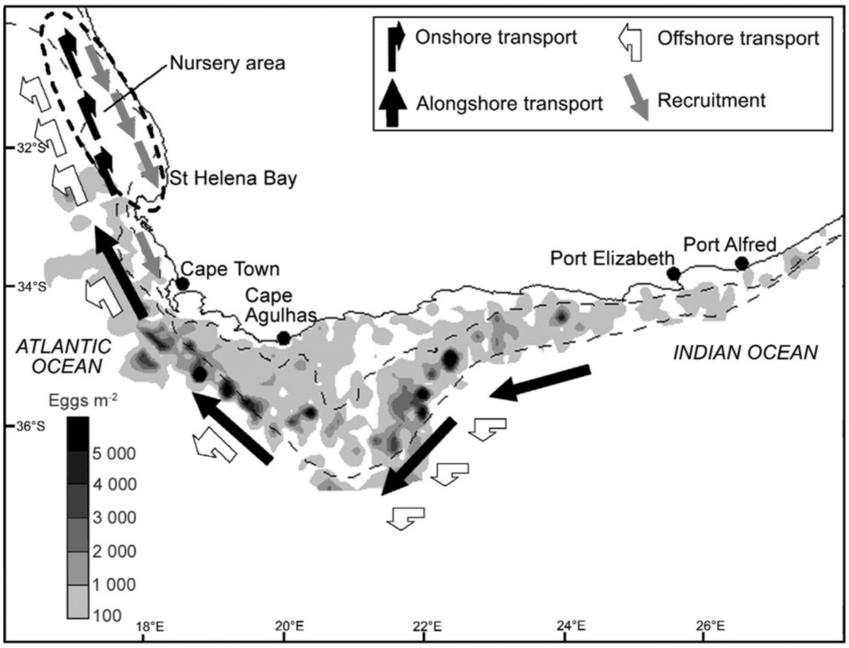


Figure 1.1: Map showing the composite distribution of anchovy eggs from pelagic spawner biomass surveys conducted over the period 1984–2000 (adapted from Roy *et al.* 2007),

Responses of endemic Benguela seabirds to human activities

Many top-predators in the Benguela upwelling system depend on small pelagic fish, including three endemic seabirds: African penguin *Spheniscus demersus*, Cape gannet *Morus capensis* and Cape cormorant *Phalacrocorax capensis* (Crawford & Dyer 1995, Crawford *et al.* 2008). All three species have shown an alarming reduction in their numbers of breeding pairs over the last few decades (Kemper *et al.* 2007, Crawford *et al.* 2014). As a result, the African penguin and Cape cormorant are listed as Endangered, and the Cape gannet as Vulnerable (www.iucnredlist.org). A combination of factors, including climate change, historical guano scraping, disturbance to colonies, marine pollution and competition with purse-seine fisheries are considered to be the major threats to these populations (Crawford *et al.* 2014). Another local breeding seabird that feeds largerly on pelagic fish is the greater crested tern *Thalasseus bergii*, known in southern Africa as the 'swift tern'. In contrast to the three endemic breeding seabirds that rely on small pelagic fish in the region, the population of greater crested terns has increased over the last few decades (Crawford 2009). For example, the number of terns breeding in the Western Cape increased from 5,700 pairs in 2000 to ca 13,200 pairs in 2008 and peaked at more than 15,000 pairs in 2010 (Figure 1.2) (Makhado *et al.* 2013, Crawford *et al.* 2014).

The different responses of the four species of seabirds to the altered distribution of their prey are likely to be related to the seabirds' life-history traits, but the influencing factors remain poorly understood. All four seabirds have a relatively high annual adult survival and longevity and typically start breeding at 3–4 years of age (Hockey *et al*. 2005). However, once breeding, African penguins and Cape gannets show high fidelity to colonies and have clearly defined breeding season. On the other hand, greater crested terns and Cape cormorants show considerable movement between breeding localities, and the latter species shows a flexible breeding phenology, when compared to the narrow breeding period typical of the greater crested terns in this region (Berry 1976, Crawford *et al.* 1994, 2002, 2005). A shift in the breeding localities of greater crested terns was apparent when anchovy and sardine became scarce off north-west South Africa in the mid-2000s (Fairweather *et al.* 2006, Roy *et al.* 2007). They shifted rapidly south in the Western Cape, from around Saldanha and St Helena Bays to off the Cape Peninsula, whereas the response of African penguins and Cape cormorants was slower (Crawford *et al.* 2014, 2016). Therefore, for greater crested terns, this plasticity, in conjunction with protracted post-fledging care, high juvenile survival due to a strong dispersal capability and an increase in fish populations around the main post-breeding areas off the south and east coasts, are suspected to be factors underlying the positive trend of this species (Crawford 2009), but supporting evidence for this hypothesis is required.

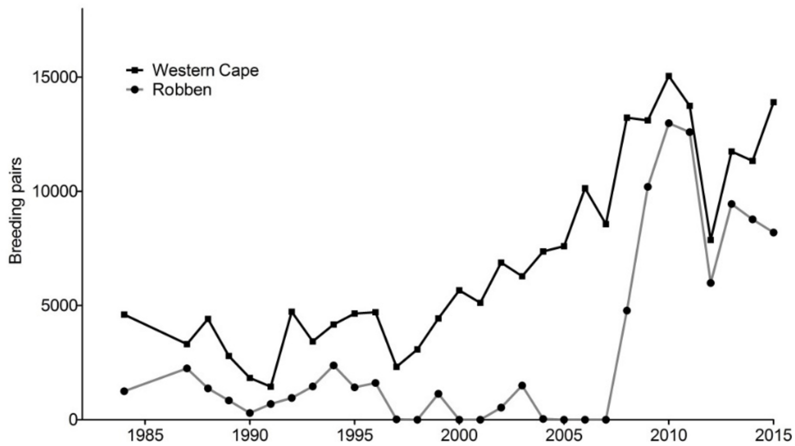


Figure 1.2: Numbers of greater crested tern breeding pairs in the Western Cape and Robben Island from 1984 to 2015. (No counts were made during 1985 and 1986). Data provided by Department of Environmental Affairs (DEA).

Energetic costs of colonial breeding

Colonial breeding is widespread in seabird species. Aggregations may be dense or loosely aggregated and colony size varies from a few to over a million (e.g. macaroni penguin *Eudyptes chrysolophus*) (Danchin *et al.* 1998, Oehler *et al.* 2008). Despite an increasing number of studies investigating the costs and benefits of breeding in a colony, the reasons for the evolution and maintenance of coloniality remain inconclusive (Danchin & Wagner 1997). Possible advantages to individuals which breed in large groups include a reduced risk of predation (through combined defense, dilution of individual risk, or both), benefit from the same favourable local environmental resources, or learn profitable foraging areas from other individuals (e.g. Wittenberger & Hunt 1985**,** Siegel-Causey & Kharitonov 1990**,** Danchin *et al.* 1998, Thiebault *et al.* 2014). Such benefits may accrue whether birds breed near individuals of the same species (single-species colony) or different species (mixed-species colony).

Central place foragers such as seabirds face high levels of energy expenditure, especially during provisioning, as they are required to return to the colony frequently to feed their offspring (Orians & Pearson 1979, Weimerskirch *et al.* 1993). Parents have to find sufficient food to sustain both their own energetic requirements and those of their growing young, and may face severe energetic demands due to the large distances between breeding colonies and foraging areas (Shealer 2002). This is particularly true for single prey loaders, which return to their nest each time they catch a prey item, which limits their movements and the extent of their foraging grounds, as well as the amount of food provisioned during each foraging trip (Stienen *et al.* 2015). In addition, single prey loaders are often exposed to kleptoparasitism, which occur nearby the colony (Brockmann & Barnard 1979, Stienen 2006, Iyengar 2008), both intra and interspecifically (Brockmann & Barnard 1979, Iyengar 2008 and references therein). The effect of intraspecific kleptoparasitism can be positive for the individual that steal the prey as the extra food obtained may provide some benefits (e.g. Shealer *et al.* 2005, García *et al.* 2011). The effect of interspecific kleptoparasitism on the victim will be negative not only through the direct loss of food, but also through energy lost, while attempting to avoid attacks (Le Corre 1997, Stienen *et al.* 2001, Blackburn 2009). The presumed advantage of breeding in association with more aggressive species, which are presumed to provide anti-predator benefits, may be interpreted as a form of parasitism rather than a mutualistic interaction (Finney *et al.* 2001).

Methods

Study species: the greater crested tern

The greater crested or swift tern (*Thalasseus bergii*) is a small seabird that breeds in dense colonies on coastlines and islands widely distributed from the southeast Atlantic Ocean east to the west-central Pacific Ocean. The nominate race of greater crested tern (*T. b. bergii*) is endemic to southern Africa. It is commonly found foraging in coastal waters up to 10 km offshore as well as in estuaries and occasionally in coastal wetlands (Walter *et al.* 1987a, Crawford *et al.* 2005). It roosts ashore along the coast and at adjacent wetlands, frequently in flocks of hundreds of birds and in association with other terns or gulls (Crawford *et al.* 2005). Breeding has been recorded at 27 localities between Swakopmund (22° 30'S; 14°31'E), Namibia, and Stag Island (33° 50'S; 26° 17'E), Algoa Bay, South Africa (Cooper *et al.* 1990, Crawford & Dyer 2000). However, most breeding occurs on islands off the Western Cape (Figure 1.3). Usually, only 6-7 localities are occupied in any one breeding season and greater crested terns are known to be nomadic between these different sites (Crawford 2003).

Breeding usually peaks in February to March in the Western Cape, with most young by April-May (Crawford *et al.* 2005). Greater crested terns breed in open nesting colonies, often in association with Hartlaub's gulls *Chroicocephalus hartlaubii* (Cooper *et al.* 1990, Gaglio & Sherley 2014) or crowned cormorants *Phalacrocorax coronatus* (Crawford *et al.* 2005). Colonies can reach up to 15,000 pairs, but they may also form smaller sub-colonies (Crawford *et al.* 2005). The nests are shallow cups in bare sand or rock and usually on open flat ground. Recently they have started to nest on roofs of buildings, also in association with Hartlaub's gulls (Crawford & Dyer 2000). Egg laying is synchronised within breeding groups, with usually one egg per clutch (mean clutch size 1.03 ± 0.18, n=146) and the incubation period averages 28 days (Crawford *et al.* 2005, Gaglio *et al.* 2015a). If adults are disturbed from the nest, their eggs become susceptible to predation by kelp gulls *Larus dominicanus*, sacred ibis *Threskiorni saethiopicus* (Urban 1986), Hartlaub's gulls (Gaglio & Sherley 2014) and common egg-eater snakes *Dasypeltis scabra* (at Robben Island, Underhill *et al.* 2009).

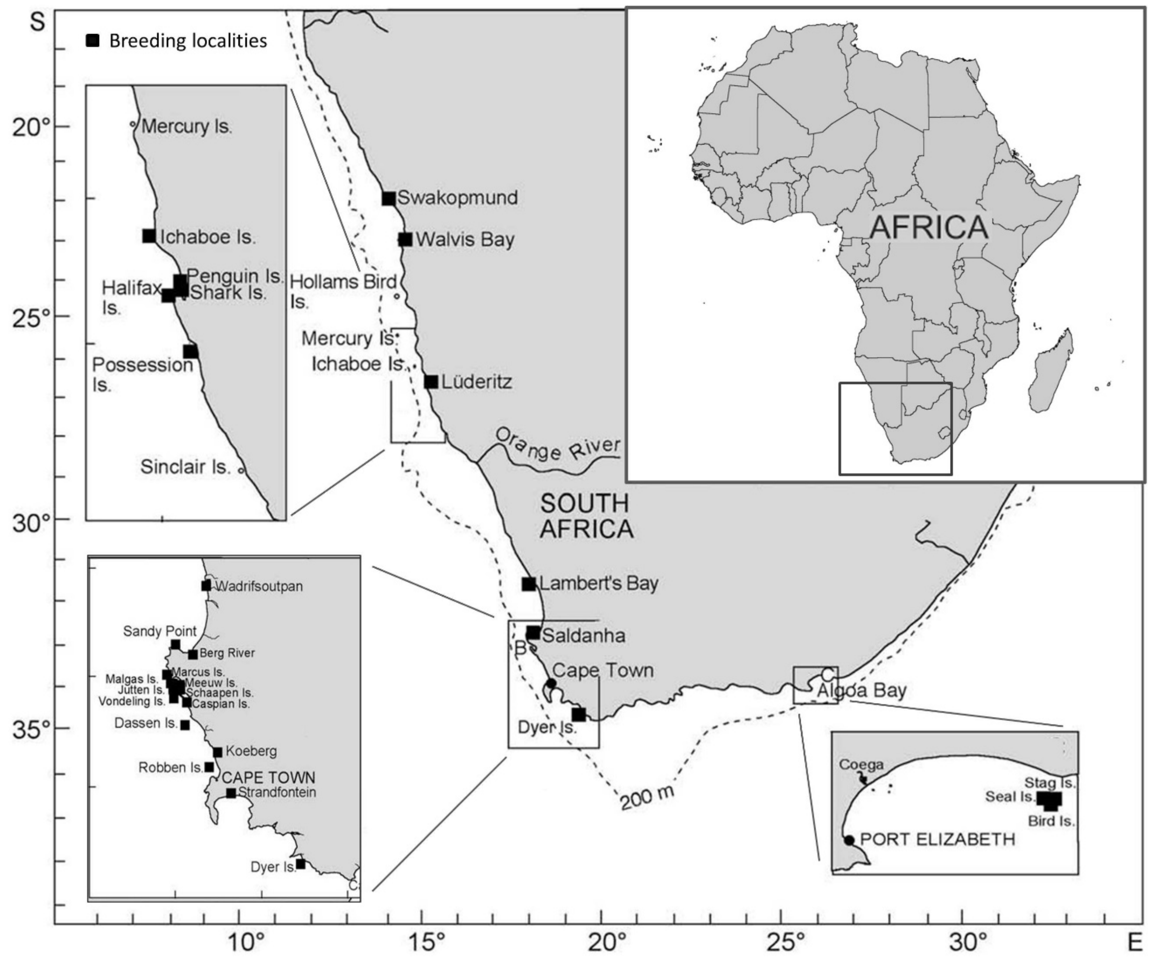


Figure1.3: Known breeding localities of greater crested terns in southern Africa (adapted from Crawford 2009).

Chicks remain in the nest after hatching for 2-4 days, then become mobile, forming loose crèches with other chicks (Heydorn & Williams 1993). The chicks grow rapidly (Nicholson 2002, Le Roux 2006) and can fly when they are ca 56 days old (Heydorn & Williams 1993). Most fledglings leave the colony with at least one parent within 19 days of fledging (Langham & Hulsman 1986) and continue to be fed by their parents for up to four months after leaving the colony, during which time they can disperse over long distances (Underhill *et al*. 1999, Crawford *et al.* 2005). This long period of post-fledging parental care presumably allows the juveniles to learn the necessary skills to feed for themselves. Greater crested terns are thought to first breed when they are 3-4 years old (Underhill *et al.* 1999, Crawford *et al.* 2002). Like most seabirds, this species show great longevity, with 109 records of southern African birds living to ≥ 15 years old. The oldest individual is 34 years from a bird banded as chick in Marcus Island (Payo payo *et al.* unpubl. data).

Greater crested terns feed mostly at sea by plunge diving to a maximum depth of ca 1 m (assumed maximum dive depth) (Crawford *et al.* 2005)., or by dipping from the surface, and food is usually swallowed in mid-air. Elsewhere, breeding adults exploit both inshore and offshore feeding grounds

(Nicholson 2002, McLeay *et al.* 2010), but little is known about the foraging areas of individuals breeding in southern Africa**.** Their diet is mainly composed of surface-schooling Clupeiformes fish (Crawford & Dyer 1995, McLeay *et al.* 2009a), but also includes cephalopods and crustaceans, while insects may be taken opportunistically (Walter *et al.* 1987a, Gaglio *et al.* 2015b). The global population of greater crested terns has not been quantified, but it is not believed to approach the thresholds for either the size criterion (fewer than 10,000 mature individuals) or the population decline criterion (declining more than 30% in ten years or three generations), for these reasons, the species is listed as Least Concern globally (www.iucnredlist.org). However, greater crested terns are vulnerable to human disturbance at breeding colonies on inhabited offshore islands (Gaglio *et al.* 2015a) and are also threatened by injury and mortality from entanglement with baited hooks, fishing lines, nets and human refuse (Cooper *et al.* 1990).

Study site: Robben Island

Breeding greater crested terns were studied on Robben Island (33°48'S, 18°22'E), located in Table Bay off Cape Town. It is the largest of the continental islands along the South African coast, with an area of 5.07 km^2 (Figure 1.3). The island is flat, with the highest point, Minto Hill, rising to 30 m above sea level (de Villiers 1971). Robben Island is dominated by sandy soils, and the vegetation include dense strands of bush with grasslands, and plantations of introduced gum (*Eucalyptus* spp.) and pine (*Pinus pinaster*) trees (Rossouw *et al.* 2000). Robben Island became a museum in 1996 and was declared a World Heritage Site in 1999 based on its historical and cultural significance (de Villiers 1971). It currently greets ca 200,000 tourists per year, who come by boat from Cape Town. The island is also an Important Bird Area (Barnes 1998), providing breeding habitat for several seabird species, including the bank cormorant *Phalacrocorax neglectus,* Cape cormorant, African penguin and greater crested tern, as well as large numbers of kelp and Hartlaub's gulls and other waterbirds (Sherley 2010). The numbers of pairs of greater crested terns breeding on Robben Island have been monitored since 1984, and since 2008 Robben Island has supported the largest southern African breeding population, reaching almost 13,000 pairs in 2010, when it accounted for ca 83% of the nominate race's population.

During this study, two colonies of different sizes occurred on Robben Island in 2013 and 2014, whereas in 2015 only one large colony was established. The two colonies were located in the same areas each year (2013-2014), with nests placed in similar sandy soils with scattered, low-lying vegetation. The 'single-species' colony was situated ca 500 m from a former kelp gull breeding colony on the north side of the island (33°79'S, 18°36'E) (Figure 1.4). It supported about 7,500 pairs in 2013 and 8,000 in 2014, but there was no breeding in this area in 2015 (possibly due to the presence of a large number of kelp gulls still breeding – pers. obs.). The other 'mixed-species' colony was an association of terns and Hartlaub's gulls situated within the human settlement on the island (33°81'S, 18°38'E) (Figure 1.4). This colony totalled ca 2,500 breeding pairs in 2013, 800 in 2014 and 8,200 in 2015, when the entire island population bred in this area (Table 1.1).

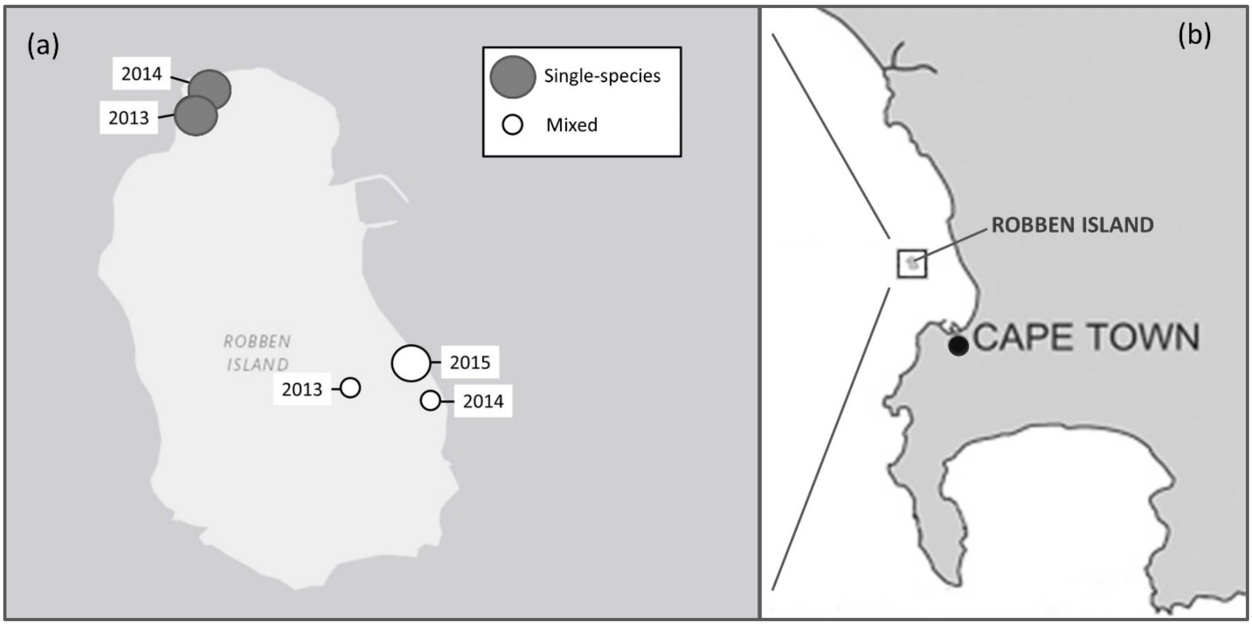


Figure1.4: Map of (a) Robben Island showing the locations of greater crested tern colonies (single-species and mixed) in the 2013, 2014 and 2015 breeding seasons; (Circle size is proportional to colony size). (b) Location of Robben Island within Table Bay (Cape Town).

Mean hatching date at the single-species colony was during the 4th week of February in 2013 and 2014. The mixed colony was generally settled 3-4 weeks later, with mean hatching date occurring during the 3rd week of March in 2013 and the 4th week of March in both 2014 and 2015 (Table 1.1). In both years when there were two colonies on the island (2013 and 2014), the colonies were only ca 2 km apart. Therefore, with the exception of size, phenology, and associations with other breeding species, they were assumed to be under similar environmental conditions (e.g. access to food resources, influence of wind, tide and temperature).

Table 1.1: Number of breeding pairs and mean hatching week of the single-species and mixed colony of breeding greater crested terns on Robben Island from 2013 – 2015.

	Single-species colony		Mixed colony	
Season	Number pairs	Hatching week	Number pairs	Hatching week
2013	ca 7000	24 Feb. – 2 Mar.	ca 2500	17 – 23 March
2014	ca 8000	23 Feb. – 1 Mar.	ca 800	23 – 29 March
2015	Not applicable	Not applicable	ca 8200	29 Mar. – 4 Apr.

Data collection: the use of non-invasive methods

Investigations of seabirds at their breeding colonies, allows for the collection of large numbers of samples in a short period of time and is to thus able to address multiple questions. However, many species of seabirds, including terns, are susceptible to disturbance while nesting. For example, human disturbance may cause whole colonies to abandon their nests, with further potential negative effects to species which breed in association or nearby the focal species (Gaglio *et al.* 2015a). The issue of disturbance by researchers has long been a concern in studies of avian species (Bennet 1938, Bart 1977, Götmark & Åhlund 1984, Götmark 1992, Carney & Sydeman 1999, Carey 2009). Several studies have highlighted the detrimental effect of reduced fitness of some species provoked by the most common research activities, such as monitoring nest attendance, banding, or handling of birds during breeding (Wilson *et al.* 1986, Wilson & McMahon 2006, Ropert-Coudert *et al.* 2007, Sherrill-Mix & James 2008). In addition, activities, may modify birds' natural behaviour, thus compromising the understanding of a species' ecological and behavioural attributes (Serventy & Curry 1984, Yoccoz *et al.* 2001). The development of non-invasive sampling methods that do not create perturbation to breeding birds is therefore of great value.

Today, digital photography offer researchers the ability to collect efficiently detailed, low cost and accurate datum. This technology overcomes many of the limitations of other methods, such as collection of regurgitations or focal observations, being user-friendly and non-invasive (Savazzi 2010). Other advantages include the finer discrimination of details in comparison to visual assessment, and the opportunity to perform retrospective evaluation, as images or videos can be stored without loss of data quality. Ecological studies using digital cameras are now shifting their attention from documenting to actual analysis and quantification (Luscier *et al.* 2006). For example, the use of digital images was implemented recently to study avian moult or monitor breeding success of seabirds, thus reducing researcher effort and disturbance, while collecting valuable data (Ryan 2014, Huffed & Merkel 2013, Merkel *et al.* 2016, Vieira *et al.* 2016). Therefore, in this thesis I used digital photography to collect data with minimal disturbance to breeding pairs. In particular, I developed and applied a non-invasive sampling method to investigate the diet of the greater crested terns, and used video-recordings coupled with focal observations to collect data on foraging and kleptoparasitism behaviour in this species.

General aims of the thesis

The main aim of this thesis is to understand the factors driving variations of population trends in seabirds by investigating the functional relationships between the diet, foraging ecology and associated energy requirements of greater crested terns.

In this thesis, I aim to develop a non-invasive diet-sampling method to gather useful, relatively inexpensive, and comprehensive diet data for breeding terns. I aim to better understand the extent to which the greater crested tern's behavioural flexibility and life-history characteristics, combined with their hypothesised low energy requirements contribute to their recent population increase in the southern Benguela. I also aim to investigate the relationships between greater crested terns and Hartlaub's gulls, which associate with terns at some breeding sites, to assess whether the presence of gulls in mixed-species colonies is detrimental to the terns through interspecific kleptoparasitism.

The specific aims of this thesis are to:

1) Develop a non-invasive sampling method to investigate diet of greater crested terns. For this aim, digital photography was used to assess the composition and size of prey consumed by greater crested terns during incubation and chick provisioning. This required a comparison between the suggested photographic sampling method to the traditional technique of collection of regurgitations from chicks, previously used to evaluate greater crested terns' diet in southern Africa (Chapter 2).
2) Study the intra and inter-annual variations of greater crested tern diet and assess the influence of environmental factors on prey composition using the photo-sampling method developed. In addition, this chapter investigates intra- and inter-annual variation in anchovy size captured by greater crested terns and assesses their overlap with fish taken by the commercial fishery in the same region (Chapter 3).
3) Investigate the foraging behaviour of breeding greater crested terns using remote video-recording (combined with visual observations from a hide) to estimate the terns' daily energy requirements and food intake with direct comparison to other three Benguela endemic seabirds breeding in the same region (Chapter 4).
4) Assess the dynamics and underlying associations of mixed colonies of greater crested terns and Hartlaub's gulls. For this study, video-recordings (combined with visual observations from a hide)

were used to assess the rates of intra- and interspecific kleptoparasitism on breeding greater crested terns (Chapter 5).

The last chapter in this thesis synthesizes the key findings of these investigations, and provides suggestions for future research. By providing a comparison with three other Benguela endemic seabird species, which rely on forage fish, outcomes from this research offer valuable insights into how greater crested terns are coping with the changes in food availability which are adversely affecting other seabird species breeding off the west coast of South Africa, as well as assess the impact of natural and human induced changes on marine ecosystem dynamics.

A brief note on chapter structure

Each chapter is written as a stand-alone paper to facilitate the publication of the work. Thus, each chapter comprises an abstract, introduction, materials and methods, results and discussion section. There is some repetition of concepts throughout the introductory sections and a little duplication in the materials and methods sections. I have removed as much repetition as possible; however, in some cases this repetition is essential for the readability of each chapter. Chapter 2 has already been published but was edited and formatted to conform to the rest of the thesis.

Chapter 2

Dietary studies in birds: testing a non-invasive method using digital photography in seabirds

Abstract

Dietary studies give vital insights into foraging behaviour, with implications for understanding changing environmental conditions and anthropogenic impacts on natural resources. Traditional diet sampling methods may be invasive or subject to biases, so developing non-invasive and unbiased methods applicable to a diversity of species is essential. I used digital photography to investigate the diet fed to chicks of a prey-carrying seabird, and compared this approach (photo-sampling) to a traditional method (regurgitations) for the greater crested tern *Thalasseus bergii*. Over three breeding seasons, I identified > 24,000 prey items of at least 51 prey taxa, more than doubling the known diversity of prey taken by this population of terns. In addition, I estimated the length of the main prey species (anchovy) from photographs, with an accuracy of < 1 mm and precision ca 0.5 mm. Compared to regurgitations at two breeding localities under the same conditions, photo-sampling produced similar estimates of prey composition and size, with species accumulation indicating that photography results in a greater range of species being recorded for the same amount of sampling effort (number of prey items recorded). The diet compositions collected by two researchers photo-sampling concurrently were also similar. Photo-sampling offers a non-invasive tool to accurately and efficiently investigate the diet composition and prey size of prey-carrying birds. It reduces biases associated with diet sampling studies and is simple to use. This methodology provides a novel tool to aid conservation and management decision-making in light of the growing need to assess environmental and anthropogenic change in natural ecosystems.

Introduction

Dietary studies are essential to understand animal ecology, temporal changes in the environment, and to establish sustainable strategies for natural resources management (Jordan 2005). In complex natural systems, top-predators can act as indicators of environmental conditions, and their diet, in particular, can provide important information on prey species abundance, occurrence and size, which may reflect processes over short time-frames (e.g. Suryan *et al.* 2002; Parsons *et al*. 2008). As such, outcomes from diet studies are important tools for monitoring changes in demographic parameters or behaviour, themselves a product of changing diet (Sherley *et al.* 2013). Moreover, dietary studies can provide powerful indicators of anthropogenic impacts and environmental change on food-webs (e.g. Piatt *et al.* 2007; Green *et al.* 2015), facilitating conservation biology and ecosystem-based management (Grémillet *et al.* 2008; Sherley *et al.* 2013). The importance of monitoring diet thus demands the development of simple, efficient, non-invasive methods applicable to a diversity of species.

Numerous techniques exist to investigate bird diets (Jordan 2005; Inger & Bearhop 2008; Karnovsky *et al.* 2012). Invasive techniques include induced regurgitations (Diamond 1984), stomach flushing of live birds (Wilson 1984), application of neck-collars on chicks (Moreby & Stoate 2000) and the dissection of birds collected specifically for this purpose (Doucette *et al.* 2011). These methods describe short-term diet composition accurately (González-Solís *et al*. 1997), despite some errors introduced by differential prey regurgitation or digestion (e.g. Jackson & Ryan 1986). More recent biochemical methods involving isotopic, lipid and DNA analyses provide complementary approaches, but generally cannot be used alone due to their coarse taxonomic resolution (Karnovsky *et al.* 2012). Moreover, these approaches typically require disturbance or capture of birds, which can impact their physiology and behaviour (e.g. Ellenberg *et al.* 2006; Carey 2009).

Accurate, non-invasive diet sampling is therefore required to give fine-scale indicators of prey availability or prey selection. One of the least non-invasive methods is to observe birds carrying visible prey with binoculars or video recording systems, from a distance. This typically involves birds feeding offspring or incubating partners (e.g. Safina *et al.* 1990; Redpath *et al.* 2001; Tornberg & Reif 2007). Such studies are generally limited to assessing chick diet, but have the potential to reveal changes in prey communities (Anderson *et al*. 2014). However, observer-based diet studies are subject to several methodological limitations (Cezilly & Wallace 1988; González-Solís *et al.* 1997; Lee & Hockey 2001) calling for further development of this approach.

Digital photography represents an excellent alternative tool to study the diet fed to chicks of prey-carrying birds, because 1) there is virtually no limit to the number of pictures that can be taken, 2) species identification is possible in most cases, 3) prey can potentially be measured accurately and precisely, 4) images can be re-analysed without loss of data quality, i.e. samples do not deteriorate over time and 5) storage is simple. Over the last decade, the use of digital photography for dietary studies has included the use of camera-traps to investigate the diet of nesting raptors (García-Salgado *et al.* 2015; Robinson *et al.* 2015), and the combined use of digital compact cameras with spotting scopes (digiscoping) to assist prey identification (made primarily by observations) for Caspian terns (*Hydroprogne caspia*) and common murres (*Uria aalge*) (Larson & Craig 2006, Gladics *et al.* 2015). However, both techniques have limitations including poor image quality and difficultly in capturing images of birds carrying prey in flight or during rapid delivery to chicks (see Larson & Craig 2006, García-Salgado *et al.* 2015).

Recent advances in performance and price reductions of digital single lens reflex (DSLR) cameras combined with autofocus telephoto lenses makes digital photography an affordable option for prey identification, even for birds in flight. In the last few years, DSLRs have been used opportunistically to identify items carried by a variety of birds (e.g. Woehler *et al.* 2013; Gaglio *et al.* 2015b, Tella *et al.* 2015) but a systematic approach and an accurate method to estimate prey dimensions are lacking. In this chapter I developed a standardised application of digital photography using DSLR cameras and telephoto lenses to investigate diet composition and prey size of breeding greater crested tern (*Thalasseus bergii*) in South Africa. I compared the efficacy of photo-sampling to the more traditional used regurgitations (Walter *et al.* 1987a), using prey identified to species level collected from chicks, and compared size of anchovy between the two methods. In addition, assessed the accuracy and precision of length measurements of the main prey obtained from photographs. The potential for observer bias in this system was also evaluated. Finally, I discuss the validity of applying this non-invasive approach to any prey-carrying bird and the potential to develop a simple and effective tool-box to accurately identify and estimate the size of any carried item.

Method

The photo-sampling method

The diet of breeding terns was investigated at Robben Island during 2013 (February–June), 2014 (January–June) and 2015 (February–June) and at Seal Island during June 2015. Adult terns returning with prey were photographed from a vantage point of 50–80 m from the edge of their colony (Figure 2.1a). At Seal Island (ca 300 pairs) all adults returning to the colony were photographed during the photo-sampling sessions. At Robben Island, colonies were much larger (> 6,000 pairs) so I could not photograph all individuals. However, I randomly photographed any flying individual carrying a prey to not bias selection to individuals carrying particularly conspicuous prey items. The distance to the flying birds ranged between 6.5 and 25 m. Total sampling effort represented ca 7 hrs of photography per week. For each individual, I typically took a sequence of 3 photos (a “photo set”) for identification and prey measurements (Figure 2.1b). I found by trial and error that 3 images provided the best trade-off to balance processing time with obtaining at least one sharp image. To avoid biasing the results and maintain independence among photo sets, ad-hoc image analysis was performed for each sampling session to discard repeated photo sets of the same adults carrying the same prey item. Recurrent birds were identified using distinguishable feather patterns, presence of colour or metal rings, type and position of prey in the bill while flying, and distinctive markings on the prey.

Photos were taken using Canon 7D and 7D Mark II cameras, fitted with Canon EF 100–400 mm f/4.5-5.6L IS USM zoom lenses. I set the cameras to (i) shutter speed priority (1/2500 s); (ii) automatic ISO (or aperture priority mode that provided shutter speeds of at least 1/2500 s); (iii) high-Speed Continuous Shooting; (iv) Autofocus on AI Servo (for moving subjects) using the AF point expansion; and (v) large Jpeg file format for high-speed recording. I set the telephoto lens to autofocus, the image stabilizer to on and the closest focal point to 6.5 m to increase autofocus speed.

Identification of prey species

All blurred or otherwise non-identifiable images (due to e.g. distance, an unfavourable position of prey in the bill or lighting) were discarded. From the remaining photographs (e.g. Figure 2.1), I determined the numerical abundance (Duffy & Jackson 1986) of prey (usually at species level) using fish guides (Smith & Heemstra 2003; Branch *et al.* 2010) and assistance from experienced observers (see Acknowledgements). In some instances, good quality photographs contained prey that could not be identified (< 0.01% of total prey items). For example, some adults returned with pieces of fish flesh, possibly originating from kleptoparasitism disputes or scavenging. These images were excluded from analyses. Approximately 45% of photo sets were suitable for prey identification; there was no evidence of bias towards particular prey types among discarded images.

Estimation of prey standard length

Dietary studies of piscivorous birds commonly measure the standard length (SL) of the fish (length from the tip of the snout to the posterior edge of the hypural plate) to compare prey size (Barret 2002, Smith & Heemstra 2003). I estimated SL from photographs for anchovy, the most common species in the tern's diet. As prey tended to flex to differing degrees in the adults' bills, direct SL measurement from the image underestimates fish length. Thus, I estimated SL from measurements of individual body parts (eye diameter, operculum width and head width, all measured dorsoventrally), which were less distorted in the image and generally in a plane parallel to the bird's bill and the camera (Figures 2.1b and 2.2). To do this, I first assessed the accuracy of predicted SLs based on these morphological measurements using cross-validation by fitting log-linear allometric regressions to a training dataset (n = 50) and comparing model predictions to a test dataset (n = 20) of anchovies measured by hand (see Appendix A). Next, I measured 37 additional anchovies with Vernier callipers (to the nearest 0.1 mm) and then photographed them held in the bill of a dead tern, for which the culmen length was known (Figure A.2).

For each image, I used the 'line selection tool' in ImageJ (Schneider *et al*. 2012) to estimate eye diameter ($\hat{E}$), operculum width ($\hat{O}$) and head width ($\hat{H}$) for each fish by scaling the pixel length in the image to (1) the length of the dead tern's culmen (62.1 mm; measured with Vernier callipers), (2) the mean culmen length for this species (61.2 mm, n = 128; Crawford *et al.* 2005) and (3) the minimum and maximum recorded culmen lengths (range: 54.5–67.6 mm, Crawford *et al.* 2005). I used the estimates of $\hat{E}$, $\hat{O}$ and $\hat{H}$ to obtain three estimates of SL ($\widehat{SL}$) using the log-linear allometric regressions (see also Appendix A), and calculated their arithmetic mean (combined $\widehat{SL}$) and used this value in further analyses (since it was generally most accurate; Appendix A).

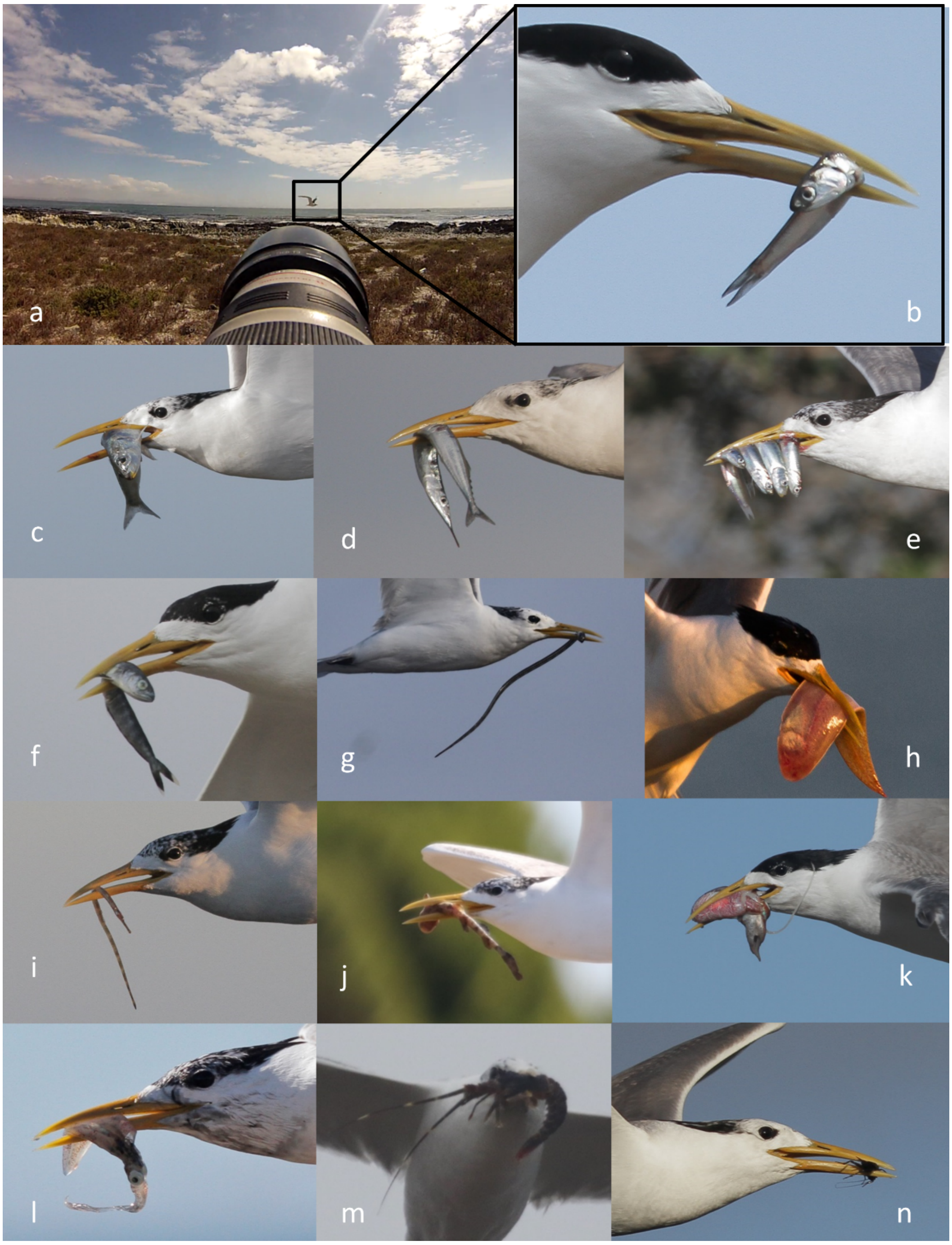


Figure 2.1: (a) Examples of capturing a photo-sample of an adult greater crested terns carrying prey to the colony without causing disturbance to nesting birds and (b) the resulting close-up image of the prey used for identification (anchovy) and standard length measurements. From c to n: Examples of tern prey items: (c) sardine; (d) Atlantic saury *Scomberesox saurus;* (e) multi-prey load (3 anchovy and 1 sardine); (f) dolphinfish *Coryphaena hippurus;* (g) snake eel *Ophichthidae* sp.; (h) sole *Austroglossus* sp.; (i) longsnout pipe fish *Syngnathus temminckii;* (j) shyshark *Haploblepharus* sp.; (k) cuttlefish *Sepia vermiculata;* (l) common squid *Loligo vulgaris;* (m) rock lobster *Jasus lalandii*; (n) two-spotted cricket *Gryllus bimaculatus*.

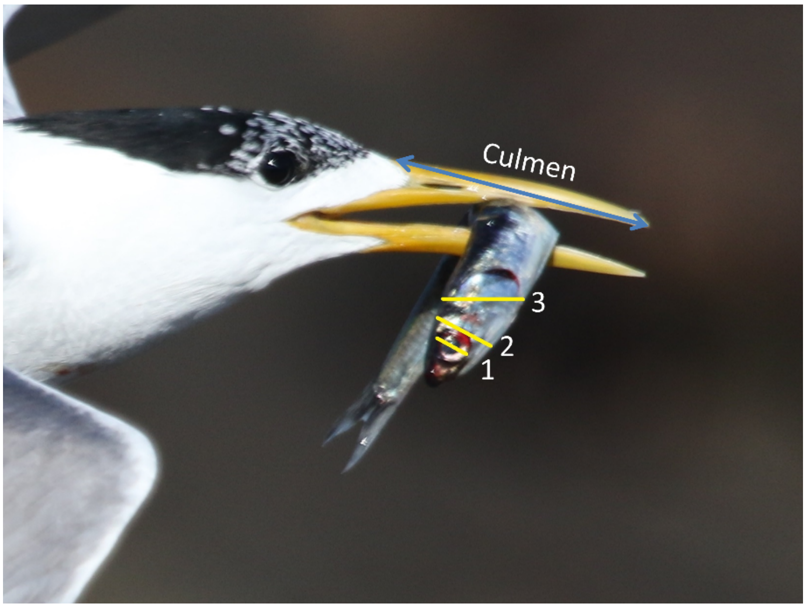


Figure 2.2: Example of the application (in ImageJ) of the 'line selection tool' to measure the linear distances for the three morphometric parameters: (1) eye diameter (E); (2) head width (H) and (3) operculum width (O).

To determine the accuracy (γ) of the combined $\widehat{SL}$ estimates from the images, I compared them to the known SL of each fish. I defined the mean percentage accuracy ($\bar{\gamma}$) of the combined $\widehat{SL}$ estimates as:

$$\bar{\gamma} = \frac{100}{n}\sum_{i=1}^{n}\left(1 - \frac{\left|SL_i - combined\ \widehat{SL}_i\right|}{SL_i}\right)$$

(eqn 1)

where *i* indexes each of the *n* = 37 fish. As the absolute difference was computed, both overestimates and underestimates of e.g. 2% would yield γ = 98%. In addition, I assessed the mean difference between the known SLs and the combined $\widehat{SL}$ estimates using permutation tests with 10,000 Monte Carlo iterations (*perm* library v. 1.0-0.0 for R).

To determine the precision (or repeatability) of the method, I repeated the measurement process in ImageJ to obtain six $\hat{E}$, $\hat{O}$ and $\hat{H}$ values and the corresponding combined $\widehat{SL}$ values for 17 of the 37 fish (using a known length on the ruler in each photograph). I calculated the combined $\widehat{SL}$ as above and used this to assess precision. Precision (τ) was defined as:

$$\tau_{f,j} = \left|\left(\frac{1}{n}\sum_{j=1}^{n} combined\ \widehat{SL}_{f,j}\right) - combined\ \widehat{SL}_{f,j}\right|$$

(eqn 2)

where *j* indexes each of the *n* = 6 combined $\widehat{SL}$ values for the *f* = 17 fish. I report mean precision (in mm) of all (6 x 17 = 102) values of $\tau_{f,j}$.

In addition, I examined whether either precision or accuracy were influenced by the SL of a fish. For accuracy, I used a linear model of the form:

$$logit(\gamma_i) = \alpha + \beta \times SL_i + \varepsilon_i$$

(eqn 3)

where α and β are estimated from the data, γ_i are the accuracy estimates (as proportions), SL_i the known standard length for fish *i* and $\varepsilon_i \sim N(0,\sigma)$ the residual error, with σ estimated from the data. For precision I used a linear-mixed model (LMM: *lme4* library for R) of the form:

$$\tau_{f,j} = \beta \times SL_{f,j} + \delta_{f,j} \times \eta_j + \varepsilon_{f,j}$$

(eqn 4)

where $\beta$is the fixed effect parameter, $\eta_j \sim N(0, \varsigma)$ the random effect parameter, $\varepsilon_{f,j} \sim N(0, \sigma)$ the residual error, $\delta_{f,j}$ the vector of fish IDs, $\tau_{f,j}$ the vector of precision values and $SL_{f,}$ the vector of known standard lengths for each measurement *j* of fish *f*, with β, σ and ς estimated from the data.

Finally, I used the above approach to estimate SL of the prey in a subset of the digital images collected in the field where the bird's bill and the head of the prey were clearly visible and approximately parallel to the camera (Figure 2.1b). For each image, I used combined $\widehat{SL}$ and assumed the length of the bird's culmen to be 61.2 mm (see above).

Comparison between photo-sampling and regurgitation-sampling

To compare photo-sampling and regurgitation-sampling, I collected images of adults carrying prey and regurgitations from chicks concurrently on 18 and 19 April 2015 at Robben Island (photo-sampling effort: 600 min) and on 9 June 2015 at Seal Island (photo-sampling effort: 132 min). Regurgitates were collected from the ground, while chicks were inside a pen during ringing operations (chicks often regurgitate when disturbed). Prey were later identified from whole-prey or diagnostic prey remains resistant to digestion such as otoliths and squid beaks using Clarke (1986), Smith & Heemstra (2003), Smale *et al.* (1995), Branch *et al*. (2010) and the Port Elizabeth Museum's reference collection. Prey items that were not identified mainly consisted of fish flesh and were excluded from our analysis. The SL of whole anchovies collected from regurgitations was measured using a ruler. I compared the number of prey items from different taxa between methods using χ^2 tests and assessed differences in the estimated anchovy SLs using permutation tests (10,000 iterations) for each island separately as the SL variance between islands was heterogeneous (Levene's test: $W_{(1,164)} = 5.8$, $p = 0.017$).

I examined prey diversity using sample-based rarefaction curves as these allow for standardized comparison across collections that differ in sample size (Gotelli & Colwell 2001). Using 1,000 random permutations of both the photo-samples and regurgitations from 18 and 19 April 2015, I produced curves of the mean (± asymptotic 95% confidence intervals, CI) species accumulation rate (species identified per sample made). I then compared this rate at samples sizes of n = 190. In addition, by fitting a Generalised Additive Model (GAM) to the photo-sample means and by assuming equal accumulation rates for extrapolation, I also compared the predicted species accumulation rate for regurgitations to the mean rate for photo-sampling at n = 1500. The chosen sample sizes approximate those obtained in the field.

Finally, to evaluate any possible observer effect on photo-sampling, two different researchers (observer-A and observer-B) simultaneously collected photographs at Robben Island on 18 and 19 April 2015. The two observers used the same equipment (Canon 7D Mark II camera, Canon 100–400 mm lens) and had similar experience in wildlife photography. All other procedures were the same as described above. I compared the samples from the two observers using χ^2 tests. Unless otherwise stated, all means are presented ± 1 SD and all statistics were performed using R v.3.3 (R Core Team 2016).

Results

Photo-sampling vs regurgitation-sampling

In total ca 160,000 photos were taken during the three breeding seasons on Robben Island, yielding images of 24,211 prey items identifiable to species (96%, 48 species) or family (98%, 49 families) level (total of 51 prey taxa; Table 2.1) and accounting for ca 30 hours per season needed to select and identify those prey items. During the regurgitation comparison trial at Robben Island, I identified 27 species from 1,510 photo-samples compared to 11 species from 198 regurgitated prey items. At Seal Island, I identified 11 species from 157 photo-samples and 6 species from 103 regurgitated prey items (Table A.3). The mean species accumulation rate at 190 samples was 0.075 (95% CI: 0.058–0.089) for photo-sampling and 0.057 (95% CI: 0.053–0.058) for regurgitations; however, at this sample size, the 95% CIs overlapped (Figure 2.3). The number of species predicted from 1,500 regurgitations was 23.4 (based on the GAM extrapolation) versus 27.0 for photo-sampling (Figure 2.3). The diet composition of main prey did not differ significantly between the two methods for Robben Island ($\chi^2 = 47$, d.f. = 42, p = 0.26) or Seal Island ($\chi^2 = 18$, d.f. = 15, p = 0.26; Table A.3).

Accuracy and precision in estimating anchovy standard length

Mean SL of the 50 anchovy used to calculate the allometric regressions between the morphometric measurements (training set) was 109.6 ± 13.5 mm (range = 83.3–130.5 mm), similar to the 20 anchovy in the test set (SL 112.8 ± 3.0 mm; range = 107.6–116.8 mm). The predicted $\widehat{SL}$s of the test set predominantly fell within the 95% prediction intervals for all three specific body part models (Figure A.1). The mean accuracy ($\bar{\gamma}$) for the combined $\widehat{SL}$ was 97.9 ± 1.7% (range 93.0–99.9%) for the training set and 97.3 ± 1.8% (range 92.5–100%) for the test set. Accuracy was not affected by SL in either case (linear models: $p > 0.05$, see Appendix A).

The mean SL of the 37 photographed anchovy was 113.4 ± 6.7 mm. With the culmen length of the dead tern (62.1 mm) as the reference, mean accuracy ($\bar{\gamma}$) for the combined $\widehat{SL}$ was 98.3 ± 1.5% (range 93.8–100%), yielding a mean combined $\widehat{SL}$ of 114.0 ± 7.1 mm (Table A.2). With the species' mean culmen length (61.2 mm) as the reference, the mean combined $\widehat{SL}$ = 112.7 ± 7.0 mm ($\bar{\gamma}$ = 98.1 ± 1.5%, range 92.2–99.9%; Figure 2.4, Table A.2). The length of a fish (actual SL) did not influence the accuracy in either case (linear models: $p > 0.05$, Figure 2.4) and neither of the combined $\widehat{SL}$s differed significantly from the actual SL (permutations tests: $p > 0.05$). The mean accuracy ($\bar{\gamma}$) reduced to 88.9 (± 3.3)% and 91.3 (± 3.2)% for the minimum (54.5 mm) and maximum (67.6 mm) recorded culmen lengths respectively (Table A.2) and these combined $\widehat{SL}$ series did differ significantly from the actual SLs (permutations tests: $p < 0.001$; see Appendix A).

The mean precision of the combined $\widehat{SL}$ estimates was 0.52 (± 0.38) mm or 99.6 (± 0.3)%, with an absolute range of 0.02–1.58 mm or 98.6–99.99%. Precision was not related to the actual SL of the fish being measured (LMM: $\chi^2 = 0.02$, $p = 0.89$).

Comparisons of prey size between photo-sampling and regurgitation-sampling

At Robben Island, 116 anchovy from photo-samples (10% of anchovy photographed) and 20 from regurgitates (12%) could be measured, while at Seal Island, the corresponding values were 21 (18%) and nine (9%) respectively. Overall, the anchovy were longer at Seal Island (mean = 120.3 ± 8.2 mm, n = 30) than at Robben Island (91.2 ± 13.2 mm, n = 136; $p < 0.001$; Figure 2.5). For Robben Island, the mean combined $\widehat{SL}$ of anchovy in the photo-samples was 91.3 ± 13.6 mm compared to 90.8 ± 11.1 mm for regurgitates (Figure 2.5). At Seal Island, they were 121.6 ± 9.3 mm and 117.4 ± 3.6 respectively. The SL estimates from the two methods did not differ statistically for either Robben Island ($p = 0.85$) or Seal Island ($p = 0.21$).

Comparisons between observers

A total of 1,510 prey items representing 22 species from the photographs taken by observer-A and 1,625 representing 21 species from observer-B were identified. Prey composition did not differ significantly between the two ($\chi^2 = 72$, d.f. = 64, $p = 0.23$). However, three species were not recorded in both; observer-A photographed one horsefish Congiopodidae sp. and one eel Ophichthidae sp., while observer-B recorded three individuals of Cape hake *Merluccius capensis.*

Table 2.1: Prey families in the greater crested tern diet identified by photo-sampling on Robben Island during the 2013, 2014 and 2015 breeding seasons. N = number of prey items identified.

Prey type	**Family**	**Species**	**N**
Fish	Engraulidae	1	16206
	Dussumieriidae	1	2557
	Scomberesocidae	1	1658
	Syngnathidae	2	866
	Clupeidae	1	545
	Carangidae	2	409
	Gonorynchidae	1	351
	Atherinidae	1	198
	Mugilidae	1	117
	Merlucciidae	1	76
	Pomatomidae	1	67
	Soleidae	Unid.	63
	Champsodontidae	1	58
	Clinidae	Unid.	63
	Clinidae	5	25
	Holocentridae	1	47
	Nomeidae	2	46
	Triglidae	Unid.	43
	Blenniidae	Unid.	38
	Myctophidae	1	23
	Gobiidae	Unid.	9
	Gobiidae	1	23
	Scombridae	1	22
	Scyliorhinidae	Unid.	16
	Macrouridae	Unid.	12
	Congridae	1	12
	Coryphaenidae	1	10
	Sebastidae	Unid.	6
	Gobiesocidae	1	6
	Trichiuridae	2	9
	Tetraodontidae	Unid.	5
	Cheilodactylidae	1	4
	Ophichthidae	Unid.	5
	Bregmacerotidae	Unid.	4
	Ophidiidae	1	3
	Ophidiidae	Unid.	1
	Sparidae	2	3
	Congiopodidae	Unid.	2
	Berycidae	1	2
	Centriscidae	1	1
	Chlorophthalmidae	1	1
	Batrachoididae	1	1
	Aulostomidae	Unid.	1
Cephalopods	Loliginidae	2	54
	Sepiidae	1	85
	Octopodidae	1	11
Crustaceans	Squillidae	1	244
	Brachyura*	Unid.	2
	Portunidae	1	1
	Palinuridae	1	3
Insects	Gryllidae	1	191
	Gryllotalpidae	1	2
	Sphingidae	1	2
	Sphingidae	Unid.	1
	Coleoptera **	Unid.	1

*Infraorder, **Order

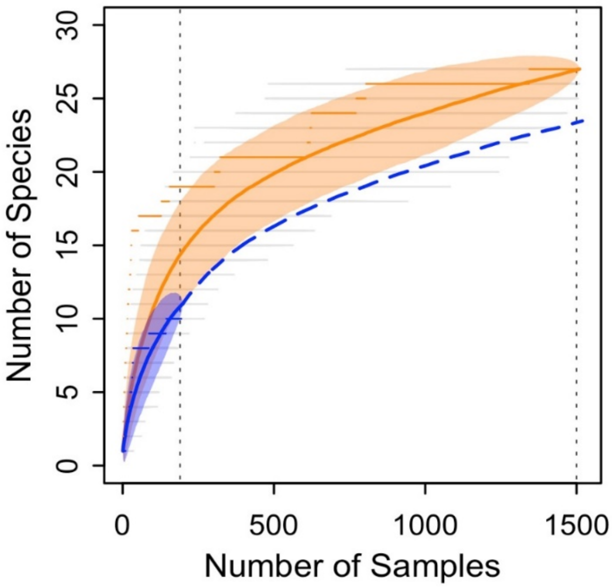


Figure 2.3: Sample-based rarefaction and species accumulation curves for greater crested tern diet at Robben Island. Accumulation curves show the observed species accumulation from 1510 photo-samples (orange points) and 198 regurgitations (blue points) collected on 18 and 19 April 2015. Rarefaction curves (solid lines) and 95% asymptotic confidence intervals (shaded areas) are based on 1,000 random permutations (shown as light grey points) of the observed data. The rarefaction curve for regurgitations is extrapolated (blue dashed line) based on a GAM fit to the photo-sampling, assuming an equal species accumulation rate beyond the range of the observed data. Vertical dotted lines show sample sizes of 190 and 1500 used to compare the methods.

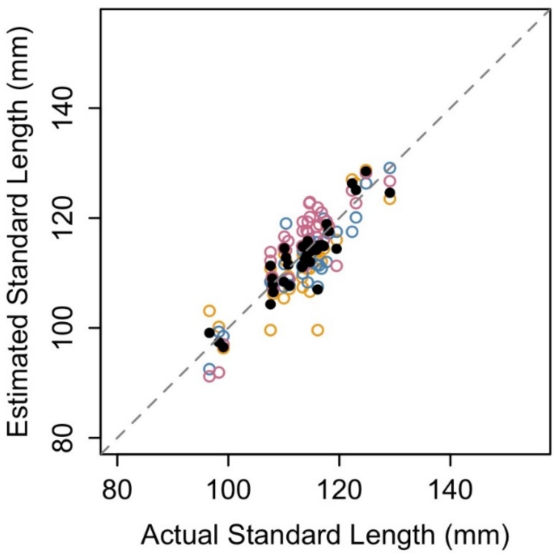


Figure 2.4: Accuracy of estimated standard length ($\widehat{SL}$) (y-axis) compared with actual SL values (x-axis) of anchovy from photographs in ImageJ using allometric regressions based on estimates of eye diameter ($\hat{E}$, open orange circles), operculum width ($\hat{O}$, open blue circles), head diameter ($\widehat{H}$, purple open circles) and the mean of all three (mean $\widehat{SL}$, black closed circles). The mean culmen length of greater crested terns (61.2 mm) was used as the reference length to scale the pixel-based length estimates in ImageJ. The grey dashed line represents 100% accuracy.

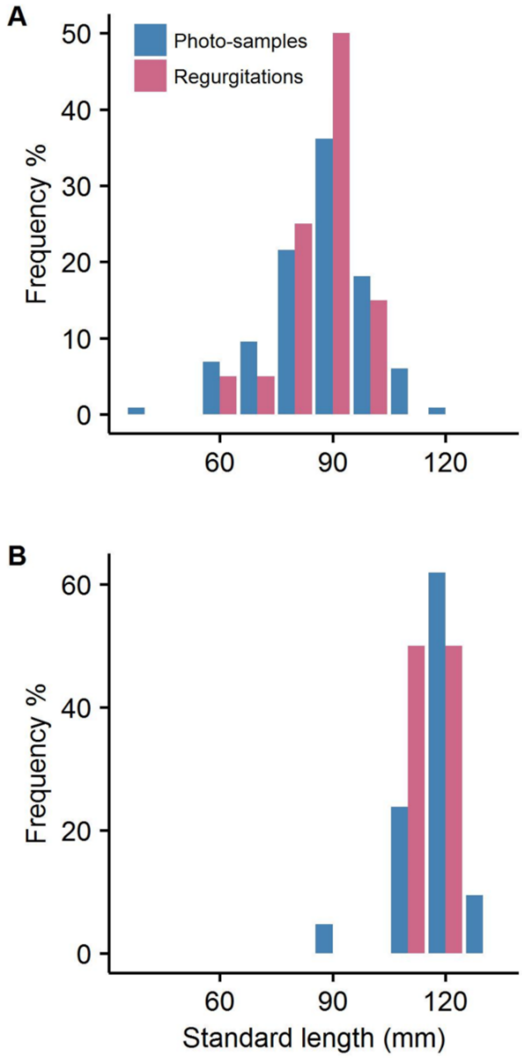


Figure 2.5: Frequency distribution of anchovy standard length from photo-samples and regurgitations (A = Robben Island; B = Seal Island).

Discussion

Photo-sampling offers an effective, low-impact alternative to traditional diet studies for birds that carry prey items in their bill, with accurate prey identification and size estimates possible. Samples can be acquired quickly and equivalent diet compositions obtained with relatively low effort (Figure 2.3). In three breeding seasons, I sampled 24,211 prey items and identified 51 prey taxa (Table 2.1) with this approach; the most comprehensive diet analysis for terns in southern Africa prior to this study identified 25 species from 1,311 regurgitated prey items in 10 breeding seasons (1977–1986; Walter *et al*. 1987a). Despite ca 55% of photos being discarded, this approach yielded an order of magnitude more samples and identified twice as many species, with minimal disturbance to breeding birds.

The photo-sampling approach has several other advantages over traditional diet sampling. First, terns often regurgitate only the posterior body and caudal fin of a fish, making identification of similar species difficult (McLeay *et al.* 2009a). Photo-sampling records the entire prey, and if there is doubt as to the identification, images can be shared easily with global experts or on specialized websites (e.g. I-spot). Second, photo-sampling can be used in a range of situations (e.g. on land or from a boat), by one individual (collection of regurgitations often involves many people), with minimal training in photography (cameras can be pre-set). Third, the photographic equipment is relatively affordable and once purchased can be used for several years, at multiple colonies and for several species. Also, although processing the photographs can be time-consuming, taking about 30 min for an average of 100 prey identified, the images can be stored and analysed multiple times if needed, without the loss of data quality or metadata (e.g. date and location).

Possible drawbacks associated with photo-sampling include the repeated photography of prey items, especially those with long handling times, leading the frequency of these items being over-estimated. This is predominately a problem in larger colonies, where it is difficult to follow the fate of individual prey items, and one that could be countered using delays (e.g. 5 mins) between photosets. When only a subset of prey is sampled, large or conspicuous prey items may induce an observer bias if they are easier to photograph, more readily identified to species level or more interesting to the photographer. Training photographers to randomise the photo-sampling as much as possible should help reduce this potential bias. Differences in photographic experience between different observers could create a possible bias and should be examined in future studies. Photo-sampling is difficult in bad weather (strong wind, rain or mist) and this may also introduce bias in some situations. Finally, one constraint of this study is that photo-sampling was applied to study chick diet and incubating birds. Although this can provide important insights into changes in prey communities (Anderson *et al.* 2014), it may not always represent adult diet, or diet outside the breeding season (McLeay *et al*. 2009a). Today, specific types of diet can be reconstructed from isotope values, if the diet consists of isotopically distinct components. The implementation of indirect methods such as measuring stable isotope ratios in e.g. blood and feathers of adults (Inger & Bearhop 2008) concurrently with photo-sampling will help to overcome the limitations imposed by photo-sampling. In addition, applying both methods concurrently on marked individuals would allow the development of trophic discrimination factors in wild animals (Newsome *et al*. 2010).

More broadly, ecologists now use digital photography to study animals across a wide range of taxa (e.g. Morrison *et al*. 2011; Marshall & Pierce 2012; Gregory *et al*. 2014). Opportunistic observations have documented novel behaviours and trophic interactions (e.g. Gaglio *et al.* 2015b; Tella *et al.* 2015), suggesting that standardised approaches to study species bringing items to a known location have great potential for ecological monitoring. This approach could also be applied to a diversity of taxa in addition to birds that carry prey (e.g. carnivores bringing prey to their offspring, or ants and termites carrying items to their nests). In any of these applications photo-sampling could provide high quality photographic data to complement the now extensive use of camera-traps.

The ecological information provided by prey size is almost as important as prey species, giving information on the targeted prey cohort and the predator's energetics. This study demonstrated that prey size (anchovy SL) can be estimated accurately (ca 98%) and precisely (ca 99%) from images. The approach could be used with a wide variety of predators and prey species to eliminate biases associated with *in situ* visual observation (Lee & Hockey 2001). Even if photo-sampling is unlikely to obtain measurements as accurately or precisely as regurgitated/dropped prey, the sample size from photo-sampling is always likely to be greater than the number of prey found undigested. A crucial step to estimate absolute prey size is identifying a reference object (e.g. culmen, eye diameter) of known size, to provide a scale for prey measurements. These reference objects should be chosen carefully and the degree to which the selected trait varies within the population assessed to constrain and minimise errors where possible (see Results). Additional studies could photograph birds of known bill length, age and sex (e.g. colour banded individuals) with prey held with different angles to the body and compare larger numbers of observers' photo-sampling concurrently to further quantify the errors associated with prey measurements. For prey species that are not distorted in images (e.g. some insects do not bend over a bird's bill), size can be estimated directly and even when absolute estimates are not possible, the method can still be used to assess changes in relative prey size, allowing for spatial and temporal comparisons.

Crucially, the photo-sampling method caused little if any disturbance to the nesting birds. Distances from animals can be selected to balance each species' sensitivity against image quality. The opportunity to record the number and size of prey brought to offspring remotely and in real time without influencing behaviour, allows for accurate monitoring of temporal variability. For threatened or declining species (e.g. many seabirds; Croxall *et al.* 2012), such non-invasive methods can help elucidate functional links between population dynamics, environmental variability and anthropogenic pressures (Saraux *et al.* 2011a). Incorporating these observations into detailed information on species composition and energy content for energetic models offers great potential for indicators of long-term and large-scale ecosystem change (Furness & Cooper 1982). Furthermore, with standardized protocols, digital images can be shared easily using digital platforms (e.g. I-spot, Google Images) to facilitate global collaborations (e.g. González-Solís *et al.* 2011; Lynch *et al*. 2015), encourage community involvement in citizen science projects (e.g. Newman *et al*. 2012), and develop data archives to answer as yet unforeseen questions. Given the growing need to assess environmental changes and human impacts on natural ecosystems (Hobday *et al.* 2015), this methodology offers a novel tool for collaborative efforts in conservation.

Appendix A

Additional methods and results for estimation of prey standard length

Allometric regressions between anchovy morphometric measurements and standard length

Eighty-seven anchovy were collected from commercial purse-seine catches obtained through the Department of Agriculture, Forestry and Fisheries. All 87 fish were straightened by hand on a flat surface and measurements of standard length (SL), operculum width (O), head width (H) and eye diameter (E) were taken using Vernier callipers to the nearest 0.1 mm. For 50 of these fish (the training set), I related each of these three morphometric measurements (O, H and E) to the SL of the fish using linear ($y = \alpha + \beta x$), log-linear ($y = \alpha + \beta \cdot ln(x)$), and power ($y = \alpha \cdot x^{\beta}$) regressions fitted with the *lm* and *nls* functions in R. I compared model fits using Akaike's Information Criterion adjusted for small sample size (AICc) and selected the model with the highest AICc weight in each case (Table A.1). All three relationships were best represented by log-linear regressions with adjusted-R^2 values between 0.88 and 0.93 (Table A.1, Figure A.1).

Table A.1: Regression equations and adjusted R^2 values from models regressing anchovy (n = 50) eye diameter, operculum width and head width against standard length (SL) based on morphometric measurements. Models for each morphometric measurement are sorted by AICc weight, with the adjusted R^2 and regression equation given for the best fitting model in each case.

Morphometric measurement	Model type	AICc value	AICc weight	Adjusted R^2 value	Regression equation
Eye diameter	Log-linear	279.5	0.94	0.92	$\widehat{SL} = -68.16 + 91.95 \times \ln(E)$
	Power	285.8	0.04	–	–
	Linear	287.2	0.02	–	–
Operculum width	Log-linear	299.0	0.66	0.88	$\widehat{SL} = -230.44 + 121.60 \times \ln(O)$
	Linear	301.5	0.19	–	–
	Power	301.9	0.15	–	–
Head width	Log-linear	276.7	0.38	0.93	$\widehat{SL} = -168.70 + 112.29 \times \ln(H)$
	Linear	277.1	0.32	–	–
	Power	277.2	0.30	–	–

$\widehat{SL}$ = estimated standard length and ln is the natural logarithm.

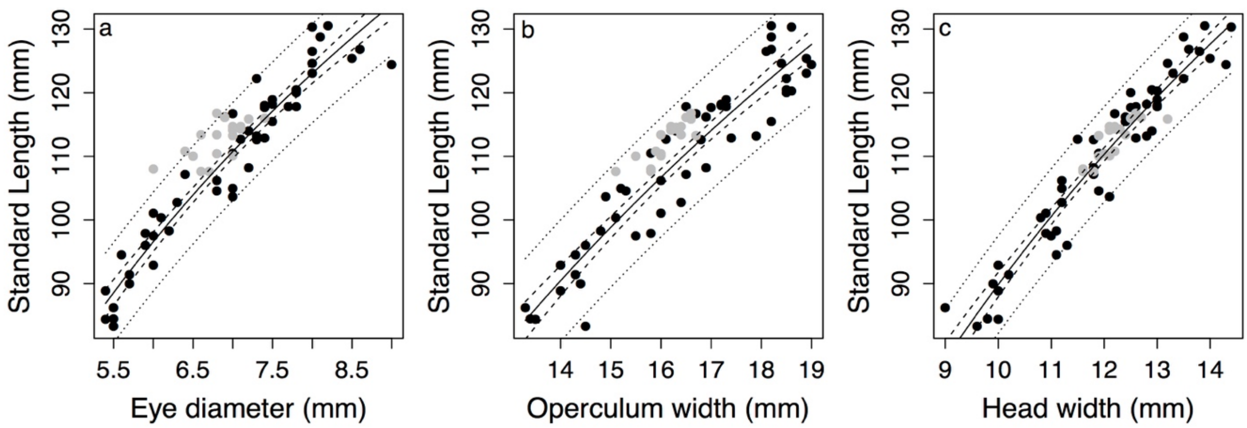


Figure A.1: Log-linear regression fits (solid lines) between measurements of each of (a) the eye diameter, (b) the operculum width, (c) the head width and the standard length (all in mm) of 50 anchovies *Engraulis encrasicolus* (black circles) measured with vernier callipers. Dashed lines show the 95% confidence intervals for the regression fit (solid line) and dotted lines show the 95% prediction intervals. Grey circles show the same measurements for 20 fish from the cross-validation dataset.

Assessing accuracy of predicted standard lengths for the training and cross-validation datasets

I used the log-linear model described above and the *predict* function in R to generate three SL estimates ($\widehat{SL}$) for each of the 50 anchovies in the training data set and each of 20 additional anchovies making up the test data set for cross-validation (Figure A.1). In addition, I combined the three estimates by taking their arithmetic mean (combined $\widehat{SL}$). I then compared these models predicted estimates ($\widehat{SL}$) to the known SL (measured with the callipers) of each fish by computing the mean accuracy ($\bar{y}$) of each of the four sets of $\widehat{SL}$ estimates following the approach in eqn 1 in the main text where n = 50 for the training dataset and n = 20 for the cross-validation dataset. I assessed the mean differences between the known SLs and each set of $\widehat{SL}$ values using permutations tests with 10,000 Monte Carlo iterations (see main text). I checked that the accuracy of the combined $\widehat{SL}$ estimates were not influenced by the size of the fish (known SL) using linear models on the logit transformed percentage accuracy (expressed as a proportion) as in eqn 3 in the main text.

For the 50 anchovy in the training set, mean (± SD) accuracy ($\bar{y}$) of ($\widehat{SL}$) was: O = 96.5 (± 2.3)%, H = 97.2 (± 2.2)%, E = 97.2 (± 2.0)% and combined $\widehat{SL}$ = 97.9 (± 1.7)% and none of the means differed significantly from the mean of the known SL (permutations tests: all p-values > 0.05). On average, the combined $\widehat{SL}$ estimates were inaccurate by 2.34 (± 1.89) mm for these 50 anchovy. For the cross-validation set, mean accuracies were E = 96.3 (± 2.8)%, O = 95.6 (± 1.5)%, H = 98.5 (± 1.1)% for the individual morphometric measurements, and combined $\widehat{SL}$,= 97.3 (± 1.8)%. The $\widehat{SL}$s based on the E and O measurements almost consistently underestimated SL (Figure A.1) and their means differed significantly from the SL of the 20 anchovy (permutations tests: E: p = 0.001; O: p < 0.001). The estimates based on H were more balanced between under and overestimates (Figure A.1) and did not differ significantly from the SL values ($p = 0.51$). For these 20 anchovy the combined $\widehat{SL}$ estimates were inaccurate by a mean of 2.97 (± 2.17) mm, which was significantly different from their known SLs (permutations tests: $p < 0.007$). Accuracy was not affected by the known SL of the fish for either the training dataset ($F_{(1,48)} = 0.12$, $p = 0.73$) or the cross-validation dataset ($F_{(1,17)} = 0.12$, $p = 0.73$).

Assessing accuracy of predicted standard lengths for the 37 anchovy photographed

Based on the above, I used these log-linear regressions to obtain estimates of SL ($\widehat{SL}$) from 37 anchovy photographed in the bill of a greater crested tern carcass (see Figure A.2 and main text). With the culmen length of the carcass (62.1 mm) set as the reference mean (± SD) accuracy ($\bar{y}$) of ($\widehat{SL}$) was: O = 98.3 (± 1.7)%, H = 96.8 (± 2.0)%, E = 97.8 (± 2.1)% and combined $\widehat{SL}$ = 98.3 (± 1.5)% and none of the means differed significantly from the mean of the known SL (permutations tests: all p-values > 0.05). On average, the combined $\widehat{SL}$ estimates were inaccurate by 0.58 (± 2.58) mm for these 37 anchovy. Accuracy was negatively related to SL for the estimates derived from the pixel measurement of eye diameter ($\hat{E}$: $F_{(1,35)} = 4.9$, $p = 0.03$), but not for the other three estimates (all p-values > 0.05).

Figure A.2: An example of the set up used to validate SL estimates of anchovies *Engraulis encrasicolus* from photographs taken in the field. Here an anchovy of known SL is held in the bill of a carcass of greater crested tern *Thalasseus bergii* with known culmen length.

With the species' mean culmen length (61.2 mm) set as the reference length, the mean (± SD) accuracy ($\bar{\gamma}$) decreased slightly to O = 97.7 (± 1.9)%, H = 96.8 (± 2.1)%, E = 96.9 (± 2.6)% and combined $\widehat{SL}$ = 98.1 (± 1.5)%. Again, none of the means differed significantly from the mean of the known SL (permutations tests: all p-values > 0.05) and the mean (± SD) inaccuracy of the combined $\widehat{SL}$ estimates was 0.64 (± 2.75) mm. Accuracy was not affected by the known SL for any of the estimates in this case (all p-values > 0.05).

For the species' minimum culmen length (54.5 mm), the mean (± SD) accuracy ($\bar{\gamma}$) values were O = 87.9 (± 4.0)%, H = 89.6 (± 4.5)%, E = 88.6 (± 4.7)% and combined $\widehat{SL}$ = 88.9 (± 3.3)%. Again, accuracy was negatively related to SL for the estimates derived from the pixel measurement of eye diameter ($\hat{E}$: $F_{(1,35)} = 4.5$, $p = 0.042$), but not for the other three estimates (all p-values > 0.05). For the maximum culmen length (67.6 mm), the $\bar{\gamma}$ values were O = 89.2 (± 4.6)%, H = 88.6 (± 3.7)%, E = 92.4 (± 3.8)% and combined $\widehat{SL}$ = 91.3 (± 3.2)%. Accuracy was positively related to SL for the estimates derived from the pixel measurement of eye diameter ($\hat{H}$: $F_{(1,35)} = 7.96$, $p = 0.008$) and combined $\widehat{SL}$ ($F_{(1,35)} = 5.48$, $p = 0.03$), but not for the other two estimates (p-values > 0.05). For the both minimum and maximum culmen lengths, all $\widehat{SL}$ means differed significantly from the mean of the known SL (permutations tests: all p-values < 0.001); however, these values represent the absolute extremes record for this species (see main text). Finally, based on the above, I used the combined $\widehat{SL}$ for all further analyses described in this chapter.

Table A.2: Estimated SLs from operculum width, head diameter and eye diameter from the (N) 37 anchovy photographed in the bill of a greater crested tern carcass a measured in ImageJ. SL = known standard length. Results obtained using as reference: carcass = bill length of the carcass photographed; min = minimum bill length knc for the species; mean = mean bill length known for the species; max = maximum bill length known for the species. All results in mm.

		Operculum width ($\widehat{O}$)				**Head diameter ($\widehat{H}$)**				**Eye diameter ($\widehat{E}$)**			
N	**SL**	**Carcass**	**Min.**	**Mean**	**Max.**	**Carcass**	**Min.**	**Mean**	**Max.**	**Carcass**	**Min.**	**Mean**	**Max.**
1	113.3	111.84	97.22	111.18	124.16	110.33	102.88	114.91	122.89	113.87	106.46	109.18	120.48
2	107.6	107.39	95.57	108.37	121.03	113.01	101.58	113.83	124.47	107.42	92.51	99.61	115.38
3	113.4	112.93	95.73	109.93	121.03	117.84	107.68	119.32	127.64	109.84	96.59	107.42	122.12
4	114.1	113.15	97.22	113.51	124.16	110.33	102.88	117.66	122.89	113.87	106.46	110.77	120.48
5	108.0	107.24	95.57	107.31	121.03	113.01	101.58	109.01	124.47	107.42	92.51	107.42	115.38
6	116.0	118.92	104.41	114.86	131.82	117.93	98.81	116.52	127.00	114.88	105.36	113.99	122.47
7	114.6	116.35	106.02	116.21	131.63	123.06	108.44	122.72	130.18	112.33	100.49	110.77	117.11
8	114.3	110.30	88.19	108.29	114.08	117.31	94.26	119.32	127.64	115.00	109.04	113.99	131.60
9	107.6	108.82	99.66	108.44	127.15	111.91	102.18	112.19	122.72	111.68	104.80	110.77	124.19
10	114.7	113.22	101.82	113.15	128.50	119.32	106.72	120.18	130.33	110.77	98.11	110.77	121.77
11	110.0	109.19	94.82	107.54	121.90	111.73	97.76	114.55	121.96	103.10	96.59	105.36	110.77
12	116.1	111.55	95.32	107.46	119.47	119.58	105.36	121.88	134.41	105.63	83.96	99.61	110.77
13	115.9	112.35	100.23	111.48	124.82	118.71	92.08	118.36	127.24	114.12	99.60	112.07	119.53
14	110.8	110.45	98.04	108.97	125.67	113.83	96.61	115.81	124.63	112.07	96.59	109.44	121.54
15	113.4	112.49	104.79	114.08	130.51	117.40	102.58	117.58	122.64	112.97	102.53	113.36	121.54
16	110.4	119.05	110.08	118.99	139.19	115.36	103.48	114.10	124.38	118.21	104.94	112.07	125.32
17	114.7	114.08	98.85	113.00	125.41	122.05	111.35	122.89	136.65	113.74	100.35	106.60	119.05
18	110.1	113.00	104.33	111.62	122.37	117.14	106.33	116.61	132.89	113.87	99.31	113.36	120.60
19	114.3	111.18	98.85	111.77	121.97	117.75	104.57	117.31	125.62	113.74	101.81	112.33	124.53
20	116.8	111.40	102.45	110.82	126.58	122.97	107.97	121.03	136.36	111.03	103.81	112.07	124.87
21	122.3	119.74	106.90	117.53	131.01	127.16	105.55	124.96	128.76	128.62	111.42	126.98	133.05
22	98.3	99.02	82.39	99.26	111.91	92.63	88.38	91.86	109.01	99.75	88.75	100.20	105.91
23	123.0	119.81	106.10	120.15	131.51	123.64	109.39	122.72	131.66	126.76	115.75	126.32	135.60
24	119.5	117.81	104.09	117.53	128.43	109.67	99.32	111.26	121.88	118.45	101.52	116.00	118.93
25	111.0	111.48	96.73	107.84	123.70	110.33	97.56	108.92	120.69	109.31	98.71	107.15	120.36
26	107.9	107.62	97.63	107.77	121.03	110.52	98.81	109.30	122.64	109.31	96.74	108.77	118.57
27	99.1	100.55	82.57	98.53	108.59	98.91	82.07	97.03	113.10	98.86	84.83	96.28	107.56
28	129.1	129.26	112.64	129.07	144.10	128.92	111.08	126.67	136.65	125.76	107.83	123.50	133.36
29	117.7	111.70	99.26	112.06	126.25	121.29	108.82	119.40	130.18	119.17	106.19	118.69	127.31
30	116.0	116.63	100.55	115.57	127.48	118.01	101.27	114.73	125.78	116.74	104.52	114.37	125.43
31	108.1	108.52	93.30	107.09	122.51	105.36	93.39	107.10	121.96	109.44	95.35	106.19	115.50
32	124.8	127.92	113.07	126.32	139.54	127.24	116.34	128.20	137.90	126.10	108.91	128.73	133.87
33	118.1	118.85	104.79	117.19	135.17	119.32	106.81	118.54	129.78	119.65	104.94	117.23	127.20
34	116.4	113.29	98.69	111.40	124.89	119.66	101.07	118.80	130.65	114.75	101.08	113.10	122.00
35	117.2	117.05	104.17	119.94	133.11	118.45	109.20	115.99	128.76	113.61	95.97	114.37	120.36
36	113.8	113.94	102.37	111.62	130.76	111.17	96.92	111.35	122.80	118.57	104.23	113.10	131.91
37	96.6	94.23	80.98	92.53	100.31	94.47	77.52	91.19	107.20	96.89	95.04	103.10	110.77

Results of the comparison between photo-sampling and regurgitation

Table A.3: Species, genera or families (numerical abundance) identified from photographs or regurgitations at Robben (Observer A, 18–19 April 2014) and Seal islands (9 June 2014).

Common name	Latin name	Robben Island		Seal Island	
		Photo-sample	Regurgitation	Photo-sample	Regurgitation
Anchovy	*Engraulis encrasicolus*	1185	170	129	96
Redeye round-herring	*Etrumeus whiteheadi*	116	10	6	1
Cape silverside	*Atherina breviceps*	41	2	0	0
Sardine	*Sardinops sagax*	21	2	7	3
Southern mullet	*Liza richardsonii*	20	1	0	0
Longsnout pipe fish	*Syngnathus temminckii*	19	0	1	0
Atlantic saury	*Scomberesox saurus*	17	1	0	1
Horse mackerel	*Trachurus capensis*	12	2	0	0
Elf	*Pomatomus saltatrix*	9	0	4	0
Beaked sandfish	*Gonorynchus gonorynchus*	9	2	5	0
Gaper	*Champsodon capensis*	8	1	0	0
Blenny	Blenniidae	5	0	0	0
Grenadier	Macrouridae	5	0	0	0
Klipfish	*Clinus* spp.	5	0	1	0
Soldierfish	Holocentridae	2	0	0	0
Sole	Soleidae	2	0	0	0
Bluebottle Fish	*Nomeus gronovii*	1	0	0	0
Gurnard	*Chelidonichthys* sp.	1	0	0	0
Lanternfish	*Lampanyctodes hectorus*	1	0	0	0
Eel	Ophichthidae	1	0	0	0
Horsefish	Congiopodidae	1	0	0	0
Rocksucker	*Chorisochismus dentex*	1	0	0	0
Carpenter	*Argyrozona* sp.	0	0	1	0
Cape Hake	*Merluccius capensis*	0	0	0	1
Pufferfish	*Amblyrhynchotes* sp.	0	0	1	0
Southern conger	*Gnathophis capensis*	0	0	1	0
Indian lizard fish	*Synodus indicus*	0	0	0	1
Fish (Total)		**1482**	**191**	**156**	**103**
Cuttlefish	*Sepia vermiculata*	9	6	0	0
Squid	*Loligo vulgaris*	3	1	0	0
Octopus	*Octopus vulgaris*	1	0	0	0
Cephalopod (Total)		**13**	**7**	**1**	**0**
Mantis shrimp	*Pterygosquilla armata capensis*	14	0	0	0
Crustacean (Total)		**14**	**0**	**0**	**0**
Two-spotted Cricket	*Gryllus bimaculatus*	1	0	0	0
Insects (Total)		**1**	**0**	**0**	**0**
Total		**1510**	**198**	**157**	**103**

Chapter 3

Coping with the odds: foraging plasticity of the greater crested tern breeding in an exploited and unpredictable environment

Abstract

Top predators are useful indicators of marine ecosystem functioning. Among seabirds, some tern species specialise on a few high-quality prey, while other species are more opportunistic, and tend to be able to cope better with reductions in the abundance of their preferred prey. The diet of breeding greater crested terns from an increasing population in the Western Cape, South Africa, was investigated between 2013 and 2015. Using a non-invasive photo-sampling method, 24,211 prey items from at least 47 different families were identified, with 34 new prey species recorded, revealing an important degree of foraging plasticity for this seabird. Fish dominated the diet, constituting 94% of prey by number, followed by cephalopods (3%), crustaceans (2%) and insects (1%). Greater crested terns targeted mainly surface-schooling Clupeiformes, with anchovy *Engraulis encrasicolus,* the most abundant prey in all three breeding seasons (65%), followed by redeye round-herring *Etrumeus whiteheadi* (10%), Atlantic saury *Scomberesox saurus* (7%), and many other uncommon species of fish including demersal fish. Prey composition differed significantly between breeding stages and seasons, with anchovy highly abundant in terns' diet at the start of the breeding season and less frequent as the season progressed. Small anchovy and fish larvae were captured by parents to feed nestlings, whereas larger prey and multi-prey loads were returned to older chicks throughout the rest of the rearing period.

Proportions of preferred prey in greater crested tern diet were influenced by time of the day and localized environmental factors, with anchovy prey being scarce on foggy days, and occurring more frequently with increasing wind speeds. The standard length of anchovy prey was 84 ± 16.8 mm (range 32-125 mm), but this also differed between breeding stages and seasons. The size of anchovy captured by fisheries was generally different to those captured by terns with only occasional overlaps of anchovy size classes. Comparison of the proportion of anchovy in tern diet (sampled intermittently from the 1980s to 2015), with hydro-acoustic anchovy biomass estimates, showed no clear relationship. This is the first study of the diet of a single prey-loading seabird that overcomes the inherent biases associated with traditional diet collection. Detailed knowledge of temporal variations in seabirds' diet provides a useful indicator linking seabird prey choice responses to changes in localised prey availability, including non-commercial species, which may enhance conservation strategies for seabirds and fish stocks.

Introduction

Marine top predators are often used as indicators of ecosystem functioning (Piatt *et al.* 2007) with the potential to support ecosystem-based management (Sergio *et al.* 2006, Fauchald 2009) as changes in their life history traits (e.g. diet, demography, behaviour or physiology) often reflect changes in the environment (e.g. Piatt *et al.* 2007). In highly dynamic and unpredictable marine systems, like upwelling ecosystems, top predators such as seabirds must adjust their diet and foraging ecology in response to seasonal and inter-annual changes in food availability. Thus, the diet of seabirds may reflect variability in food-web composition due to natural or human-induced environmental change (Ludynia *et al.* 2010, Green *et al.* 2015).

Although seabirds have evolved several life-history characteristics to help to buffer scarce and/or unpredictable forage resources, seabirds can still be negatively affected by reductions in food availability (e.g. Cury *et al.* 2011). Such negative impacts are particularly evident during breeding, when prey availability and localized environmental factors affect seabird foraging success, owing to feeding range restrictions imposed by central-place foraging (Labbé *et al.* 2013). Variation in food supply around breeding colonies can have strong impacts on populations of seabirds with short foraging ranges, such as terns (Monaghan *et al.* 1992, McLeay *et al.* 2009b). Some specialist seabird species target a few high-quality prey species (Shealer 1998), making them vulnerable to stochastic availability of their preferred prey and other abiotic constraints (Ramos *et al.* 2002, McLeay *et al.* 2009b). Other seabird are more versatile, enabling them to buffer short-term changes in the availability of favoured prey species by switching to other prey of lower quality, which can be obtained with less effort, especially when foraging areas are restricted near the colony (Safina *et al.* 1990, Lyons *et al.* 2005). This opportunistic feeding can be sufficient to maintain adult condition and survival, but is not optimal for the growth and survival of chicks (Furness & Tasker 2000, Grémillet *et al.* 2008).

The greater crested tern *Thalasseus bergii bergii* is a coastal seabird with an extensive breeding range that includes the Benguela upwelling system. It is an inshore forager, which acquires food from near the water surface (Crawford *et al.* 2005). When breeding, adults predominantly return to their nests with single prey items and, infrequently with multi-prey loads, carried in their bills (Duffy 1987). They feed mainly on schooling Clupeiformes fish, which are also targeted by industrial purse-seine fisheries (Walter *et al.* 1987b, Griffiths *et al.* 2004). Like all other terns, greater crested terns are visual predators, seizing fish that are near the sea surface, but they also use foraging flocks of other seabirds as cues to locate prey (i.e. local enhancement; Thiebault *et al.* 2015). They furthermore may benefit from the hunting behaviour of underwater predators like penguins, dolphins and predatory fish, which force prey to the surface (Haney *et al.* 1992, Ryan *et al.* 2012).

Localized environmental factors can also limit the ability of greater crested terns to find food for themselves and their offspring. For instance, fog may prevent terns from locating fish schools or foraging flocks of other seabirds (Minich 2001 and references therein). Prey such as anchovy and redeye round-herring *Etrumeus whiteheadi* exhibit diel-vertical movements, potentially altering their accessibility during the day (Stenevik *et al.* 2007, Zimmer *et al.* 2008). In addition, seasonal variation in abundance of anchovy recruits may influence the availability of this key prey source during the breeding season (van der Lingen & Huggett 2003, Hutchings *et al.* 2014). Tidal cycles are also found to influence delivery rates in relation to foraging areas used by different seabird species (Taylor 1983) and adverse weather conditions (e.g. rough seas) may impact the foraging behaviour of seabirds by altering prey detectability or prey behaviour or by increasing the energetic costs of foraging (e.g. strong winds) (Gilchrist *et al*. 1998, Stienen *et al.* 2000, Robinson *et al.* 2002).

Greater crested terns display a variety of foraging methods including plunge diving, surface seizing, aerial and ground foraging, scavenging (e.g. from fishery discards or seal catches), kleptoparasitism and perch hunting foraging (Crawford *et al.* 2005, Gaglio *et al.* 2015b, Ryan 2017). This suggests some form of opportunism against the uncertainty of locating food in a stochastic system (Erwin 1977), which may play a role in their ability to find sufficient food for their offspring, especially when their favourite prey is scarce or irregularly distributed (Götmark 1990). In southern Africa, little is known about the greater crested tern's foraging ecology, and there have been only two studies of its diet (Walter *et al.* 1987a, Crawford & Dyer 1995), with no published information from the last two decades. Results of prey studies collected from greater crested terns in Australia suggest that adults select higher quality prey for their chicks than for themselves (McLeay *et al*. 2009a). This is predicted to increase their foraging effort to meet the chicks' energy requirements, particularly when high quality food is scarce (Grémillet *et al.* 2008, Ludynia *et al.* 2010).

In the Benguela upwelling region, populations of breeding seabirds that feed on anchovy and sardine *Sardinops sagax*, such as the African penguin *Spheniscus demersus*, Cape cormorant *Phalacrocorax capensis* and Cape gannet *Morus capensis*, have decreased since the 1980s, largely due to reductions in prey availability (Cury *et al.* 2011, Crawford *et al.* 2014 and references therein). Competition with fisheries and environmental changes have caused a spatial mismatch between prey distributions and the breeding colonies of these three species (Cury & Shannon 2004, Watermeyer *et al.* 2008, Blamey *et al.* 2012, Crawford *et al.* 2014, Crawford *et al.* 2016). In contrast, the greater crested tern population has increased over the last two decades (Crawford 2009, Crawford *et al.* 2014), a period for which there is no published information on this species' diet.

In order to assess how the greater crested tern is coping with local changes in food availability, I investigated this species' prey composition and how it varies between breeding stages and years in relation to the abundance of their preferred prey. Moreover, I assessed overlap with fisheries that target the same prey species. Finally, I investigated the influence of localized environmental factors on tern diet.

Methods

The study was conducted at Robben Island, where most of the nominate race of greater crested terns breed (Chapter 1). Prey carried by terns visiting the breeding colony was recorded during three successive breeding seasons: February–May 2013, January–May 2014 and March–May 2015. The study of environmental factors was done similarly over the three breeding seasons. Prey identity and multi-prey loads were assessed with a novel non-invasive photo-sampling technique, which consists of taking a sequence of 3 photos (photo-set) of adults returning to the colony with prey, allowing also an accurate estimation of anchovy standard length (SL) (see Chapter 2, Gaglio *et al.* 2016). Photo-sampling was carried out for several days per week (range 1–7 days) from incubation until the chicks fledged. Generally, each photo-sampling session lasted about 1 hr and was carried out randomly at different times of the day between civil dawn and civil dusk (ca 06h00-20h00 in February–March; ca 7h00-18h00 in April–May), a period when photography is possible and when terns are known to forage (Nicholson 2002) (Table B.1). An index for breeding stage was obtained from a combination of visual inspection at the two colonies and detailed observations of images from camera-traps placed within the colony (camera-traps were set to photograph nest contents every day for 1h in the morning and 30 min in the afternoon) (Figure B.1).

Environmental factors

Several environmental factors were investigated to assess their influence on prey returned by terns to their breeding colonies. Visibility was measured by the presence/absence of fog within one hour preceding the photo-sampling and was determined by the observer's ability to distinguish specific landmarks located 500 m away from the observer. Time of day may affect both the visual detection of prey and the abundance of prey species that undergo diel vertical movements (Elliot & Gaston 2015). To investigate diet changes in relation to time of day, prey photographs were categorised into seven two-hourly periods commencing from the beginning of civil light. Hourly wind speed measurements were provided by the South African Weather Service. Tidal stage, defined as hours before and after high tide (range from -5 to 6), was obtained from www.tides.mobilegeographics.com.

Abundance and size of anchovy

Relationship with anchovy hydro-acoustic survey

To test the effect of food availability on tern diet, I used data on anchovy biomass (in tonnes) obtained from annual hydro-acoustic surveys conducted by DAFF (provided by J. C. Coetzee). Since the 1980s, annual surveys have been conducted in May to estimate the distribution and biomass of the 'young-of-the-year' recruits, and in November to estimate the anchovy spawner biomass. The surveys usually are conducted from Hondeklip Bay (30°19'S, 17°16'E) to Port St Johns (31°62'S, 29°53'E) with the coastline broken up into six areas or 'strata' for the November surveys and up to nine strata for the May surveys. In this chapter, I used three anchovy biomass estimates from areas which fall either inside or outside tern's foraging range, in order to investigate both large and small scale influencing factors. Those areas were: 1) from Cape Columbine to Cape Point (stratum B); 2) from Cape Columbine to Cape Agulhas (strata B + C) and 3) from Hondeklip to Port Alfred (strata A + B + C + D) (Figure 3.1a). For a long-term comparison with acoustic surveys, results of this study were placed in context using historical tern diet data from Walter *et al.* (1987a) and Crawford & Dyer (1995).

Comparison to anchovy caught by fisheries

Potential resource competition between the purse-seine fishery and greater crested terns on anchovies was assessed by examining the correspondence in anchovy size classes to establish if they were targeting similar prey size. Size classes of anchovy caught by terns were compared to those of purse-seine catches quantified between February and May during 2013, 2014 and 2015 (data provided by C. D. van der Lingen; Department of Agriculture, Forestry and Fisheries [DAFF]). Comparisons with fishery catches were restricted to within ca 40 km of Robben Island, as this is the maximum foraging range known for greater crested tern (McLeay *et al.* 2010) (Figure 3.1b).

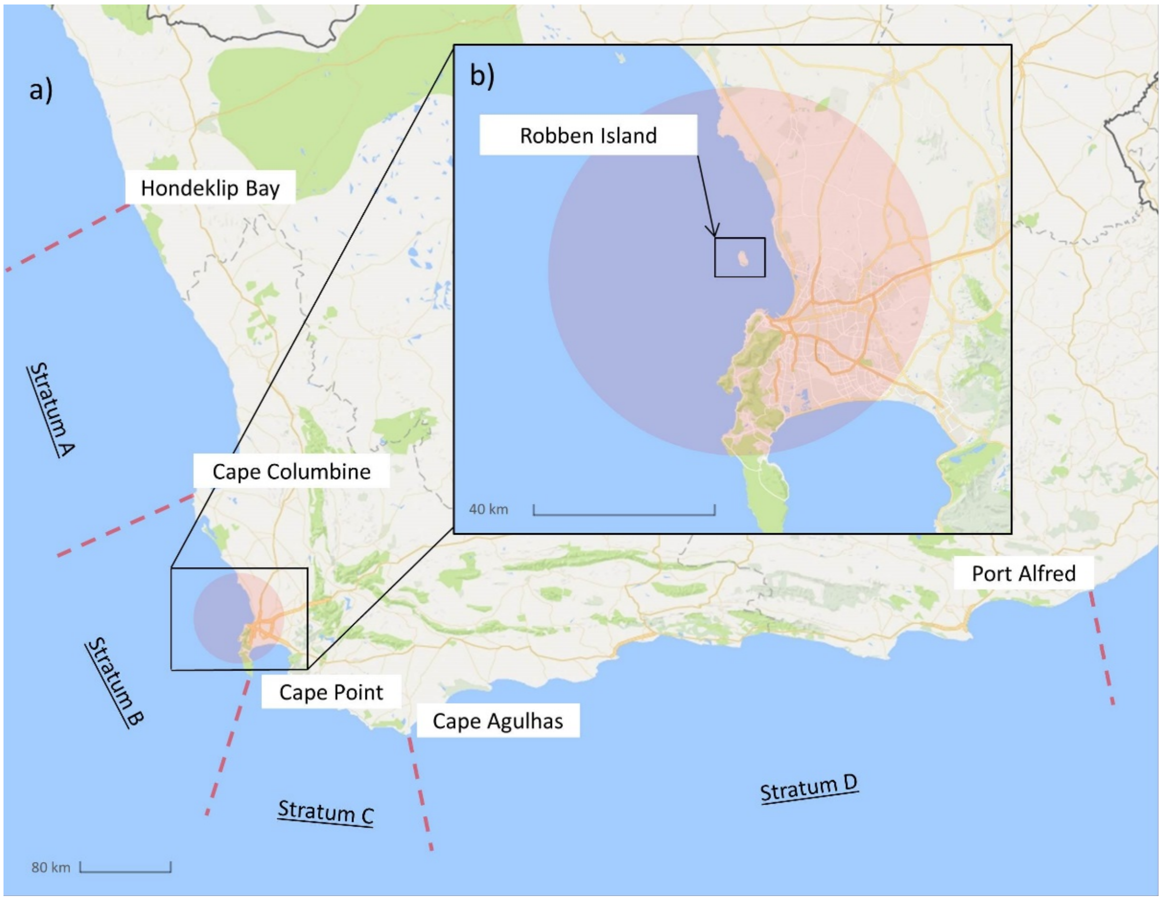


Figure 3.1: Location of Robben Island in the Western Cape (a) and position in Table view (b). Red dotted lines in map (a) indicate the pre-defined strata used to split the coastline of the fish survey data (see Methods). Red circle in map (b) indicate the range of 40 km around Robben Island to assess overlap of anchovy standard length with fisheries (see Methods).

Data analysis and statistics

The contributions of prey species were assessed by counting the numbers of individuals per species by the total prey photographed. Fish prey were divided into pelagic species (dwellers of the pelagic zone of the ocean, including pelagic-neritic and pelagic-oceanic species or demersal species, which occur in the pelagic zone when juveniles), demersal fish (dwellers of the sea floor) and bentho-pelagic fish (species living throughout the water column). Where possible, prey were identified to species or family; very small transparent fish were lumped together as fish larvae (probably anchovy larvae). All fish species that comprised > 5 % of the overall diet were analysed separately. Multi-prey loads were classified as: (i) anchovy double-prey loads (two anchovy carried by the adult), (ii) anchovy multi-prey loads (more than two anchovies carried by the adult), (iii) other species multi-prey loads (two or more non- anchovy prey items carried by the adults), (iv) mixed-species multi-prey loads (load with different species carried together by the adult).

Greater crested terns typically breed synchronously within a colony (Crawford *et al.* 2005), allowing the assessment of the week around median hatch date for each colony. Breeding stages were classified into four categories: incubation (during which time prey returned are used for displaying or courtship purposes), early-provisioning (the mean week when chicks are provisioned in the nest cup), mid-provisioning (the mean week subsequent to early provisioning when chicks begin to leave the nest, this period was used to avoid overlaps between nestling and mobile differences in large colonies) and late-provisioning (the period when adults provision mobile chicks, which are often at this stage grouped in crèches).

As prey composition constituted counts, chi-squared tests were used to assess differences between diet during incubation and during the chick-rearing period within and between seasons. Chi-squared tests were also used to compare counts of the main prey between clear and foggy days at the same stage of breeding. ANOVA followed by Tukey post-hoc tests were performed to compare proportions of prey across times of day as well as to compare mean anchovy SL between seasons, breeding stages and colonies. In order to visualize the importance of each prey group returned to the colony in relation to breeding stage, differences in species composition were plotted in an ordination via non-metric multidimensional scaling (NMDS). NMDS is an unconstrained ordination technique that allows the use of dissimilar measures appropriate for ecological data sets, with the use of distance measures to graphically represent relationships in multidimensional space of groups with similar diets (Quinn & Keough 2002, Karnovsky *et al.* 2012). The Bray–Curtis dissimilarity measure, after Hellinger transformation (Bocard *et al.* 2001), was used with NMDS ordination (with a maximum of 100 iterations) to compare weekly diet variation according to breeding stages, among the sampling weeks for the two colonies and all years combined. Interpretation of the NMDS plot relies on relative distances between objects, with objects closer together being more similar (Quinn & Keough 2002, Arthur & Balazs 2008). I used the function ordiellipse of the R vegan Package to plot ellipses to show the centroid corresponding to each breeding stage.

The influence of environmental variables on the probability of anchovy captured by greater crested terns was assessed using generalised additive models (GAM) to accommodate potential non-linear relationships between continuous explanatory variables and the response (Wood 2006). I included the presence or absence of anchovy for each individual observation as a binary response (i.e. Y = anchovy, N = other prey) using a binomial error distribution with a logit link function to accommodate the non-normal error distribution. Smoother terms included two environmental variables, wind speed and tide, and a temporal variable, week, calculated as the chronological week number commencing from the last week of January (i.e. the beginning of the breeding season; Crawford *et al.* 2005). The latter variable was included to control for seasonal variation in anchovy abundance, which may be influenced by the movements of recruits through this region during the tern's breeding season (van der Lingen & Huggett 2003, Hutchings *et al.* 2014). Explanatory variables expressed as factors included visibility (clear vs foggy days), breeding stage, colony and year. GAMs were fitted using the package 'mgcv' (Wood 2006) in R (R Core Team 2016) with the smoother functions generated using penalised regression splines and the degree of smoothness determined by Generalized Cross Validation criteria (Wood 2006). Collinearity between continuous explanatory variables was assessed using variance inflation factors (Zuur *et al.* 2009) with a minimum threshold set to 3. Proportion tests (non-parametric 2-sample test for equality of proportions) were used to test for proportion differences between anchovy SL classes captured by fisheries and greater crested terns. I used linear logistic regressions (binomial family) on the logit transformed data to assess relationships between proportions of anchovy in the terns' diet and biomass in the spawner and recruitment hydro-acoustic surveys. The significance level was set at $P < 0.05$ for all statistical tests. All computations were carried out in R v 3.3.1 (R Core Team 2016).

Results

Diet of tern chicks and incubating adults

Photo-sampling of tern diet was carried out on 125 days, capturing ca 50,000 photo-sets that yielded images of 24,211 prey items (see Chapter 2). Annual sampling effort varied between 2,954 prey identified in 2013, 9,738 in 2014 and 11,914 in 2015. Prey brought back to the colony were dominated by fish (96%), represented by at least 38 families and 53 genera, including 13 pelagic, 34 demersal and 6 bentho-pelagic fish species (Table 3.1). Pelagic fish accounted for most prey (94% of all prey photographed), with demersal fish (5%) and bentho-pelagic fish (< 1%) (Table 3.1). Anchovy was the dominant prey followed by redeye round-herring, Atlantic saury, long-snout pipefish *Syngnathus* *temminckii*, sardine and horse mackerel *Trachurus capensis* (for details see Table 3.1). Larvae fish (presumably anchovy larvae) accounted for 0.5% of the diet and all non-fish prey (classified as 'other species') accounted for < 4 % and included three species of cephalopods, three crustaceans and four groups of insects (Table 3.1; Figure B.2).

Table 3.1: Numbers and proportions of prey species (and Family) photographed in the bill of adult greater crested terns while returning to the colony. Data include habitat of prey species and include prey recorded at both colonies combined between 2013 and 2015 in Robben Island.

Common name	**Family**	**Habitat**	**N 2013**	**%**	**N 2014**	**%**	**N 2015**	**%**	**N TOT**	**TOT %**
Anchovy	Engraulidae	Pelagic	2420	81.92%	6527	67.03%	7259	60.93%	16206	**65.518%**
Redeye round-herring	Dussumieriidae	Pelagic	92	3.11%	648	6.65%	1817	15.25%	2557	**10.338%**
Atlantic saury	Scomberesocidae	Pelagic	45	1.52%	1245	12.78%	368	3.09%	1658	**6.703%**
Long-snout pipefish	Syngnathidae	Bentho-pelagic	41	1.39%	597	6.13%	227	1.91%	865	**3.497%**
Sardine	Clupeidae	Pelagic	57	1.93%	69	0.71%	419	3.52%	545	**2.203%**
Horse mackerel	Carangidae	Pelagic	57	1.93%	150	1.54%	201	1.69%	408	**1.649%**
Beaked sandfish	Gonorynchidae	Demersal	35	1.18%	23	0.24%	49	0.41%	224	0.906%
Beaked sandfish larvae		Pelagic	1	0.03%	13	0.13%	103	0.86%	127	0.513%
Cape silverside	Atherinidae	Pelagic	3	0.10%	69	0.71%	126	1.06%	198	0.800%
Southern mullet	Mugilidae	Demersal	7	0.24%	21	0.22%	89	0.75%	117	0.473%
Cape hake	Merlucciidae	Demersal	14	0.47%	27	0.28%	35	0.29%	76	0.307%
Elf	Pomatomidae	Pelagic	6	0.20%	23	0.24%	38	0.32%	67	0.271%
Sole spp.	Soleidae	Demersal	37	1.25%	21	0.22%	5	0.04%	63	0.255%
Gaper	Champsodontidae	Demersal	6	0.20%	13	0.13%	39	0.33%	58	0.234%
Klipfish spp.	Clinidae	Demersal	11	0.37%	14	0.14%	33	0.28%	58	0.234%
Agile klipfish	Clinidae	Demersal	1	0.03%	0	0.00%	0	0.00%	1	0.004%
Bearded klipfish	Clinidae	Demersal	10	0.34%	1	0.01%	2	0.02%	13	0.053%
Bull klipfish	Clinidae	Demersal	1	0.03%	2	0.02%	0	0.00%	3	0.012%
Cancelloxus klipfish	Clinidae	Demersal	4	0.14%	0	0.00%	1	0.01%	5	0.020%
Grass klipfish	Clinidae	Demersal	0	0.00%	0	0.00%	1	0.01%	1	0.004%
Snaky klipfish	Clinidae	Demersal	0	0.00%	3	0.03%	4	0.03%	7	0.028%
Soldierfish spp.	Holocentridae	Demersal	0	0.00%	2	0.02%	45	0.38%	47	0.190%
Bluebottle fish	Nomeidae	Pelagic*	3	0.10%	33	0.34%	9	0.08%	45	0.182%
Cape gurnard	Triglidae	Demersal	13	0.44%	5	0.05%	25	0.21%	43	0.174%
Blenny spp.	Blenniidae	Demersal	2	0.07%	2	0.02%	34	0.29%	38	0.154%
Lantern fish	Myctophidae	Pelagic	1	0.03%	1	0.01%	21	0.18%	23	0.093%
Goby spp.	Gobiidae	Demersal	7	0.24%	0	0.00%	2	0.02%	9	0.036%
Pelagic goby	Gobiidae	Demersal	9	0.30%	0	0.00%	14	0.12%	23	0.093%
Chub mackerel	Scombridae	Pelagic	0	0.00%	4	0.04%	18	0.15%	22	0.089%
Shyshark spp.	Scyliorhinidae	Demersal	3	0.10%	2	0.02%	11	0.09%	16	0.065%
Grenadier spp.	Macrouridae	Demersal	0	0.00%	0	0.00%	12	0.10%	12	0.049%
Southern conger	Congridae	Demersal	3	0.10%	2	0.02%	5	0.04%	11	0.044%
Southern conger larvae		Pelagic	0	0.00%	0	0.00%	1	0.01%	1	0.004%
Dolphinfish	Coryphaenidae	Pelagic	0	0.00%	10	0.10%	0	0.00%	10	0.040%
Sebastes sp.		Demersal	1	0.03%	1	0.01%	4	0.03%	6	0.024%
Rocksucker	Gobiesocidae	Demersal	1	0.03%	2	0.02%	3	0.03%	6	0.024%
Cutlassfish (Silver scabbardfish)	Trichiuridae	Bentho-pelagic	1	0.03%	1	0.01%	3	0.03%	5	0.020%

Cutlassfish (Largehead hairtail)	Trichiuridae	Bentho-pelagic	0	0.00%	1	0.01%	3	0.03%	4	0.016%
Pufferfish spp.	Tetraodontidae	Demersal	0	0.00%	2	0.02%	3	0.03%	5	0.020%
Redfingers	Cheilodactylidae	Demersal	2	0.07%	2	0.02%	0	0.00%	4	0.016%
Snake eel	Ophichthidae	Demersal	0	0.00%	0	0.00%	3	0.03%	4	0.016%
Snake eel larvae		Pelagic	0	0.00%	1	0.01%	0	0.00%	1	0.004%
Codlet	Bregmacerotidae	Pelagic	1	0.03%	0	0.00%	3	0.03%	4	0.016%
Kingklip	Ophidiidae	Demersal	1	0.03%	1	0.01%	1	0.01%	3	0.012%
Carpenter seabream	Sparidae	Demersal	0	0.00%	0	0.00%	2	0.02%	2	0.008%
Horsefish sp.	Congiopodidae	Demersal	0	0.00%	1	0.01%	1	0.01%	2	0.008%
Short alfonsino	Berycidae	Bentho-pelagic	2	0.07%	0	0.00%	0	0.00%	2	0.008%
Brotulid sp.	Ophidiidae	Demersal	0	0.00%	1	0.01%	0	0.00%	1	0.004%
Greater pipefish	Syngnathidae	Bentho-pelagic	0	0.00%	1	0.01%	0	0.00%	1	0.004%
Pilot fish	Carangidae	Pelagic	0	0.00%	0	0.00%	1	0.01%	1	0.004%
Shadow driftfish	Nomeidae	Bentho-pelagic	1	0.03%	0	0.00%	0	0.00%	1	0.004%
Slender snipefish	Centriscidae	Pelagic	1	0.03%	0	0.00%	0	0.00%	1	0.004%
Spotted greeneye	Chlorophthalmidae	Demersal	0	0.00%	1	0.01%	0	0.00%	1	0.004%
Streepie	Sparidae	Demersal	0	0.00%	1	0.01%	0	0.00%	1	0.004%
Toadfish sp.	Batrachoididae	Demersal	0	0.00%	0	0.00%	1	0.01%	1	0.004%
Trumpetfish sp.	Aulostomidae	Demersal	1	0.03%	0	0.00%	0	0.00%	1	0.004%
Unidentified larval fish			12	0.41%	10	0.10%	94	0.79%	116	0.469%
Unidentified fish			5	0.17%	6	0.06%	36	0.30%	47	0.190%
Fish spp (Total)			***2918***	98.78%	***9559***	98.16%	***11171***	93.76%	23777	96.127%
Cape hope squid	Loliginidae	Pelagic	12	0.37%	31	0.32%	11	0.09%	54	0.214%
Cuttlefish	Sepiidae	Pelagic	12	0.41%	36	0.37%	37	0.31%	85	0.344%
Octopus	Octopodidae	Bentho-pelagic	6	0.20%	1	0.01%	4	0.03%	11	0.044%
Cephalopod spp (Total)			***30***	1.02%	***77***	0.79%	***398***	3.34%	505	2.042%
Mantis shrimp	Squillidae	Demersal	3	0.10%	13	0.13%	228	1.91%	244	0.986%
Crab spp.	Brachyura **	Bentho-pelagic	0	0.00%	0	0.00%	3	0.03%	3	0.012%
Rock lobster	Palinuridae	Demersal	0	0.00%	0	0.00%	3	0.03%	3	0.012%
Crustaceans spp (Total)			***3***	0.10%	***13***	0.13%	***234***	1.96%	250	1.007%
Two spotted cricket	Gryllidae	Terrestrial	3	0.10%	85	0.87%	103	0.86%	191	0.772%
African mole cricket	Gryllotalpidae	Terrestrial	0	0.00%	1	0.01%	1	0.01%	2	0.008%
Lepidoptera sp.	Sphingidae	Terrestrial	0	0.00%	0	0.00%	3	0.03%	3	0.012%
Coleoptera sp.	Coleoptera *	Terrestrial	0	0.00%	0	0.00%	1	0.01%	1	0.004%
Insect spp (Total)			***3***	0.10%	***89***	0.91%	***112***	0.94%	204	0.825%
Totals			*2954*		*9738*		*11914*		***24736***	

* Infraorder, ** Order

Inter- and intra-annual variation in prey composition

Prey proportions differed significantly between the three years (χ^2 = 2597.8, d.f. = 14, p < 0.001). In 2013, anchovy constituted 83% of the diet by number, compared to 67% in 2014 and 62% in 2015. Redeye round-herring increased from 3% in 2013 to 7% in 2014 and 15% in 2015, while sardine showed little variation (2013 - 2015: 2% – 0.7% – 4%). Other type of prey increased across the three years (2013 - 2015: 1% – 2% – 6%), and fish larvae were relatively abundant in 2015 (0.8%) (Table 3.1).

There was a significant difference in the composition of prey returned to the colony between incubation and the provisioning periods (χ^2 = 998.55, d.f. = 6, p < 0.001, Figures 3.2a,b). In all years, the proportion of anchovy in the diet peaked during the early and/or mid-provisioning weeks at both colonies (except at the mixed colony in 2014; Figures 3.2a,b). During late provisioning, larger fish (mainly redeye round-herring and Atlantic saury) occurred more frequently than in the first two weeks of chick-provisioning, with particular abundance of Atlantic saury in 2014, in both colonies (single-species colony 32%; mixed colony 29%). In all three seasons other type of prey were rare during incubation, and were most abundant during late provisioning (Figures 3.2a,b). These patterns are evidenced by the non-metric multidimensional scaling plots (NMDS) of weekly numerical abundance for both colonies and all years combined (Figure 3.3). NMDS illustrates that during incubation, diet was dominated by anchovy contributions and, to a lesser extent, by horse mackerel and redeye round-herring. During early provisioning, anchovy was favoured above all prey, and during mid-provisioning, diet centred mostly on anchovy and sardine. Diet was more variable during late provisioning, and included large fish species such as Atlantic saury, redeye round-herring, sardine and other type of prey more abundant in this period (Figure 3.3).

At the single-species colony, the occurrence of fish larvae was mainly recorded during early provisioning and in minor proportions during mid- provisioning, whereas at the mixed colony larvae were recorded in similar proportions at both the early and late provisioning in 2014, and larger proportions were recorded in 2015 although presence of larvae were already observed from the last week of the incubation period (Figures 3.4 a,b). The occurrence of adults carrying multi-prey loads was a notable observation. Of the total prey items returned by an adult, 792 prey items (0.03%) were part of a multi-prey load. Most of these loads consisted of two anchovies (n = 460; 58% of all multi-prey loads) with a maximum record of 11 anchovies carried in one trip (Figure B.3). In general, multi-prey loads were scarce during incubation, but became more apparent during late provisioning in both colonies, although in 2014 occurrences of multi-prey loads were predominantly recorded during the first stages of provisioning at both colonies (Figure 3.5).

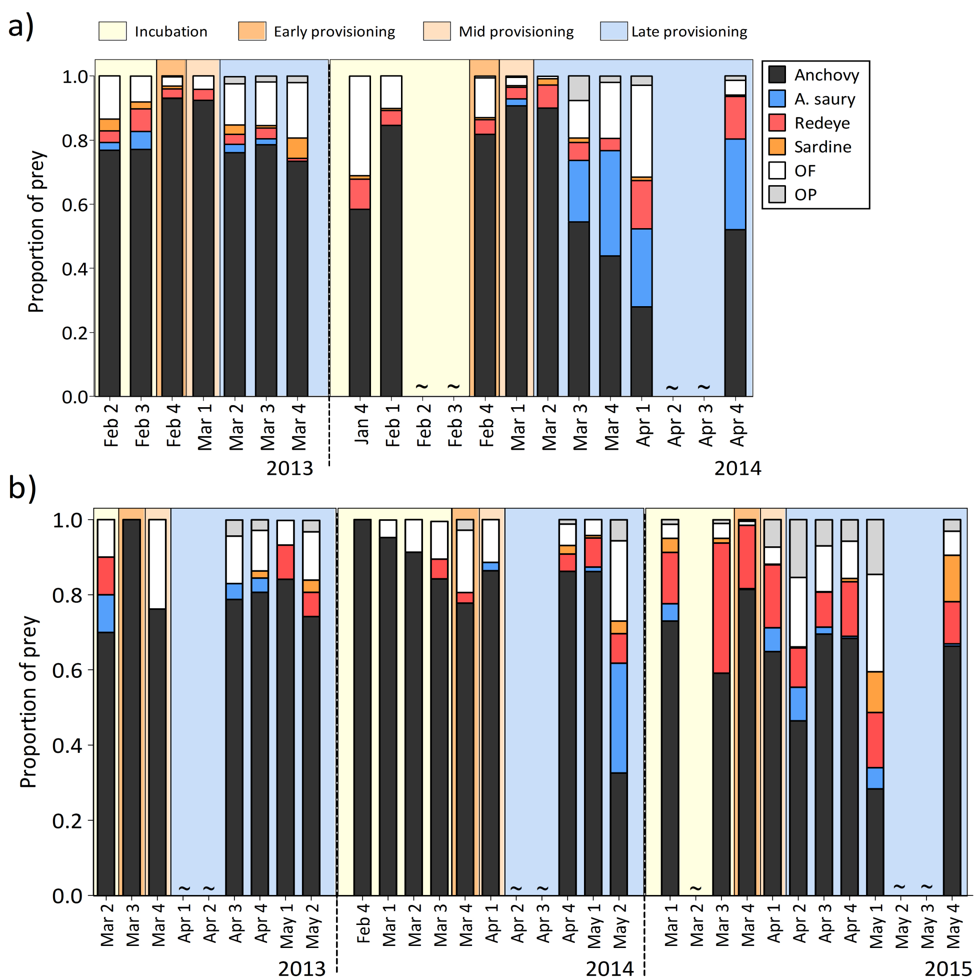


Figure 3.2: Fine-scale weekly variation in greater crested terns' diet by mean percent number (% N) of the 4 major fish prey (anchovy, Atlantic saury, redeye round-herring, sardine), other type of fish (OF) and other prey (OP). Sampling locations were at the single-species colony (a) and mixed colony (b) on Robben Island across breeding seasons and stages. Breeding phases are illustrated as (i) incubation period, (ii) early, (iii) mid and (iv) late provisioning.

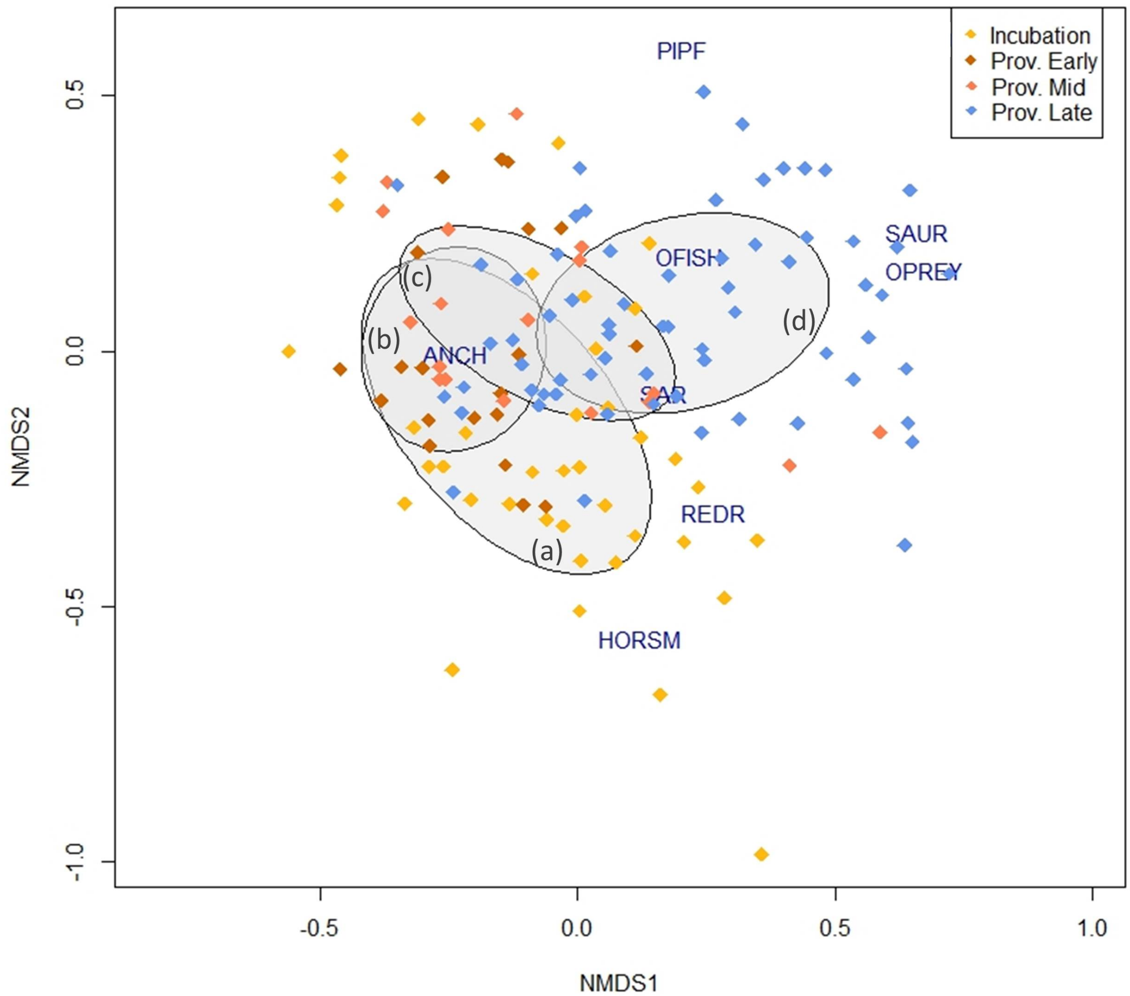
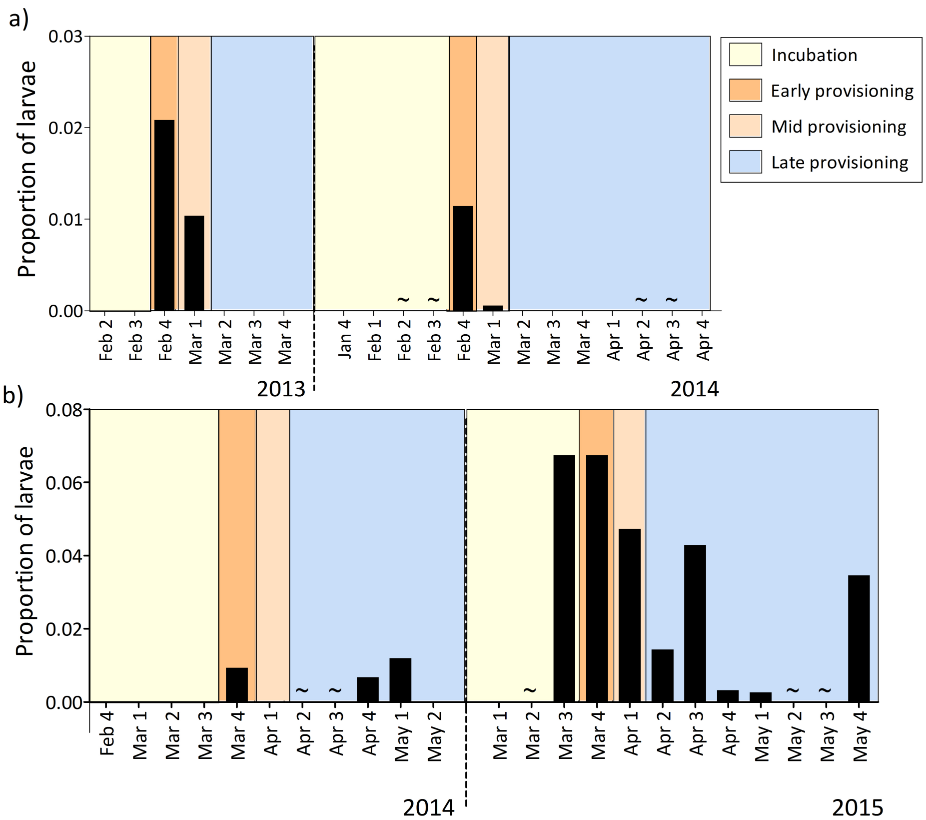
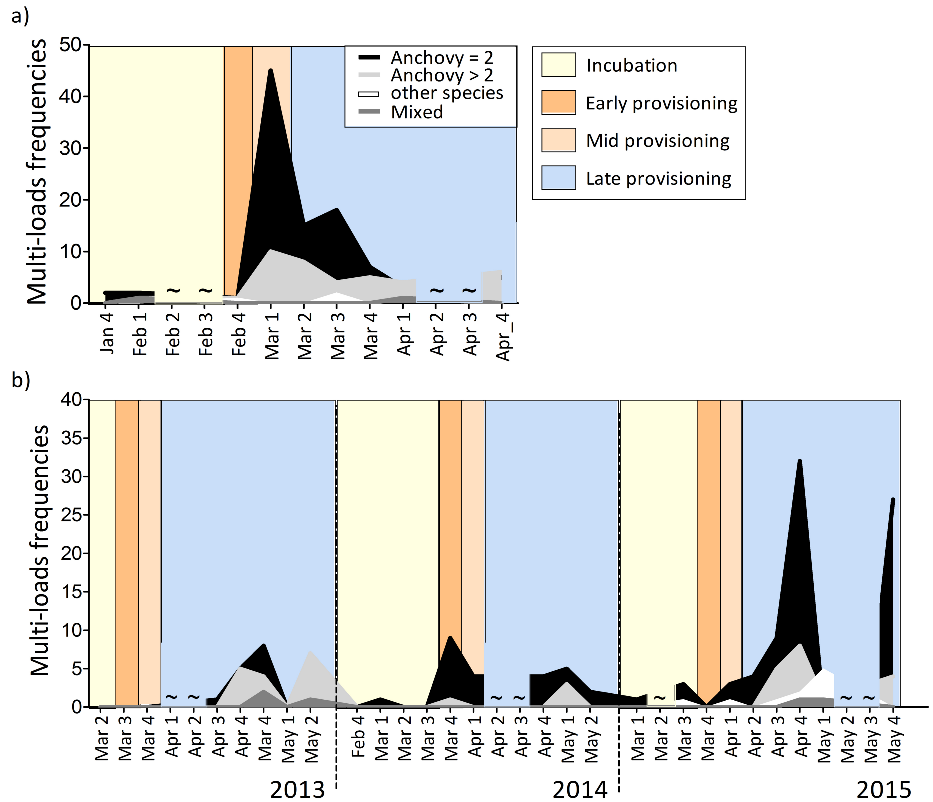


Figure 3.3: Non-metric multidimensional scaling plots (NMDS) of weekly mean percent number showing differences in prey composition by breeding stages of greater crested tern diet across three breeding seasons (2013-2015) on both colonies on Robben Island. Sample points represent each sampled week divided by the stage of the colony (see legend). Position of points is related to the relative weekly contribution of each of the eight major prey groups. Grey shaded ellipses were used to highlight the centre of gravity of breeding phases: a) Incubation; b) Early provisioning; c) Mid-provisioning; d) Late provisioning. (Prey species: ANCH = Anchovy; REDR = Redeye round-herring; SAUR = Atlantic saury; HORSM = Horse mackerel; SAR = Sardine; PIPF = Pipefish; OFISH = other fish; OPREY = other prey).



* no data available from 2013 at mixed colony

Figure 3.4: Dietary contribution in terms of mean percent number (%N) of larvae in (a) single-species colony (2013-2014) and (b) mixed colony (2014-2015) in Robben Island across breeding seasons and stages. Breeding phases are illustrated as (i) incubation period, (ii) early, (iii) mid- and (iv) late provisioning.



* no data available from 2013 at single-species colony

Figure 3.5: Numbers of multi-prey loads at the (a) single-species colony and (b) mixed colony in Robben Island across breeding seasons and stages. Loads are classified as: Anchovy double-prey loads, anchovy multi-prey loads, other species multi-prey loads, mixed-species multi-prey loads. Breeding phases are illustrated as (i) incubation period, (ii) early, (iii) mid- and (iv) late provisioning.

Prey composition in relation to environmental factors

Overall, 87% of photo-sampling was conducted on clear days and 13% in foggy conditions (when landmark located 500m away was not visible). During foggy days, pelagic fish (mainly anchovy) were returned in lower proportions, while demersal fish and other prey occurred more frequently (χ^2 = 962, d.f. = 7, p < 0.001; Figures 3.6 and B.4). The proportion of anchovy was significantly less abundant early in the morning compared to the rest of the day (ANOVA: $F_{(6,264)}$= 4.5 p < 0.001; Table 3.2). The proportion of redeye round-herring was high during the first hour after twilight (ca 15%) and again at the end of the day (ANOVA: $F_{(6,229)}$ = 2.3 p = 0.03; Figure 3.7). Other type of prey were also considerably more abundant during the early morning (ANOVA: $F_{(6,120)}$ = 7.6 p < 0.001; Table 3.2), and there was no clear pattern in the proportions of other fish across the day. These patterns were found in all months investigated for all four prey groups with the exception of anchovy, which was higher early in the day during February and March, compared to April (ANOVA: $F_{(3,267)}$= 5.35 p = 0.001; February–April Tukey test, p = 0.002, March–April. Tukey test, p = 0.006).

Tests of covariance using variance inflation factors between all continuous variables used in the GAM were all < 3, providing justification for including all these variables in the model. There was a positive influence of wind speeds > 5 m s^{-1} on the proportion of anchovy returned to the colony (Figure 3.8a). The influence of tide, although significant, was very weak with slightly higher probabilities of anchovy returned during the first peak of low tide (-5 hrs) and the subsequent neap tide (3 hrs) (Figure 3.8b). The proportion of anchovy returned to the colony generally decreased over the course of the breeding season, with a first peak of anchovy occurring during week 6 (1st week of March) and a second peak occurring in week 12 (3rd week of April) (Figure 3.8c).Foggy conditions had a negative influence on the proportion of anchovy returned (Table 3.3). The model showed a significant inter-annual effect; more anchovy were returned to the colony in 2013, compared to 2014 and 2015 (Table 3.3). There was a strong inter-colony difference with a lower probability of anchovy being returned to the single-species colony when compared to the mixed colony. Finally, the model confirmed previous results with significantly more anchovy being returned during early provisioning compared to incubation and late provisioning, while no differences were found when comparing mid- with early provisioning (Table 3.3).

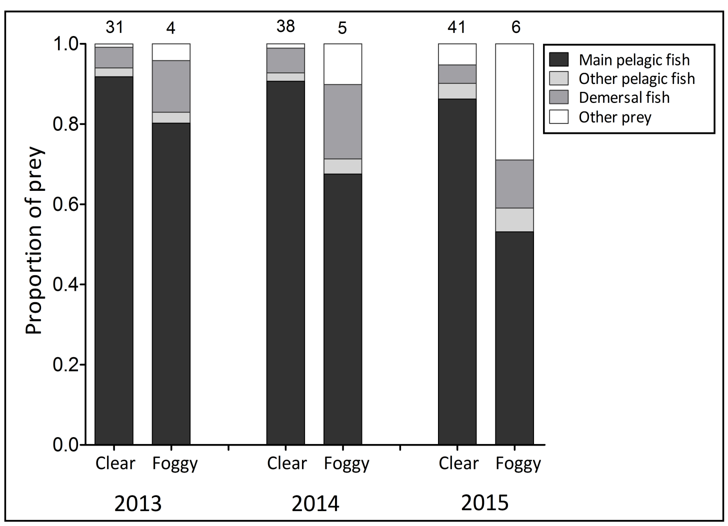


Figure 3.6: Comparison of mean percent number of four prey groups (main pelagic fish, other pelagic fish, other demersal fish and other prey) returned to the colony by greater crested terns on clear and foggy days recorded in Robben Island between 2013-2015 breeding seasons. Numbers of sampling days are shown above each bar.

Table 3.2: Tukey test p-values from comparisons of proportions of anchovy and other prey returned to the colony by greater crested terns according to time periods from the beginning of civil twilight (e.g. 1 - 3 = first hour compared to the third hour after the beginning nautical twilight).

Time periods	**1 - 3**	**1 - 5**	**1 - 7**	**1 - 9**	**1 - 11**	**1 - 13**	**3 - 5**	**3 - 7**	**3 - 9**	**3 - 11**	**3 - 13**
Anchovy	0.02	**<0.01**	0.18	**0.02**	**<0.01**	**0.03**	**0.03**	0.15	0.99	0.96	0.99
Other prey	**<0.01**	**<0.01**	**<0.01**	**<0.01**	**<0.01**	0.16	0.27	**0.01**	0.51	0.83	0.99
Time periods	**5 - 7**	**5 - 9**	**5 - 11**	**5 - 13**	**7 - 9**	**7 - 11**	**7 - 13**	**9 - 11**	**9 - 13**	**11 - 13**	
Anchovy	0.51	0.99	0.73	0.60	0.93	0.99	0.99	0.99	0.97	0.99	
Other prey	0.95	0.99	0.93	0.36	0.95	0.32	**0.04**	0.97	0.54	0.84	

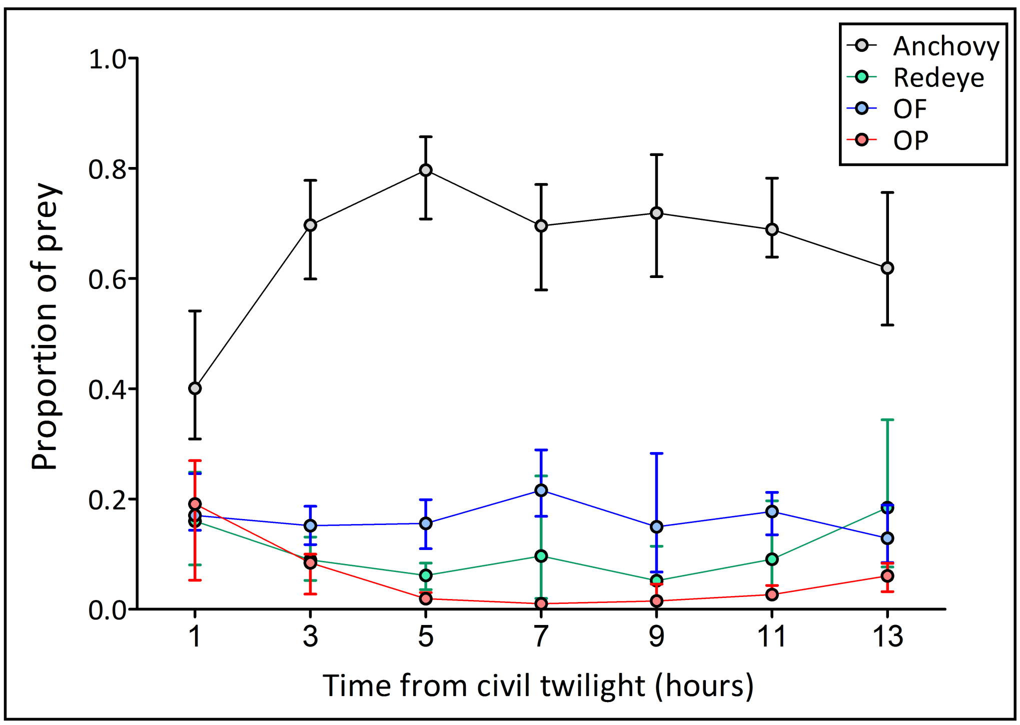


Figure 3.7: Diurnal patterns in mean (± SE) percent number of prey (anchovy; redeye round-herring; OF = other fish; OP = other prey) returned to the colony by greater crested terns in Robben Island between 2013-2015.

Table 3.3: Parametric coefficients of fixed effects used in the Generalised additive models (GAM) fitted to assess the influence of non-linear variables (wind speed, tide and week) on the presence of anchovy in the diet of greater crested terns. B. stage refers to breeding stage.

Model term	**Estimates**	**Std. Error**	**P value**
Intercept	3.01	0.09570	< 0.001
Weather (foggy)	-0.90	0.06644	< 0.001
Year (2014)	-0.70	0.06305	< 0.001
Year (2015)	-1.71	0.08112	< 0.001
Colony (single-species)	-1.61	0.08549	< 0.001
B. stage (incubation)	-1.44	0.10158	< 0.001
B. stage (late)	-0.39	0.09982	< 0.001
B. stage (mid)	-0.06	0.07913	0.41

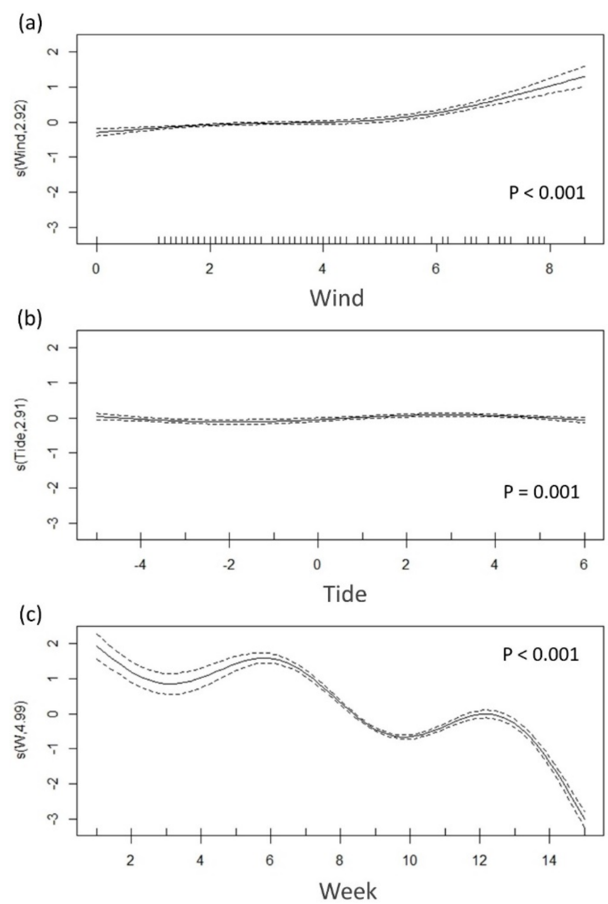


Figure 3.8: (GAM) partial predictions for the probability of returning an anchovy in the greater crested terns' diet according to (a) wind speed, (b) tide and (c) week from beginning of breeding. Tidal stage (b) is defined as hours before and after high tide (high tide = 0). Week (c) indicate the sequence of weeks commencing from the last week of January (1) until the 2nd week of May (15). Data from 2013- 2015 breeding season in Robben Island.

Relationship with anchovy hydro-acoustic survey

There are only a few dietary studies for greater crested terns in southern Africa; comparisons between anchovy hydro-acoustic biomass estimates and the proportion of anchovy in tern diet were possible only for 1985–86; 1991–1993 and 2013–2015. Linear logistic regression models showed no significant relationships between the proportions of anchovy in the tern's diet and biomass of anchovy surveyed (spawner or recruits) near the colony (either Cape Columbine to Cape Point, or Cape Columbine to Cape Agulhas) or in the total area between Hondeklip and Port Alfred (Figure 3.12, all p-values > 0.05).

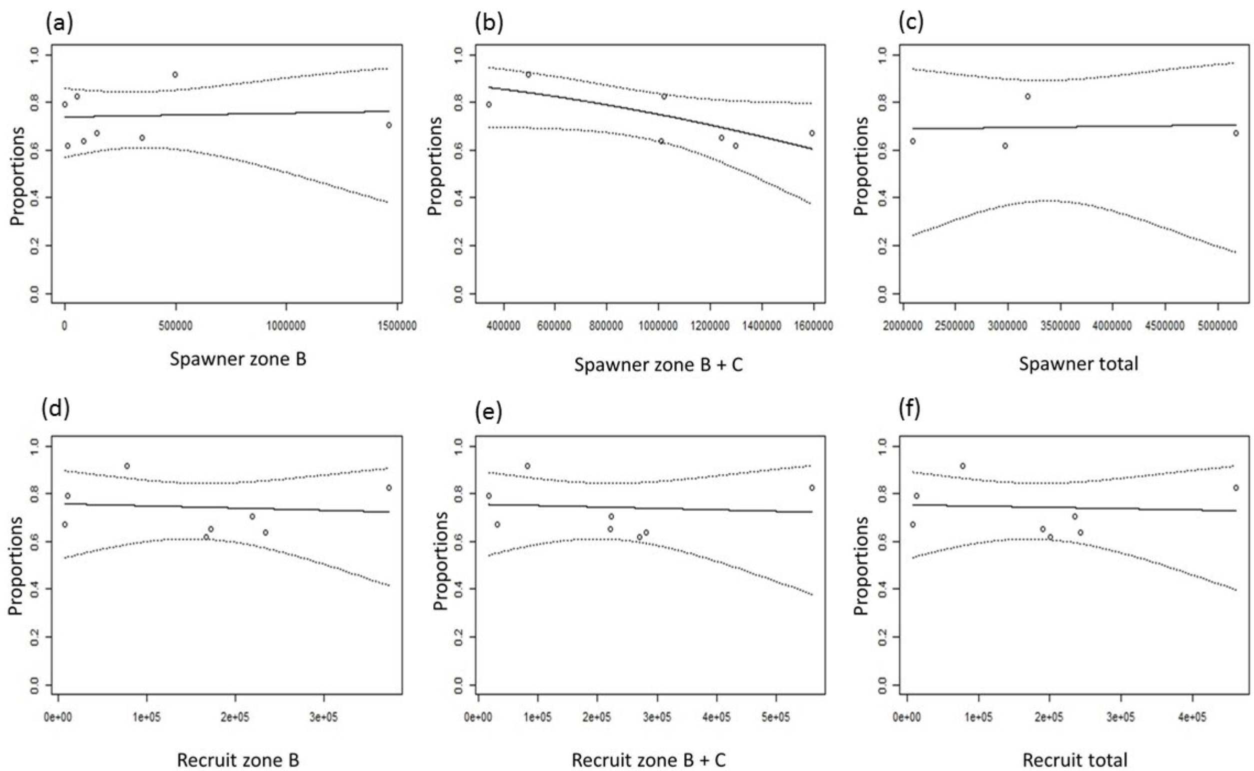


Figure 3.12: Multi-plot logistic regressions (including 95% confidence intervals), showing the relationship between anchovy in the greater crested terns' diet (proportion by number) and (a) Anchovy spawner biomass in stratum B; (b) Anchovy spawner biomass in strata B + C; (c) Anchovy spawner biomass all strata (total; from A to D); (d) Anchovy recruitment biomass in stratum B; (e) Anchovy recruitment biomass in strata B + C; (f) Anchovy recruitment biomass all strata (total; from A to D).

Anchovy size comparisons between tern prey and fisheries

Anchovy standard length ranged from 32 mm to 125 mm with an overall mean of 83.9 ± 16.8 mm in all years and seasons. Inter-annual differences in anchovy SL (n = 886) were significant (ANOVA: $F_{(2,883)}$= 93.69, $p < 0.001$) with larger anchovies recorded in 2015 (mean ± SD: 92 ± 16 mm) followed by 2013 (84 ± 16 mm) and 2014 (76 ± 15 mm) (Tukey test $p < 0.001$; Figure 3.9). Between breeding stages, the anchovy brought back during incubation at both colonies was significantly larger (85 ± 13 mm) (Table 3.4) than those recorded during early and mid-provisioning (early: 77 ± 20 mm; mid: 74 ± 15 mm), but similar in size to those delivered when provisioning older chicks (late provisioning, 85 ± 14 mm; Table 3.4). Similar patterns were apparent in both colonies, but only at the mixed colony were differences significant (Table 3.4, Figures 3.10a,b).

Sizes of anchovy captured by the purse-seine fleet (median SL 95 mm; range 40 – 135 mm) during the tern breeding season, within 40 km of Robben Island, appeared similar to those fish returned to the colonies by greater crested terns (median SL 84 mm; range 32 – 125 mm; Figure 3.11). However, overall significant differences were seen in most of the months that were compared (Table 3.5 and Figure 3.11).

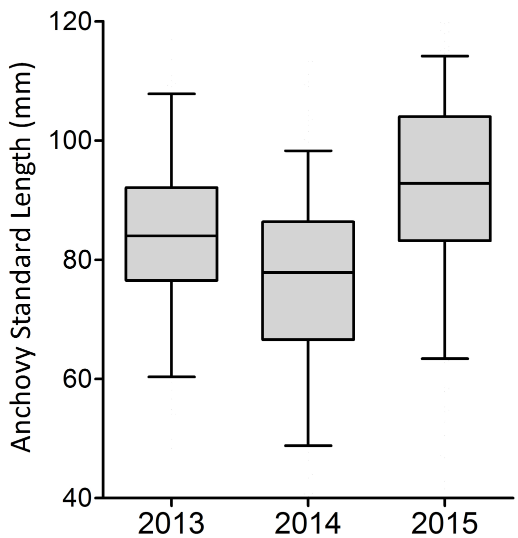


Figure 3.9: Seasonal comparison of mean (5–95 percentile) anchovy standard length from photo-sample recorded in the diet of greater crested terns across three breeding seasons (2013-2015) in Robben Island.

Table 3.4: Tukey test p-value from comparisons of anchovy standard length estimated from photo-samples compared across breeding stages and colonies in all years in Robben Island. Breeding phases are referred as (i) incubation period, (ii) early, (iii) mid- and (iv) late provisioning.

Breeding stage	Comparison all years				Comparison between colonies	
	Diff	Lowr	Upr	P adj	Single-species	Mixed
Incubation – Early	9.21	4.23	14.18	**< 0.001**	0.36	**< 0.001**
Incubation – Mid	-10.22	-14.59	-5.85	**< 0.001**	0.50	**< 0.001**
Incubation – Late	0.45	-3.48	4.40	0.99	0.90	0.57
Early – Mid	-1.01	-5.48	3.46	0.93	0.90	0.90
Early – Late	9.67	5.60	13.73	**< 0.001**	0.08	**< 0.001**
Mid – Late	-10.68	-13.97	-7.39	**< 0.001**	**< 0.001**	**< 0.001**

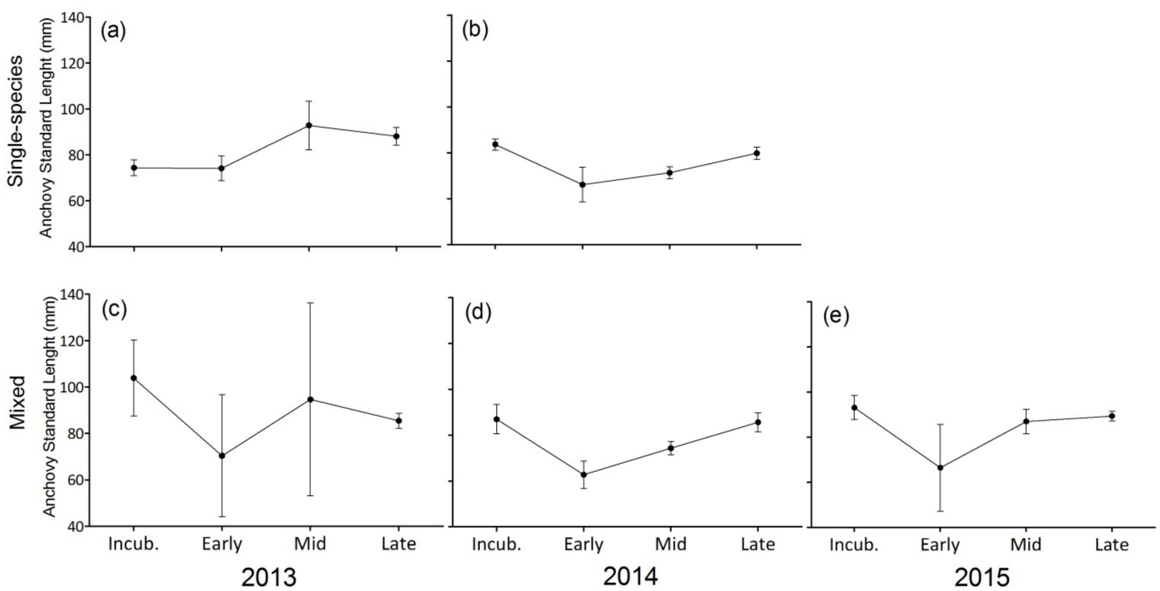
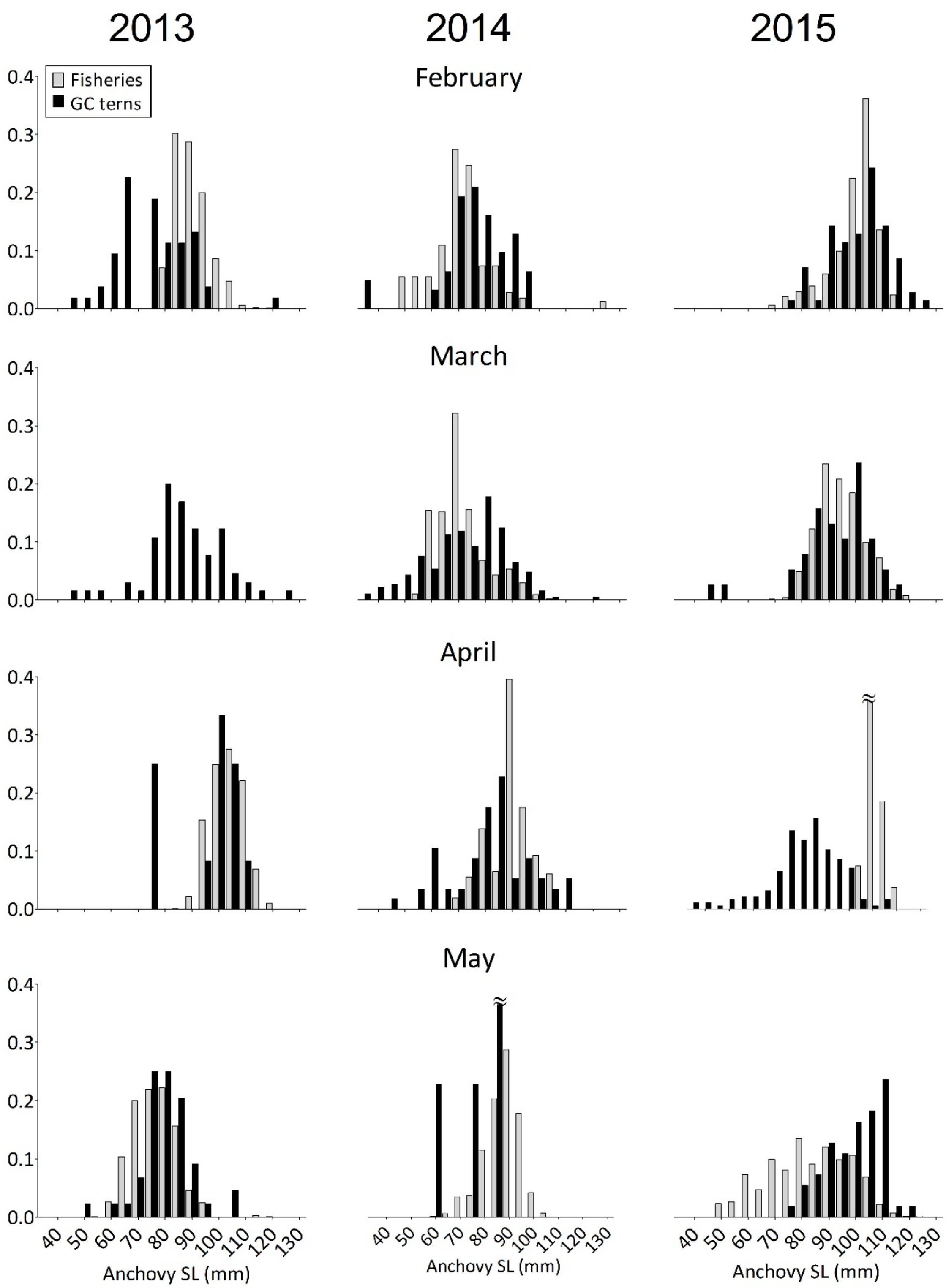


Figure 3.10: Anchovy standard length in the diet of greater crested tern across four breeding stages. Breeding phases are referred as (i) incubation period, (ii) early, (iii) mid- and (iv) late provisioning. Data from the single-species colony in (a) 2013 and (b) in 2014 and at the mixed colony (c) in 2013, (d) in 2014 and (e) in 2015 across breeding stages in Robben Island.



* no data from fisheries in March 2013

Figure 3.11: Comparison of frequency of anchovy standard length classes captured by greater crested terns and purse-seiners in a radius of 40 km around Robben Island between February and May in 2013-15 breeding season.

Table 3.5: Chi square for proportion (prop. test) comparison between fisheries and greater crested terns' anchovy standard length classes by months in all years.

	2013			2014			2015		
Month	χ^2	*d.f.*	*P*	χ^2	*d.f.*	*P*	χ^2	*d.f.*	*P*
February	85.96	3	**<0.001**	11.558	3	**0.009**	4.96	2	0.084
March	-	-	-	25.414	3	**<0.001**	9.55	3	**0.023**
April	37.37	2	**<0.001**	27.376	3	**<0.001**	162.30	3	**<0.001**
May	7.53	3	0.057	17.953	1	**<0.001**	52.59	3	**<0.001**

* no data from fisheries in March 2013

Discussion

This study gives a detailed description of the prey exploited by greater crested terns in the largest breeding site in southern Africa during three successive years. As with previous studies in the Western Cape, my investigations found that greater crested terns mainly target small schooling Clupeiformes, especially anchovy and, to a lesser extent, redeye round-herring, two of the most common mid-trophic fish species in the Benguela upwelling system (Cury et al. 2000, Crawford *et al.* 2014). Despite the dominance of Clupeiformes in their diet, greater crested terns demonstrated considerable foraging plasticity with the ability to capture demersal fish as well as cephalopods and arthropods. Previous knowledge of greater crested tern diet in southern Africa came from the collection of chick regurgitations and observations of food provision of chicks (Walter *et al.* 1978a, Crawford & Dyer 1995); this is the first diet study since 1993, and gives novel information on prey composition during incubation.

A study of chick regurgitations collected from 1977 to 1986 sampled 1,311 prey items, of which 86% were fish, mostly Clupeiformes (Walter *et al.* 1987a). Anchovy was scarce in the diet between 1977 and 1979, but then increased, reaching about 90% in 1986 (Figure 3.13). In this decade of investigation, 25 prey species were recorded, including two species of cephalopods (*Sepia australis, Loligo reynaudi*), two crustaceans (mantis shrimp *Pterygosquilla armata* and mud prawn *Upogebia africana*) and one insect (*Gryllus bimaculatus*). The only subsequent diet study conducted between 1991 and 1993, (Crawford & Dyer 1995) found that anchovy constituted more than 60% of the prey by mass, with Atlantic saury, sardine and mantis shrimp also important food items. This diet composition was similar to that found in my study.

Factors affecting the temporal variations in greater crested tern diet

A major strength of my study comes from monitoring tern diet throughout the breeding season, which showed large variation in the relative abundance of prey types and sizes of anchovy returned to the nest in both colonies. Interestingly, the proportions of the main prey by breeding stages were similar at the two colonies, despite the delayed onset of breeding at the mixed colony, which is often an indicator of inexperienced individuals that attempt breeding later than more experienced birds (e.g. Perdeck & Cavé 1992). In particular, the proportions of the most abundant prey varied significantly between incubation and chick provisioning, supporting the ontogenetic differences in food requirements between adults and chicks reported for greater crested terns in Australia (McLeay *et al.* 2009a). Such ontogenetic differences also have been documented in other seabird species (e.g. Votier *et al.* 2003, Barrett *et al.* 2007, Cherel *et al.* 2008, Fijn *et al.* 2012). In kittiwakes *Rissa tridactyla*, Bugge *et al.* (2011) found that the frequency of occurrence of energy-rich prey was significantly greater in chick diets (77%), than in adults (26%). In this study, the preponderance of small anchovies and fish larvae delivered during early chick provisioning was presumably related to the limited gut capacity of hatchlings, still providing the benefit of an high calorific value prey (Batchelor & Ross 1984). The proportions and sizes of anchovy returned during mid- provisioning was similar to that of early provisioning, but there was a slight shift towards sardine, another high-quality prey. Australian anchovy *Engraulis australis* and sardine were also the most abundant prey of greater crested terns breeding in Australia (McLeay *et al.* 2009a). Chick regurgitations confirmed that fish were generally smaller during early provisioning, compared to when chicks were larger and more mobile.

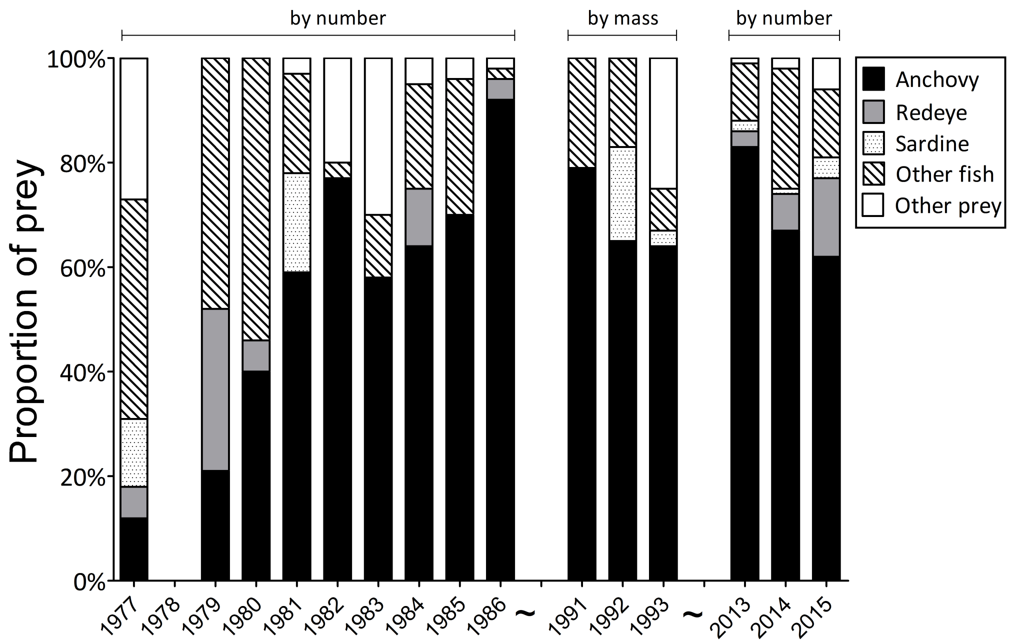


Figure 3.13: Proportions of main prey in the greater crested tern diet from previous studies (by mean percent number 1977-86; Walter *et al.* 1987a) (by mass 1991-93; Crawford & Dyer 1995) and this study (by mean percent number 2013-2015) in Western Cape (South Africa). Historical diet is broken up in five major prey groups (anchovy, redeye round-herring, sardine, other fish, other prey). Note absence of data from 1987-1990 and 1994-2012

A broader variety of species including larger fish species, such as redeye round-herring and Atlantic saury occurred frequently in my investigations during late provisioning. At this stage parents delivered significantly larger anchovies (mean SL = 85 ± 14 mm). This apparent specialization in prey fed to chicks was detected in all years; similar strategies have been reported for other seabird species (Golet *et al.* 2000, Bugge *et al.* 2011), including terns (Ramos 1998, Stienen *et al.* 2000). Delivering larger prey to large chicks reflects the increased energetic demands for these chicks, when parents have to maximise the efficiency of each foraging trip, bringing back as much food as possible as predicted by central place foraging models for single prey loaders (Orians & Pearson 1979, Shealer 1998, Davoren & Burger 1999). This period also saw the highest frequency of multi-prey loads (as reported by Duffy 1987). Different energy requirements of chicks may influence the type of prey returned to the colony during the course of the day (Dunn 1973). Dunn (1973) proposed that the peak feeding activity at dawn may result from lack of food during the night and hunger states of both adults and chicks in the early morning. This notion is supported by the great diversity of prey types returned to the colony early in the morning and the peak abundance of anchovy around mid-morning. Adults presumably perform a short trip to capture what is available close to the colony to meet their chicks' immediate food needs, before heading out for a more profitable trip (Gaglio *et al.* 2015b)

Previous studies on the Australian population of greater crested terns showed that this species is vulnerable to the depletion of its favoured prey (McLeay *et al.* 2009b). McLeay (*et al.* 2009b) reported that disease-related mortality in adult sardine, which reduced sardine biomass by ca 70% over three seasons, slowed chick growth rates in females and caused significantly lower rates of recruitment to the breeding colony (McLeay *et al.* 2009b). Adult prey choice is ultimately influenced by the spatio-temporal availability of prey in the system (e.g. Gaston & Elliot 2014) and the extent to which this may influence greater crested terns' diet, should not be discounted. Most anchovy delivered by greater crested terns were recruits (SL < 100 mm), which were recorded during all breeding stages (Figures 3.9 and 3.10). Based on the known movements of anchovy recruits through this system (Hutchings *et al.* 2014), young-of-the-year anchovy would only be expected to reach Robben Island after May, by which time most tern chicks have fledged (Hutchings *et al.* 1998, van der Lingen *et al.* 2003, Hutchings *et al.* 2014). My findings contradict this general trend, with anchovy (mostly recruits) decreasing in abundance as the breeding season progresses from February to May. During late provisioning, parents may buffer scarcity of anchovy by targeting alternative prey (e.g. Atlantic saury), which presumably is found at more distant feeding grounds, as parents generally perform longer foraging trips during this period (Chapter 4).

Among seasonally breeding species, breeding is often timed to coincide with the peak availability of food (Lack 1968). This timing may be related to the weeks leading up to the onset of breeding, when adult body condition can play a significant role in mediating breeding success (Drent & Daan 1980; Sorensen *et al.* 2009). The onset of breeding may also be timed to pre-empt subsequent breeding stages where food supplies are more critical for chick or fledgling survival (Passuni *et al.* 2016). Unfortunately, few studies have investigated the temporal abundance of anchovy around Robben Island in the periods leading up to and including the terns' breeding season (Campbell 2016). An exception was the icthyofaunal study by van der Lingen and Huggett (2003), which included monthly quantification of anchovy and sardine eggs and larvae ca 30km south of Robben Island between 1995 and 2001. This study revealed a clear peak in the abundance of anchovy larvae during January and February, which may influence the timing of greater crested terns' breeding (i.e. the onset of breeding or for the subsequent early provisioning stage).

The prey choice of single prey loaders have been elsewhere been shown to be influenced by physical conditions while foraging (Paiva *et al.* 2006). For example, strong winds increase prey catch rates in sandwich *Thalasseus sandvicensis*, common *Sterna hirundo* and Damara terns *Sternula balaenarum* (Dunn 1973, Braby 2011). My study revealed an increased proportion of anchovy returned at wind speeds > 5 m s^{-1}. Possible explanations for this observation may include that elevation of zooplankton in the water column may influence the vertical location of anchovy (Taylor 1983, van der Lingen 2002), or increase flight efficiency allowing them to travel further. Alternatively, at high wind speeds there is reduced detection of prey, hence they have to rely on other cues for prey location (e.g. through local enhancement, Thiebault *et al.* 2014). Along the coast of the Western Cape, greater crested terns are likely to frequently encounter Cape cormorants and African penguins, which rely mostly on anchovy (Crawford & Dyer 1995). Therefore, the positive correlation between the proportion of anchovy in the diet and increased wind speeds may be linked to the prey preferences of these species. The low proportion of anchovy returned to the colony on foggy days (Table 3.3, Figure 3.6) concurs with this hypothesis where adults may not only struggle to find prey when it is foggy (particularly early in the morning at low light levels), but are not able to detect other feeding groups. On foggy days, high proportions of demersal fish and other type of prey occurred more frequently, implying for a more opportunistic foraging behaviour (Figure B.4).

Prey diversity and ecology

The photo-sampling technique I utilised, enabled the identification of numerous species, revealing at least 28 new species of fish, 1 cephalopod, 2 crustaceans and 3 species of insects in the terns' diet. A large diversity of prey has also been reported in the diets of greater crested terns in Australia (Chiaradia *et al.* 2002, McLeay *et al.* 2009a), reflecting considerable foraging plasticity. In addition to the typical plunge diving and surface dipping in flight, they can dive from perches (sit-and-wait) (Ryan 2017) and take prey in flight as well as from the ground (Crawford *et al.* 2005, Gaglio *et al.* 2015b). The large number of prey species I recorded reflects high foraging plasticity with potentially strong adaptive significance to cope with temporal or long-term reduced availability of favoured prey.

After anchovy, the second most abundant prey in the tern's diet was redeye round-herring, which is an important prey fish in the southern Benguela system (Roel & Armstrong 1991, Griffiths *et al.* 2004). It was particularly abundant in the terns' diet during mid- to late chick provisioning. The high abundance of redeye round-herring delivered to the colony in the morning suggests that adults catch this fish near the surface at dawn, before schools descend into deeper water (Safina *et al.* 1990, Elliot & Gaston 2015). The occasional presence of redeye round-herring during the day may be linked to the fact that the juveniles of this species are found near the surface in mixed shoals comprising anchovy and juvenile sardine in inshore waters (C. van der Lingen pers. comm.). In addition, other predators such as African penguins, may force this and other mid-water species such as Lantern fish *Lampanyctodes hectorus* to the surface for short periods of time, making them temporarily available for terns (Klages 1992, Ryan *et al.* 2012). Atlantic saury was particularly abundant while adults were provisioning fledglings, similar to observations on Cape gannets in the Benguela or in roseate terns *Sterna dougalli* in the Azores (Green *et al.* 2015, Martins *et al.* 2004). Saury is one of the most cost-effective prey in this system, due to their relatively large size and high energy content (Batchelor & Ross 1984). Interestingly, saury normally have an offshore distribution; however, longitudinal migration of this fish, which brings shoals closer in shore during autumn (Berruti *et al.* 1993), may provide increased availability to terns during the later stages of the breeding season as apparent in my study.

This study was the first to record long-snout pipefish in the diet of greater crested terns diet, which accounted for 3.5% (by number) of the prey recorded. Members of the Syngnathide are captured by terns in other systems (Safina *et al.* 1990, Stienen *et al.* 2000), but the low energy content of this family is considered a poor alternative to small pelagic fish such as anchovy or sardines (Harris *et al.* 2007, 2008). The rigid and bony structure of this fish can even suffocate chicks (Harris *et al.* 2008). In southern Africa, long-snout pipefish is widespread in coastal waters, which is presumably where adults find this species (Branch et al. 2010). Other bottom dwellers species, such as redfingers *Cheilodactylus fasciatus*, rocksukers *Chorisochismus dentex*, blennidae, clinidae or soleidae were also probably captured in coastal habitats including tidal pools. Some of the demersal fish species recorded inhabit the sea surface when juvenile including beaked sandfish *Gonorynchus gonorynchus* and bluebottle fish *Nomeus gronovii* (Branch *et al.* 2010) and are possibly captured by terns at this life stage. Like beaked sandfish, juvenile Cape hake *Merluccius capensis* can occur near the surface during the daytime (Cram & Schülein 1974). Alternatively, small hake may be captured early in the morning as they migrate to the surface at night to feed on fish and crustaceans (Branch *et al.* 2010). Another explanation may imply the interactions with local fisheries as discarded bycatch or because the trawling operations force individuals to the surface (Montevecchi 2002, Grémillet *et al.* 2008). In Australia, greater crested terns scavenge discards from trawlers, which can contribute up to 70% of their diet during the fishing season (Blaber *et al.* 1995). In southern Africa, crested terns rarely scavenge from fishing boats (Ryan & Moloney 1988, Crawford *et al.*

2005); however, those interactions may be the only explanation for the rare occurrence of deep-sea species such as Macrouridae spp. Despite the fact that shrimps are common prey for terns exploiting fishery discards in Australia (Blaber *et al.* 1995), the occasional presence of mantis shrimps in the tern's diet likely results from these crustaceans periodically migrating into surface waters (Walter *et al*. 1987a, Jackson 1988). The occasional presence of large numbers of terrestrial prey (e.g. crickets), suggests that insects may be opportunistically captured from temporary high density areas in the vicinity of the colony (Gaglio *et al.* 2015b).

Coping in an exploited environment

The size of anchovies captured by provisioning parents, compared to those captured by fisheries in the 40 km area, surrounding Robben Islandwere significantly different for most of the months compared. In addition, terns also caught smaller anchovies (including larvae), mostly during early provisioning, and these size classes were significantly different from those targeted by fisheries.

The number of breeding greater crested terns was previously found to correlate with the combined biomass of commercially targeted small pelagic fish (anchovy and sardine; Crawford 2003). In this study, no correlations were found between the proportions of anchovy captured by greater crested terns and the biannual hydro-acoustic surveys. This may due to the large gaps of diet data collected over the last few decades (Figure 3.13) or to the fact that the fish surveys only provide estimates of prey availability over a large area and short temporal scale and hence are not detailed enough to assess fish availability for an inshore forager.

Despite one prey species (anchovy) dominating their breeding diet, greater crested terns are versatile foragers that can effectively take advantage of temporarily abundant prey (Gaglio *et al.* 2015b, Ryan 2017). This foraging plasticity may be an important characteristic in locations where Clupeiformes have become scarce. For example, in the northern Benguela off Namibia terns feed their chicks on juvenile pelagic goby, which is locally abundant, although lower in energetic content (J.-P. Roux pers. comm.). This adaptability may underpin the tern's ability to cope with recent environmental changes in the Benguela upwelling system (Griffiths *et al.* 2005). In such exploited areas, greater crested terns may be important ocean sentinels indicating human-induced alterations in common and rare species (Lescroël *et al.* 2016). The systematic and detailed recording of their prey offers a window into changes in the availability of their main prey and their biology. The non-invasive technique applied in this study is a useful tool to monitor prey that occur near or in the vicinity of breeding colonies, including prey that are not commercially exploited and hence seldom studied.

Conclusions

This is the first study of the diet of a single prey-loading seabird to overcome the inherent biases associated with traditional diet collection, and the method allows for intensive sampling over extended periods with little disturbance (Gaglio *et al.* 2016). The study greatly increased our knowledge of prey caught by the southern African population of greater crested tern during the breeding season, and offers new insights into the relationships between predators and prey in the Benguela upwelling system. The seasonal variation in prey composition and prey size highlights the need for systematic sampling of seabird diet throughout the breeding season. Long-term studies of food composition will contribute to our understanding of how greater crested terns cope with the apparent variation in food availability better than other seabird species breeding in the same marine ecosystem and relying on the same primary food resource.

Appendix B

Table B.1: Time spent (in hours) photo-sampling for each week of the month. Sampling data is shown per colony and years.

Colony		**Single-species**	**Mixed**
Year	**Week of the month**	**Hours of sampling**	
2013	February 2	2.5	-
	February 3	12.0	-
	February 4	16.2	-
	March 1	1.6	-
	March 2	2.1	2.4
	March 3	9.0	2.4
	March 4	4.5	2.0
	April 3	-	2.0
	April 4	-	3.1
	May 1	-	2.0
	May 2	-	2.0
2014	January 4	3.0	-
	February 1	4.1	-
	February 4	4.0	1.1
	March 1	6.7	2.1
	March 2	4.1	1.0
	March 3	5.0	1.2
	March 4	3.2	6.0
	April 1	5.4	4.4
	April 4	4.2	4.0
	May 1	-	5.0
	May 2	-	1.3
2015	March 1	5.6	NA
	March 3	10.1	NA
	March 4	5.3	NA
	April 1	13.1	NA
	April 2	3.0	NA
	April 3	7.1	NA
	April 4	11.8	NA
	May 1	7.5	NA
	May 2	12.5	NA

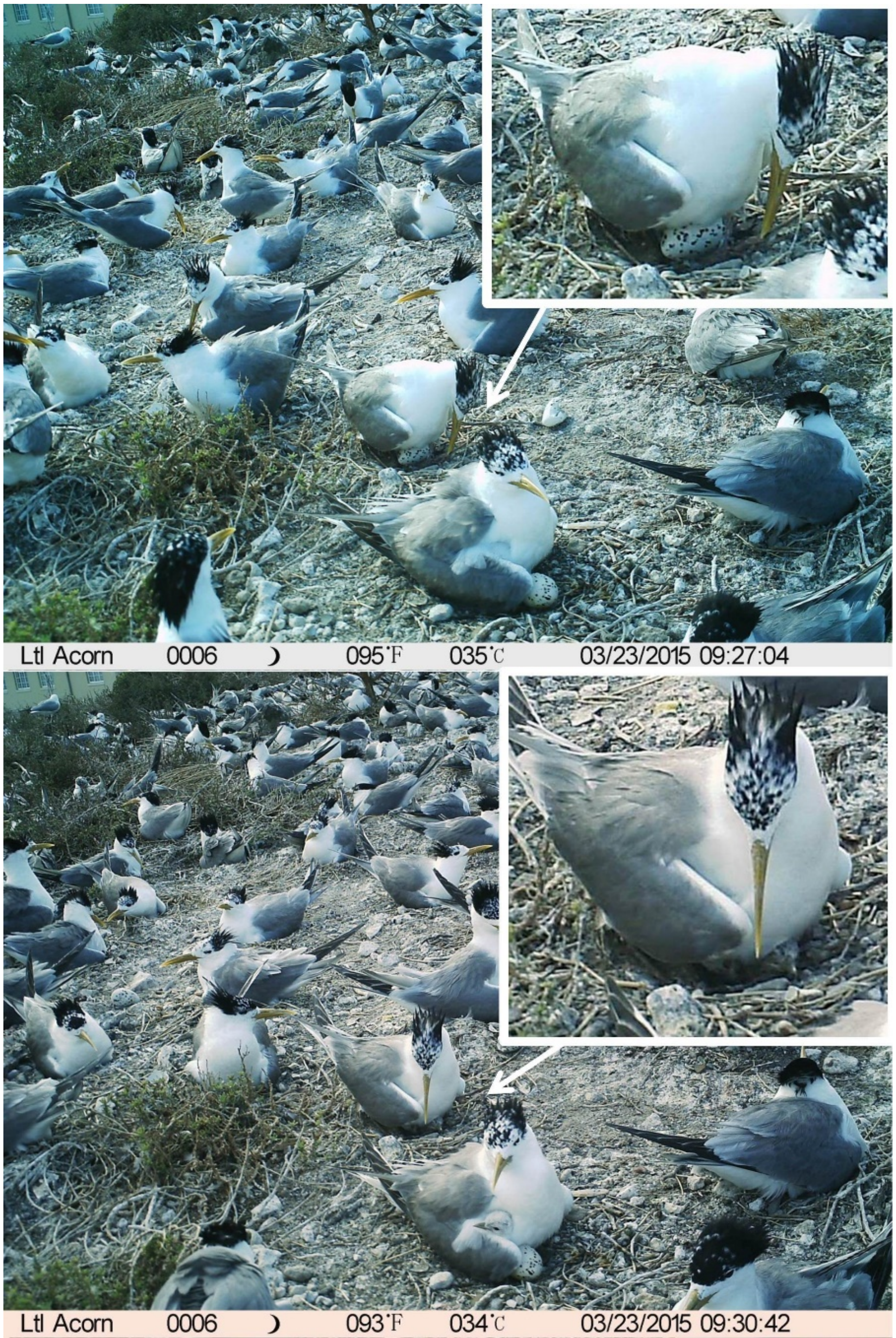


Figure B.1: Example of camera-trap photographs recording the breeding stage of a subsample of nest within the colony. (Top image) photograph recorded on the 03/23/2015 at 9:27:04 illustrate an adult sitting on egg. (Bottom image) photograph of the same nest recorded on the same day about 3minute and 30 seconds later, illustrate that the egg hatched.

Figure B.2: Examples of prey returned to the colony by adult greater crested terns. From A to N: A) klipfish *Clinidspp*; B) octopus *Octopus vulgaris*; C) Cape hope squid *Loligo vulgaris reynaudii*; D) rocksucker *Chorisochismus dentex*; E) spotted greeneye *Chloropthalamus punctatus*; F) greater pipefish *Syngnathus acus*; G) kingklip *Genypterus capensis*; H) redfingers *Cheilodactylus fasciatus*; I) southern conger *Gnathophis capensis*; J) crab Brachyura; K) toadfish *Batrichthysapiatus*; L) hawk-moth Sphingidae; M) grenadier Macrouridae; N) silver scabbardfish *Lepidopus caudatus.*

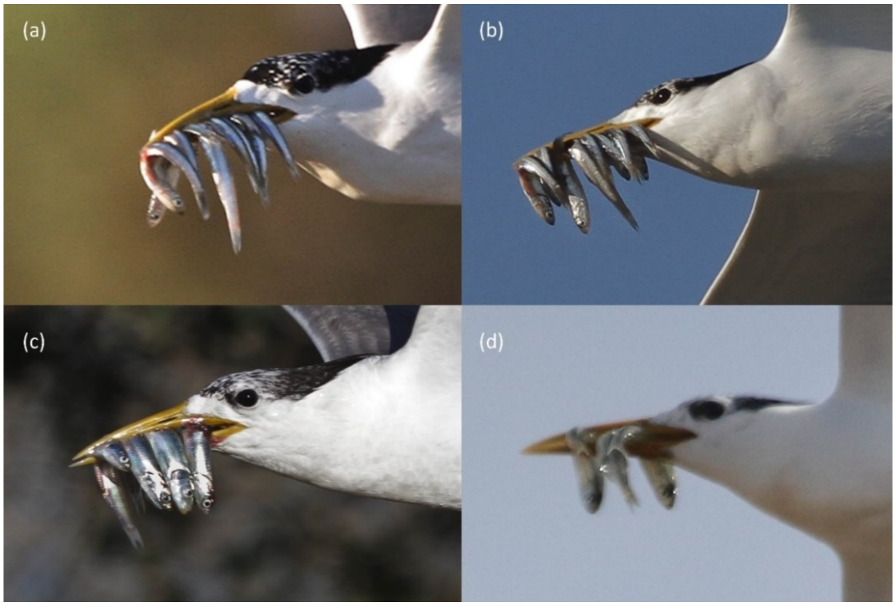


Figure B.3: Examples of multi-prey loads returned to the colony by adult greater crested terns in Robben island (2013-2015). Figure (a) and (b) illustrates same multi-prey loads which includes eight anchovies. (c) Mixed-species prey load which includes three anchovies and one sardine. (d) Other species multi-prey load which includes three individuals of Cape silverside.

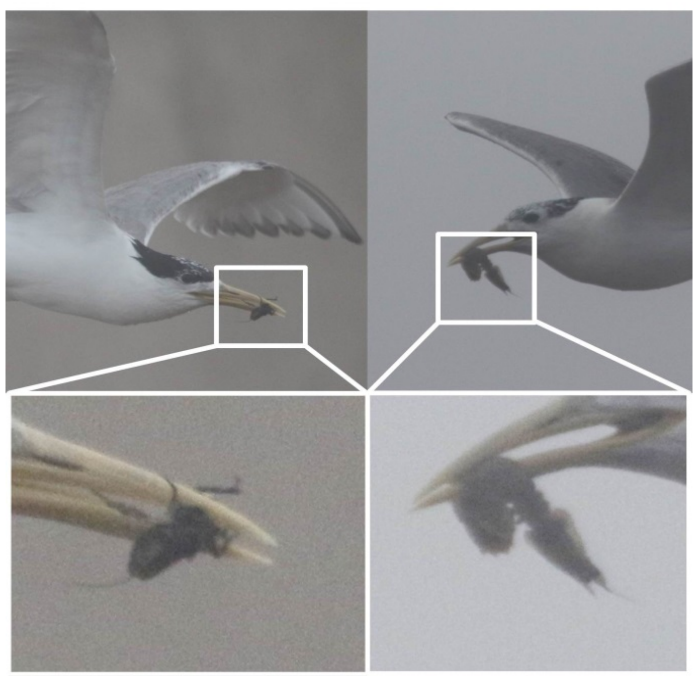


Figure B.4**:** Examples of typical prey returned to the colony by adult greater crested terns in Robben Island (20130-2015) during foggy days. (Left) two spotted cricket *Gryllus bimaculatus*; (Right) mantis shrimp *Pterygosquilla armata.*

Chapter 4

Do low energy requirements contribute to the recent increase of the population of greater crested terns breeding in the Benguela region?

Abstract

Investigating the energy needs of marine top predators is key to understanding their role within food networks and mechanisms associated with their survival and population dynamics. Numerous techniques are used to estimate energy expenditure and food consumption of animals, but the application of those methods to free-ranging seabirds is often invasive and impractical. I used time-energy budget models to estimate daily energy expenditure and food consumption across breeding stages of greater crested terns *Thalasseus bregii* breeding in the Benguela region. Time-energy budget models were built for breeding terns based on activity budgets obtained from non-invasive methods of video-recording and focal observations.

Results showed that foraging trips were fewer and significantly longer during incubation than during chick provisioning stages, and the number of foraging trips doubled from early to late chick provisioning. The time-energy budget models showed that the energy needs of adults increased throughout the breeding season, due to the increased foraging effort (total time spent away from nest). Daily Food Intake of adult greater crested tern increased from ca 142 $g \cdot d^{-1}$ of fish (during incubation) to 179 $g \cdot d^{-1}$ for early provisioning and 199 $g \cdot d^{-1}$of fish during late provisioning. Chick daily food intake estimated from observations, increased from early (20 $g \cdot d^{-1}$of fish) to late provisioning (45 $g \cdot d^{-1}$ of fish). In contrast, modelled mean chick daily metabolizable energy intake was 87 $g \cdot d^{-1}$ over the chick's entire growth period.Sensitivity analyses indicate that estimates of daily food intake are largerly driven to a large extent by estimates of time flying and prey calorific value. Breeding terns require a much lower amount of energy at both individual (range 18–36%) and at population level (range 1–8%), compared to the other endemic Benguela seabirds that rely on forage fish.

The low energy requirements of greater crested terns calculated in this study, coupled with the terns' foraging plasticity, may have contributed to their recent increase, allowing them to cope with changes in the availability and abundance of their main prey.

Introduction

To understand the adaptive advantage of a given behaviour performed by an animal, the energetic cost of that behaviour must be measured (Randall *et al.* 2002). Determining the energetic needs of an individual also enables the calculation of food consumption, which is ecologically important for understanding the role of a species within food networks (Brown *et al.* 2004). The study of metabolism has applications, which extend beyond its role in evolutionary and behavioural ecology (Gordon & Bartol 2004). In conservation, knowledge of an animal's energetic requirements can allow for the integration of their needs into management plans, particularly when the species depend upon a resource also consumed by man (Grémillet *et al.* 2003). For example, investigations of the overlap of fish consumption between breeding Australian gannet *Morus serrator* and commercial fisheries, in southeast Australia have been pivotal for the conservation of that ecosystem (Bunce 2001). Today, as the impact of human activities and environmental changes threaten an increasing number of species globally, there is a growing urgency to investigate the energy requirements of species dwelling in heavily impacted ecosystems (Krebs & Davies 1993, Brander 2007).

Knowledge of energetic needs is particularly important for birds as they usually operate at the upper trophic levels, exerting top–down control on lower trophic levels and/or react to bottom–up forcing (Britten *et al.* 2014). Investigations of the energetic needs of birds therefore allow us to explore the relationships between environmental constraints (e.g. climate change), food web characteristics (e.g. resilience) and the responses of birds, which affect their energy balance (Einoder 2009). However, such questions can only be answered with accurate metabolic estimates of individuals in the wild. Numerous studies have estimated daily energy expenditure (kJ/ bird^{-1}/d^{-1}) and daily food intake (g/ bird^{-1}/d^{-1}) in birds using a variety of methods, including pellet analysis and reconstructing prey sizes consumed (Privileggi 2003, Gagliardi *et al.* 2007) or more invasive techniques including respirometry, doubly labelled water and overall dynamic body acceleration (Keller & Visser 1999, Gleiss *et al.* 2011, Enstipp *et al.* 2005). Nevertheless, it is usually very laborious to estimate the energetic expenditure related to all the behaviours displayed by free-ranging animals, making birds a particularly challenging group to study. Therefore, a model approach offers an adequate non-invasive alternative to estimate bird energy expenditures in the wild (e.g. Furness 1978, Fort *et al.* 2011). Estimating energy expenditure from energy budgets (e.g. Grémillet *et al*. 2000, 2003), predicts bird energy expenditure more accurately than allometric equations or thermodynamics modelling (Fort *et al.* 2011). In theory, time-energy budgets are easily built as the product of the duration of each behaviour performed by the animal in the field and the respective energy cost of each activity, summed across different activities (Croxall & Briggs 1991). However, this requires a thorough knowledge of time-activity budgets and of the energetic costs of specific behaviours.

Worldwide, many marine environments have been severely altered by human activity (McCauley *et al.* 2015). The average state of global fish stocks is poor and declining, and overfishing is a major ecological concern, with only 35% of the fisheries currently fishing above the critical threshold of sustainability (Worm *et al.* 2016, Costello *et al.* 2016). The loss of low trophic level species has dire consequences for food webs and for predator communities that rely on this resource, with large impacts on top predators, including marine mammals and seabirds (Hobday *et al.* 2015). In the North Sea, for example, competition with the largest single-species industrial fishery (lesser sandeel *Ammodytes marinus*) was largely responsible for the low breeding success and the decline of black-legged kittiwakes *Rissa tridactyla* and numerous other seabird populations (e.g. Rindorf *et al.* 2000, Frederiksen *et al.* 2004, Anderson *et al.* 2014). Therefore, the use of energetic models to better quantify seabird consumption, in terms of prey biomass and quality,offers great potential to integrate their needs into an ecosystem approach to fisheries (Fort *et al.* 2011).

In the Benguela upwelling system off southern Africa, declines in population sizes and recent distribution changes of several endemic seabirds including the African penguin *Spheniscus demersus*, Cape gannet *Morus capensis* and Cape cormorant *Phalacrocorax capensis* (Crawford *et al.* 2014) have been attributed largely to the decreased availability of lipid-rich pelagic fish species, affecting the birds' foraging behaviour (Pichegru *et al.* 2007, Mullers *et al.* 2009a, Cohen *et al.* 2014) and demographic parameters (e.g. Crawford 2007, Crawford *et al.* 2011, Sherley *et al.* 2013, 2014). In parallel, the breeding population of a small, single prey loader, which also relies on forage fish, the greater crested tern *Thalasseus bergii,* has tripled over the last few decades in this region (Crawford 2009, Crawford *et al.* 2014). Low fidelity to breeding sites was hypothesised as a characteristic supporting the ability of this species to adapt to a recent eastward shift in the distribution of anchovy population in southern Africa (Crawford 2009). However, most of the population still breeds off the west coast of the Western Cape, an area where other seabird populations generally have decreased. Considerable foraging plasticity (Chapter 3), and their nomadic behaviour between breeding sites (Crawford 2003) appear to have contributed to their success, helping this species to maintain high annual survivorship in the face of ecosystem-wide changes (Payo Payo *et al.* unpubl. data.) This differentiates them from other threatened Benguela endemic seabirds, which generally return to the same breeding site once they start to breed

(Crawford *et al.* 1994, 2002) or show declined adult and juvenile survival, as a result of changes in the Benguela ecosystem (Distiller *et al*. 2012, Sherley *et al*. 2014, 2017). Perhaps, as important, their small body size (<400 g), single egg clutch, short foraging range (ca 10 km) and short breeding period (68 days) (Crawford *et al.* 2005), suggests that breeding terns have overall lower energy requirements, when compared to the other endemic breeding seabirds. In addition, other life history characteristics including extended post-fledging care, which allows juveniles to disperse long distance, may have contributed to maintain an high juvenile survival for this species (Characteristics summarized in Table 4.1). However, assessments of the energy requirements and food intake are lacking for this species, but are needed to better understand how future environmental change may impact the Benguela ecosystem.

In this chapter, I report the foraging activity budget of the southern African population of breeding greater crested terns using non-invasive methods. Based on the duration and cost of each activity performed by breeding adults, I compute the daily energy expenditure and the daily food intake of adults during their different breeding stages. Estimates of mean fish mass delivered to chicks, obtained from photo-sampling methods (Chapter 2, Gaglio *et al*. 2016), and mean daily feeding rates are used to assess chicks' daily food intake and results are compared to model calculations. Finally, I compare these results to the food requirements of other Benguela endemic seabirds, at individual and population levels, thus improving our knowledge of food partitioning within marine ecosystem food-webs and helping with the development of conservation planning.

Table 4.1: Characteristics and life-history traits of four seabird species breeding in the Benguela system (data from Hockey *et al.* 2005).

Species	**Greater crested tern**	**African penguin**	**Cape gannet**	**Cape cormorant**
Body size (kg)	ca 0.4	ca 3.3	ca 2.6	ca 1.3
Clutch size	1	2	1	2.5
Foraging range (km)	ca 10	ca 40	ca 200	ca 40
Foraging techniques	Several*	Pursuit diving	Plunging, scavenging	Pursuit diving
Fidelity to colony	N	Y	Y	N
Post-fledging care	Y**	N	N	Y
Breeding period (days)	68 days	115 days	141 days	84 days

* Surface-Seizing, Dipping, Plunge-Diving, Scavenging , kleptoparasitism, diving from perches.
**up to 4 months

Methods

Time-activity budgets and feeding rates

Time activity budgets were assessed using non-invasive methods, including video recordings of nest cup activities and observations of mobile chicks from a hide on Robben Island, from February to May during three breeding seasons (2013, 2014 and 2015). Video cameras filmed for 12 $hrs \cdot d^{-1}$ (06h30–18h30) (during incubation and early provisioning) to estimate foraging trip duration (time spent away from nest), as well as the average number of trips performed by each parent per day and daily chick feeding rates (the rate at which fish were successfully delivered by both parents in a day). Video cameras were affixed to tripods and powered via two deep-cycle 12V batteries and an AC/DC power inverter. The whole system was placed 20 – 50 m from and focussed on a group of 6 – 8 nests (Figure 4.1). Comparable data on trip duration, number of trips and feeding rates was collected from a hide, during late provisioning, using focal observations with binoculars on individual chicks (distance range 10 – 30 m). At this stage, chicks gathered in crèches are left unattended and both parents forage at sea at the same time (Heydorn & Williams 1993). Mobile chicks were followed for as long as possible (range 3.0–9.5 hrs) and trip durations and hourly feeding rate estimates were gathered from observations of chicks, which were followed for at least 3 hrs (Hall *et al.* 2000). In this period, the duration of one trip was defined as the time elapsed between the first feeding event and third feeding event observed, as I assumed the second feeding event was the start of the alternate parent's trip. The hourly feeding rates were then multiplied by 12 (maximum hours of foraging activity for a breeding adult, as chick feeding does not take place after dusk or before dawn; Nicholson 2002), to estimate comparable number of prey fed to mobile chicks per day. In these observations, the identification of each focal individual was possible as chicks were banded with metal and engraved colour rings, as as part of routine ringing operations carried out by Department of Environmental Affairs (DEA) at the Robben Island colony, or upon a few occasions by the unique characteristics due to their bare part of plumage coloration.

A single foraging trip was measured, to the nearest second, from the moment a bird left the nest (disappeared from the video frame), until its arrival back at the nest (assuming that for each trip the partner always switched nesting duties). As terns spend little time at the nest when switching with their partner (2.6 ± 3.3 min and 8.2 ± 7.2 min on average during incubation and early provisioning, respectively) and assuming that a small amount of time is spent roosting away from the nest, the time spent away from the nest was considered to be a reliable proxy of foraging trip duration, which is an important component of daily energy expenditure (DEE) (Fyhn *et al.* 2001, Rishworth *et al*. 2014).

However, to avoid biases from adults resting at the colony (but not visible in the video), only trips over 10 min were used, to exclude periods when birds may have left the nest for reasons other than foraging (human disturbance or predator avoidance; McLeay *et al.* 2010).

During incubation and early provisioning, a single foraging trip was measured, to the nearest second, from the moment a bird left the nest (disappeared from the video frame), until its arrival back at the nest. As terns spend little time at the nest when switching with their partner (2.6 ± 3.3 min and 8.2 ± 7.2 min on average during incubation and early provisioning, respectively) and assuming that a small amount of time is spent roosting away from the nest, the time spent away from the nest was used as a proxy of foraging trip duration, which is an important component of daily energy expenditure (DEE) (Fyhn *et al.* 2001, Rishworth *et al*. 2014). However, to avoid biases from adults resting at the colony (but not visible in the video), only trips over 10 min were used, to exclude periods when birds may have left the nest for reasons other than foraging (human disturbance or predator avoidance; McLeay *et al.* 2010).

Video recordings were analysed using VLC media player (VideoLAN project). Three breeding stages were recognised: incubation, early-provisioning and late-provisioning (defined in Chapter 3). As greater crested terns do not forage at night (Nicholson 2002), if birds had already left the nest by the start of filming at dawn, nautical twilight was used as an estimate of their departure time, and the same assumption was used for the last foraging trip (Stienen *et al.* 2000, McLeay *et al.* 2010). Nautical twilight is defined when the centre of the sun is 12˚ below the earth's horizon (Hull *et al.* 2001). The time of twilight on a given date at each colony was obtained from https://www.timeanddate.com.

Figure 4.1: (Top) Set up of the video-camera placement near the greater crested tern colony; (bottom) Snapshot of the video monitoring nest-cup activities of greater crested terns in the foreground (Hartlaub's gulls *Chroicocephalus hartlaubii* breeding in the background). Numbers indicate ID of nests monitored.

Time-energy-budget models

Time-energy budgets models were built for adult greater crested terns to calculate the amount of food that individuals needed to consume daily in order to rear one chick in a season (Daily Food Intake – DFI g·d^{-1}) (specific input values are shown in Table 4.5). Budgets were based on the bioenergetics model elaborated by Grémillet *et al.* (2003). Considering the duration (*D*) and metabolism per time unit (*M*) of each activity:

$$Daily\ energy\ expenditure = \sum_{k=1}^{n}(D_k \times M_k)$$

Daily energy expenditure – DEE (kJ·d^{-1}) was then converted into DFI. Anchovy, the main prey species of crested terns in the Western Cape (Walter *et al.* 1987a, Crawford & Dyer 1995, Gaglio *et al.* 2016, Chapters 2 & 3), has a calorific value (*Cp*) of 6.22 ± 0.65 kJ.g^{-1} (wet mass) (Prosch 1986, Balmelli & Wickens 1994, Pichegru *et al.* 2010a). Using an assimilation efficiency (*Ea*) of 0.77 ± 0.34 (Visser 2002), I calculated daily food intake (g·d^{-1}):

$$Daily\ food\ intake = \frac{DEE}{Cp \times Ea}$$

To estimate the energy necessary for the adult to warm the bird's fish load (*L*), I assumed that fish were at a water temperature (*Tw*) of 14°C (average temperature of inshore sea surface waters all year round in the Western Cape, Monteiro *et al.* 2006) and used a fish specific heat capacity (*HC*) of 4.2 J.g.°C^{-1}, a bird body temperature (*Tb*) of 40°C and a metabolic efficiency (*Em*) of 0.75 (Grémillet *et al.* 2003). The energy of food warming for self-consumption (kJ) was thus calculated as:

$$Food\ warming\ energy\ = \frac{(Tb\ - Tw) \times HC \times L}{Em}$$

I estimated energetic needs for the incubation, early and late provisioning phases, considering that adult DFI was the amount of fish necessary to sustain chick maintenance and growth as well as their own expenditure, as derived from their time-activity budget. For the model, I assumed the number of chicks fledged per breeding pair was the hypothetical maximum reproductive output of 0.9 (Crawford *et al.* 2005). Chick energetic requirements were estimated using an allometric equation for seabirds (Visser 2002) that gives mean chick daily metabolizable energy intake (kJ) over chick growth period in relation to asymptotic chick mass (*A,* g) and days taken to fledge (*F*):

$$Chick\ daily\ metabolizable\ energy\ intake\ = \frac{(11.09 \times A^{0.771}) \times (F^{0.747})}{F}$$

Activity costs

Metabolic rates of different activities collected from the literature are presented in Table 4.2. The two main methods used to measure activity costs were respirometry and the double-labelled water technique. An estimate of the cost of resting at the colony was taken from Enstipp *et al.* (2006) and the cost of flying was estimated with Flight 1.25 (Pennycuick 2008) using a wingspan of 1 m and an aspect ratio of 10.4. This software uses aerodynamic modelling and species-specific body mass (greater crested tern body mass input value = 380 g) and dimension to calculate the energetic cost of flying.

Chick estimated DFI from photo-sampling method

Standard length of the main prey (anchovy) was calculated from photographs (Chapter 2; Gaglio *et al.* 2016). Mass was estimated from anchovy standard length using a yearly species-specific regression (provided by C. van der Lingen, DAFF) (Table 4.3). To estimatedchick DFI, I used the mean mass of anchovy returned to the colony according to breeding stage multiplied by the average number of prey delivered to offspring during that stage.

Statistical analysis

The Shapiro test for normality was used to assess whether behavioural data were normally distributed (shapiro.test) using the package 'nortest'. Where behavioural data was not-normally distributed, comparisons between colonies and breeding stages (of trip durations, daily trips, feeding rates and time budgets) were performed using permutation tests with 10,000 Monte Carlo iterations (perm library v. 1.0-0.0 for R).

Two sample t-tests were used to analyse differences in anchovy mass between early and late provisioning. Sensitivity analyses of time-energy-budget models were run to assess the impact of different parameters on the estimated energy budget. The variation (expressed in %) of the model output (DFI) was calculated one parameter at a time, (maintaining the other parameters constant) by substituting the mean value of the specific parameter by the mean + SD and mean – SD to obtain the range of variation (Enstipp *et al.* 2006). In order to calculate the range of variation for daily food intake, time at the colony was increased or decreased in response to variation in daily time spent flying or resting at the colony. The maximum variation of the model was calculated for the most demanding condition (using mean + SD of time-activity budget parameters and body mass and mean – SD of assimilation efficiency and calorific value of prey). The minimum variation of the model was calculated for the least demanding condition (using mean – SD of time-activity budget parameters and body mass and mean + SD of assimilation efficiency and calorific value of prey). Statistical analyses were conducted in R (v. 3.3.1) (R Core Team 2016), with the significance level set at $P < 0.05$ for all tests.

Table 4.2: Greater crested tern input values (mean ± SD) and references used to calculate time-energy budgets**.**

Parameter	**Value**	**Method**	**References**
Body mass (kg)	0.4 ± 0.03	Measured	Anthony Tree, pers. c
BMR ($W \cdot kg^{-1}$)	6.7	Respirometry	Ellis (1980)
Costs (× BMR) ($W \cdot kg^{-1}$):			
at the colony	2.0	Estimated	Enstipp *et al.* (2006)
flying	5.2	Modelling	Pennycuick(2008)
diving	5.2	Modelling	Pennycuick(2008)
Incubation (days)	28	Measured	Hockey *et al.* (2005)
Early provisioning (days)	4	Measured	Hockey *et al.* (2005)
Late provisioning (days)	36	Measured	Hockey *et al.* (2005)
Fledging (days)	40	Measured	Hockey *et al.* (2005)
Asymptotic chick mass (g)	370	Modelling	le Roux 2004
Mean chick MEI ($kJ \cdot d^{1}$)	417	Estimated	Visser (2002)
Chicks fledged per pair	0.9	Estimated	Hockey *et al.* (2005)

BMR: basal metabolic rate, MEI: metabolizable energy intake.

Table 4.3: Length weight regressions for anchovy sampled during pelagic recruit surveys (May/June) 2013–2015. Data from Department of Agriculture, Forestry and Fisheries.

Year	**WBM**	r^2	**n**
2013	$0.0050*CL^{3.2438}$	0.976	2,560
2014	$0.0072*CL^{3.0834}$	0.934	2,096
2015	$0.0061*CL^{3.1618}$	0.975	3,618

WBM = aCL^b, where WBM in g and CL in cm; r^2 and n values given

Results

Time activity budget in relation to breeding stage

A total of 374 nests during incubation and 240 nests during early provisioning were monitored in 35 days of video-recording at both colonies providing 1,127 foraging trips during incubation and 1,704 foraging trips during early provisioning. In this study, I found no significant differences in trip durations and feeding rates between the two colonies (permutation test all p values > 0.1), thus all data were pooled in further analysis. During late provisioning, as chick were mobile, they were much harder to document and only 34 mobile chicks were monitored during 16 days of focal observations providing a total of 91 foraging trips (data from 2014-2015 at mixed colony only).

Results show that the foraging behaviour of breeding greater crested terns changed across the different breeding stages. During incubation, trips were significantly longer than trips during the early and late provisioning periods (permutation tests: $p < 0.001$; Fig 4.2). Incubating adults spent an average of 4.7 (± 3.00)(range 0.1 – 13.5) hrs away from their nest, while their partners incubated, and performed a mean (± SD) of 1.5 (± 0.56 d^{-1}) (range 1 – 4 d^{-1}) trips per day (Fig 4.2). Foraging trips during the early provisioning were much shorter (1.8 ± 1.74 hrs, range 0.05 – 11.6 hrs, n = 1,704; permutation test $p < 0.001$), however significantly more daily trips (4.1 ± 1.79 d^{-1}, range 1 – 8 d^{-1}) were performed when compared to incubation (permutation test: $p < 0.001$). Consequentially, the resulting total time spent away from their nest during incubation and early provisioning were similar (permutation test: $p = 0.08$) (Figure 4.2). During late provisioning, chicks are left alone, while both adults were provisioning food to their chick. The number of trips per day (4.5 ± 2.41 d^{-1}, range 1 – 9 d^{-1}) performed by each parent was similar to early provisioning (permutation test: $p = 0.25$) but the duration of each foraging trip (2.3 ± 1.4 hrs, range 0.1 – 12 hrs) was significantly longer than during early provisioning (permutation test: $p = 0.005$), resulting in a significant increase in the total time spent away from their chick, during this period (permutation test: $p < 0.001$; Table 4.4; Figure 4.2).

Modelling time-energy-budget

Outputs of the time-energy budget models showed a steady increase in energy needs throughout the breeding season, when considering the total energy requirements of both adults and offspring together (Figure 4.3, Table 4.5). During incubation, the estimated DEE of an adult was 683 $kJ \cdot d^{-1}$, with an estimated DFI of 142 g of fish. During early provisioning the estimated DEE of an adult was similar (674 $kJ \cdot d^{-1}$), but the estimated total DFI for an adult, including chick contribution was 37 grams more (179 $g \cdot d^{-1}$). Thereafter, during late provisioning adult estimated DEE increased to 768 $kJ \cdot day^{-1}$ with a total estimated DFI of 199 $g \cdot d^{-1}$ of fish (Figure 4.3).

Using an allometric equation for seabirds (Visser 2002) the modelled mean chick daily metabolizable energy intake, was estimated at 417 ($kJ \cdot d^{-1}$). This value was used to compute the average chick estimated DFI (ca 87 g.d^{-1}) over the chick's entire growth period (Table 4.5). Sensitivity analyses showed that variation in time flying and prey calorific value had the largest effect on estimates of DFI during all breeding stages (see Table 4.6).

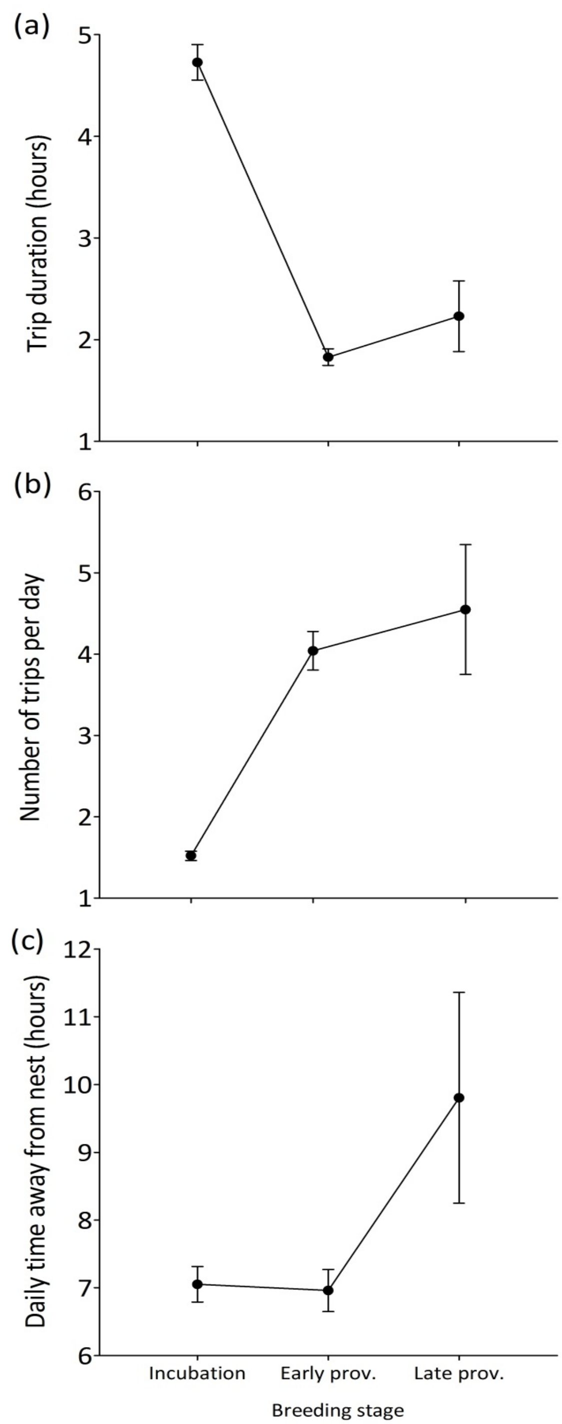


Figure 4.2: Foraging efforts related to breeding stages. (a) Average daily trip duration, (b) number of trips per day and (c) total time spent away from the nest per day related to breeding stage (incubating, early provisioning and late provisioning) for individual greater crested terns breeding at Robben Island (2013 – 2015). Bars represent the 95% confidence intervals.

Table 4.4: Number of nests monitored, foraging trip durations and trips per day (mean ± SD), performed by individual greater crested terns at Robben Island (2013 – 2015).

Breeding stage	2013	2014	2015	Total
Incubation (n nests)	229	98	47	374
Trip duration (hrs) (mean ± SD) (n)	5.0 ± 3.17 (657)	4.2 ± 2.71 (338)	4.7 ± 2.76 (134)	4.7 ± 3.00 (1127)
Average trips per day (mean ± SD)	1.4 ± 0.51	1.4± 0.68	1.4 ± 0.39	1.5 ± 0.56
Early provisioning (n nests)	73	72	95	240
Trip duration (hrs) (mean ± SD) (n)	2.1 ± 1.81 (478)	1.7 ± 1.66 (581)	1.8 ± 1.74 (645)	1.8 ± 1.74 (1704)
Average trips per day	3.9 ± 1.80	4.6 ± 1.89	3.8 ± 1.62	4.1 ± 1.79
Late provisioning (n chicks)	–	19	15	34
Trip duration (hrs) (mean ± SD) (n)	-	2.6 ± 1.56 (36)	2.0 ± 1.31 (55)	2.3 ± 1.44 (91)
Average trips per day	-	3.6 ± 1.96	5.8 ± 2.46	4.5 ± 2.41

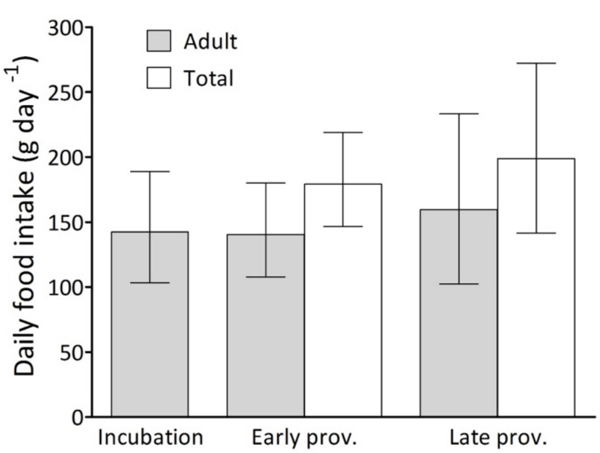


Figure 4.3: Daily Food Intake related to overall breeding stage (incubating, early provisioning and late provisioning) for adult greater crested terns provisioning offspring at Robben Island (Total DFI = Single Adult DFI + 50% Chick DFI). Error-bars represent the range of variation of the time-energy-budget models (see Table 4.6 for sensitivity analysis).

Table 4.5: Parameters used to calculate time-energy budgets of greater crested terns related to breeding stage (incubating, early provisioning and late provisioning). Cost of activities and the outputs of time-energy budget models of greater crested tern: estimated Daily energy expenditure (DEE), field metabolic rate (FMR) expressed as the multiple of BMR, estimated daily food intake (DFI) and catch per unit effort (CPUE), i.e. the amount of food caught relative to time spent at sea.

Parameter	Incubation	Early	Late
Time (min.day^{-1}):			
- at the colony	1019 ± 120	1039 ± 187	851 ± 916
- flying	420 ± 188	400 ± 180	588 ± 752
- diving	1 ± 0.01	1 ± 0.01	1 ± 0.01
Cost resting at colony (kJ·d^{-1})	317.9	324.4	265.4
Cost flying (kJ·d^{-1})	340.6	324.5	476.9
DEE (kJ·d^{-1})	683.8	674.1	767.7
FMR (W·d^{-1})	3.04	3.00	3.42
Adult DFI (g·d^{-1})	142.3	140.3	159.7
Chick DFI (g·d^{-1}) *	-	39.0	39.0
Total DFI (g·d^{-1})	142.3	179.3	198.8
CPUE (g·min^{-1})	0.34	0.45	0.34

* Chick DFI provided by one adult and calculated from averaged MEI (Visser 2002)

Table 4.6: Sensitivity analysis of time-energy-budget models of greater crested terns (see Methods for details).

Parameter	Incubation (%)	Early provisioning (%)	Late provisioning (%)
Body mass	± 8.7	± 6.5	± 6.8
Time flying	± 13.5	± 10.6	± 39.3
Time diving	± 0.01	± 0.01	± 0.01
Assimilation efficiency	± 4.8	± 4.4	± 3.6
Calorific value of prey	± 13.5	± 13.5	± 10.6
Maximum variation	+ 46.6	+ 39.7	+ 73.6
Minimum variation	– 39.2	– 32.6	– 57.2

Estimating chick estimated DFI from photo-sampling method

To assess sensitivity of modelled mean chick estimated DFI, feeding rates and mean anchovy mass was estimated from observations in the field (see methods). The average mass of anchovies brought to the chick during early provisioning (mean ± SD 4.3 ± 3.0 g, n = 126), was significantly smaller than anchovy returned during late provisioning to mobile chicks (5.2 ± 2.9 g, n = 629; two-sample t-test p = 0.002; Figure 4.4). Feeding rates averaged 4.5 (± 2.3) fish per day (range 1–13) returned to the nestling during early provisioning. Significantly more fish were returned during late provisioning (8.4 ± 5.13 fish per day;

range 1–19; permutation test: $p < 0.001$; Table 4.7). Chick DFI estimates from observations increased from early to late provisioning: chick DFI was ca 20 $g \cdot d^{-1}$ of anchovy during the early stage (range: 3–50 $g \cdot d^{-1}$) and ca 45 $g \cdot d^{-1}$ during late provisioning (range: 8–110 $g \cdot d^{-1}$).

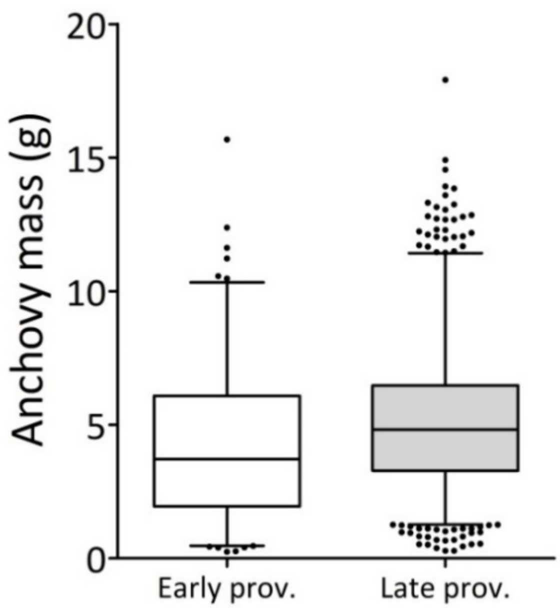


Figure 4.4: Comparison of mean anchovy mass (g) estimated from a photo-sampling method in the diet of greater crested terns across three breeding seasons (2013 – 2015) at Robben Island during early and late provisioning. Bars represent the 95% confidence intervals.

Table 4.7: Average daily (and hourly) fish returned to a chick (mean ± SD) made by both adults greater crested terns in a breeding pair at Robben Island (2013 – 2015) during early and late provisioning. Estimated daily feeding rates assume 12 hrs of foraging activities per day.

Breeding stage	**2013**	**2014**	**2015**	**Total**
Early provisioning				
Average fish returned to chick (daily)	3.4 ± 1.84	5.9 ± 3.16	4.3 ± 2.05	4.5 ± 2.30
Late provisioning				
Average fish returned to chick (hourly)	-	0.6 ± 0.32	0.8 ± 0.51	0.7 ± 0.42
Estimated average fish returned to chick (dail	-	7.2 ± 3.93	10.0 ± 6.12	8.4 ± 5.13

Discussion

This chapter investigates the time activity budgets and associated energy requirements across breeding stages of the southern Africa population of greater crested terns. The results suggest that adults face increasing energetic constraints following the progress of the season. During incubation, when trips are mainly used for self-feeding or courtship (Ponchon *et al.* 2014), terns undertook relatively few, long foraging trips. At this stage, nest duties changes occurred at a rate of 0.12 per hour, which is at the lower range of findings reported for the Australian population of this species (0.13 – 0.18 per hour, Nicholson 2002). During early provisioning, adults performed significantly more trips, but of shorter duration, resulting in equivalent total time spent away from the colony by both parent in this period, compared to incubation. During late provisioning, both adults performed longer foraging trips, while chicks were left unattended, presumably due to adults balancing their own energetic needs, after the intense period of feeding small chicks (Lyons *et al.* 2005). Together, they doubled the frequency of feeds compared to early provisioning, and delivered larger fish (as shown in Chapter 3) on each trip, greatly increasing the rate of energy delivery to their chick at his most energy demanding stage (Shaffer 2004). The increase in trip duration from early to late provisioning, could reflect longer commuting times to foraging grounds further away from the colony, where bigger fish are available and which help to maintain chick growth and condition (Takahashi *et al.* 2003, Burke & Montevecchi 2009). Alternatively, the increased trip duration may possibly be indicative of an increasing time spent self-feeding to recover from a potential energy deficit state during the early provisioning period, when trips were more frequent.

The at-sea fine-scale foraging behaviour of terns has been studied using GPS data loggers in only a few species (e.g. McLeay *et al.* 2010, Fijn *et al.* 2016). McLeay et al. (2010) used GPS to record temporal and spatial foraging patterns in the Australian population of greater crested terns. Despite the different methodologies, McLeay found that adults provisioning nestlings (early provisioning) spent an average of 1.5 (± 1.2) hrs per foraging trip, which is similar to my results (1.5 ± 2.0 hrs). Interestingly, in this study, a direct comparison between methods to assess the duration of foraging trips (use of GPS and observed time away from the nest), showed shorter trips recorded by GPS compared to observations, but results were not significantly different (McLeay *et al.* 2010). Nicholson (2002) found, for the same Australian population, that during early provisioning, a chick received ca 4 feeds per day, similar to what was found for the same stage in my study (4.5 ± 2.3). However, during late provisioning, feeding rates, showed large seasonal variations (from 3 to 6 feeds·d^{-1}), with generally less prey returned in a day, compared to the southern African conspecifics (8.4 ± 5.13 prey d^{-1}) (Nicholson 2002). Estimates of feeding rates in Damara terns *Sternula balaenarum* (in southern Africa) and little terns *S. albifrons,* (in southern Portugal) show a larger number of fish (estimated 17 prey·d^{-1}) returned for both species, compared to greater crested terns (Paiva *et al.* 2006, Braby 2011). This high feeding rate is possibly due to the need to maintain a high amount of energy for increased delivery rates to offspring, as those sternula species usually rely on lower energy content prey (Atherina spp), compared to those of greater crested terns (Braby 2011, Paiva *et al.* 2006, Chapter 2 & 3).

In general, the outcomes of this study agree with predictions of central-place foraging models, which presume that adults should increase energy amounts delivered to chicks, which positively correlates to the total amount of time spent away from the colony (Orians & Pearson 1979, Leopold *et al.* 1996). In addition, the variability in foraging effort may also be related to the need to adjust to prey availability variations and the influences of localized environmental factors (e.g. visibility, wind, tide discussed in Chapter 3), which may inhibit foraging efficiency (Stienen *et al.* 2000, Baptist & Leopold 2010, Saraux *et al.* 2011b, Stienen *et al.* 2015).

Changes in DEE and DFI according to breeding stage

The steady increase in estimated Daily Energy Expenditure (DEE) and Daily Food Intakes (DFI) of breeding greater crested terns with the progress of breeding, is likely to be associated with the intensification of the time spent flying and is reflective of the increase in energy demands of growing chicks, as previously observed in many seabird species (e.g. Rishworth *et al.* 2014, Collins *et al.* 2016). Crawford *et al.* (1991), estimated the DFI of resident seabird in the Benguela region, including non-breeding greater crested terns. Results from Crawford *et al.* (1991) estimated that a non-breeding greater crested terns would require ca 140 g·d^{-1} intake, which is similar to the estimates of DFI for incubating parents in this study, which amounted to ca 142 g·d^{-1}. A detailed comparison of estimated DEE and DFI to that of other populations of greater crested terns at different temporal or spatial levels was not possible, due to the absence of studies on greater crested tern's energetics requirements.

Modelled metabolizable energy intake for chick was calculated as a daily average based on chick fledging mass and numbers of days to fledging, for the entire chick growth period, which represents the total amount of metabolizable energy needed for successfully raising a chick. Assuming that diet consisted entirely of anchovy, the modelled amount of food needed over the fledging period would total to ca 86 g·d^{-1}. However, this model is limited as it is insensitive to the variations in energy needs for chicks, which typically increases considerably from early to late provisioning (Klasseen *et al.* 1989). In contrast, variations of chick food intake were confirmed by results of estimated DFI obtained from video-recordings and observations in this study, which amounted to ca 20 $g \cdot d^{-1}$ during the early stages and to ca 45 $g \cdot d^{-1}$ during late provisioning stages. The differences between modelled and observed chick estimated DFI indicate that more sensitive models should be implemented, which should account for variations in energy needs according to chick age.

Do breeding greater crested terns have lower energy requirements than threatened Benguela seabirds?

A comparison of the energetic demands of breeding greater crested terns with the other three Benguela endemic seabirds that rely on pelagic fish, illustrates how the other species need a much larger amount of energy to successfully raise their offspring (Table 4.8).

According to the outcomes from this chapter, greater crested tern chicks require ca 3.5 kg of anchovy to fledge. In comparison, an African penguin, which weighs 8 times more (3.2 kg; Hockey *et al.* 2005), than a greater crested tern and may raise two chicks (Pichegru *et al.* 2013, Sherley *et al.* 2013), needs a much larger amount of food for both self-sustaining and offspring provisioning (Table 4.8). Based on the food intake of captive chicks, Cooper (1977) estimated that the necessary food intake for a single penguin chick to fledge was 22.5 kg of anchovy. A recent investigation on wild individuals by Bouwhuis *et al.* (2007) estimated the total amount of food, which adults have to provide to a chick between hatching and fledging is approximately 17 kg of anchovy (Bouwhuis *et al.* 2007).

Like African penguins, Cape gannets are major avian predators in the Benguela region (Hockey *et al.* 2005). With adults weighing an average of 2.6 kg (Pichegru *et al.* 2007), this species has the greatest flight cost reported for a seabird, and previous studies shows that raising a single chick increases adult estimated DEE by approximately 28% (Adams *et al.* 1991, Grémillet *et al.* 2008, Mullers *et al.* 2009b, Navarro 2010). Bioenergetics models indicate that the DFI of Cape gannets varies according to food quality with 652 $g \cdot d^{-1}$ of fish needed by one provisioning parent and 99 $g \cdot d^{-1}$ for the chick when diet is based exclusively on anchovy (Okes *et al.* 2009).

Like African penguins and Cape gannets, Cape cormorants (1.2 kg; Hockey *et al.* 2005) mainly feed on anchovy, which they hunt typically within 20–30 km off the colony (Ryan *et al*. 2010, Cook *et al.* 2012). Using allometric equations (Ellis & Gabrielsen 2002), the estimated DFI for provisioning Cape cormorants totalled approximately 547 $g \cdot d^{-1}$ of anchovy for adults and approximately 210 $g \cdot d^{-1}$ per average brood size of two chicks (Visser 2002). Therefore, estimated chick DFI amounted to 5.8 kg of fish per single chick for the whole provisioning period.

In addition, it is important to acquire detailed data of population sizes in order to estimate the energy requirements of the whole community breeding in this system (Laugksch & Duffy 1984, Crawford *et al.* 1991). With approximately 15,000 breeding pairs occurring in the Benguela region, the whole breeding population of crested terns would require ca 3,000 $kg \cdot d^{-1}$ of fish, which is ca 65 times less than the Cape gannet population and ca 35 times less than the Cape cormorant population breeding in the region (Table 4.7). Breeding African penguins, despite a recent decrease in numbers (Crawford et al. 2014), also require approximately 12 times more food (DFI of 37,900 $kg \cdot d^{-1}$), than the greater crested tern breeding population (Table 4.8). These comparisons highlight the relatively small amount of fish needed for breeding greater crested terns (both individually and at population level), which may contribute to their recent increase in an exploited environment. These apparent differences in the food requirements between greater crested terns and other endemic seabirds, which rely on anchovies and other small pelagic fish, constitute a key factor for understanding seabird food consumption in the Benguela region and assisting the development of plans for the conservation of threatened species (Crawford *et al.* 1991, Lescroël *et al.* 2016).

Table 4.8: Comparison of adult and brood Daily Food Intake (DFI) at individual and population level among four seabird species breeding in the Benguela system (see References in Table).

Species	**G. crested tern**	**African penguin**	**Cape gannet**	**Cape cormorant**
Provisioning adult DFI (mean)	198.8 $g \cdot d^{-1}$	758.0 $g \cdot d^{-1}$	652 $g \cdot d^{-1}$	547.0 $g \cdot d^{-1}$
(Chicks fledged) DFI (modelled)	(1) ca 87 g**	(1.5) ca 330 g	(1) ~ 165 g	(2) ca 210 g**
Number of breeding pairs*	ca 15,000	ca 50,000	ca 300,000	ca 190,000
Breeding population DFI	2,982 $kg \cdot d^{-1}$	37,900 $kg \cdot d^{-1}$	375,000 $kg \cdot d^{-1}$	103,930 $kg \cdot d^{-1}$
References	This study	Nagy *et al.* 1984 Bouwhuis *et al.* 2007	Mullers et al. 2009 Pichegru *et al.* 2007	Ellis & Gabrielsen 2002*** Visser 2002

* Data from DEA, ** MEI modelled from Visser (2002), diet ***Estimated from

Limitations of the study

In this study, a modelling approach was used to estimate the daily energy requirements of breeding greater crested terns. Several models were used, and the range of different input parameters result in limitations in the resulting estimates. For example, the flight model used to estimates of flight costs has been shown to occasionally misrepresent estimate energy expenditure, in comparison to empirical estimates (Mcwilliams *et al*. 2004, Schmidt-Wellenburg *et al.* 2007) Uncertainties in constructing time-energy budgets are attributable to several parameters, including the inaccuracy of activity duration (e.g. time spent resting away from the nest) (Goldstein 1988) and estimated activity cost for each behaviour and individual thermoregulatory expenses. More specifically for terns, these parameters may lack precision as energetic investigations on terns are limited to only a few species and are based on a small sample size (Flint & Nagy 1984). Moreover, my non-invasive approach may underestimate behaviours that have a relatively high energetic cost during a foraging trip (e.g. the hovering before diving). This is evident when comparing my estimates to empirical measurements from sooty terns *Onychoprion fuscatus* (Flint & Nagy 1984), which shows higher energy expenditure during flight (ca 64 $W \cdot kg^{-1}$) relative to my computation for greater crested terns (ca 35.6 $W \cdot kg^{-1}$). Besides these limitations, it was observed that terns spend very little time on the sea surface, which is largely exclusive to diving activities (pers. obs.), hence the time spent away from the nest is mostly spent flying.

Another limitation was the assumption that time budgets were representative of the full day of activity. Unfortunately, it was not possible to follow provisioning adults for an entire day, especially once the chicks left the nest cup, reducing the confidence in these parameter estimates. To overcome such limitations, animal-borne data logger (e.g. GPS, accelerometers) could be implemented, provided they do not affect bird behaviour. However, despite gaining potentially detailed information of activity budgets from data loggers deployed in only a few individuals, for this study I favoured the use of non-invasive methods (such as video-recording and observations from a hide), which are less expensive and may provide a better population-level inference, as data logger studies often rely on a small sample size (Hebblewhite & Haydon 2010, Collins *et al.* 2016).

In this study, feeding rates were based on successful delivered prey only. However, as terns bring a single prey held in their beak to the colony, they are often subject to kleptoparasitic interactions (Brockmann & Barnard 1979), which may result in extra energy costs In Chapter 5, I investigate two colony sites with different rates of kleptoparasitism from neighbouring gulls. To meet the energy requirements of growing chicks, adults may have to compensate for the food loss from kleptoparasitic gulls by changing some components of their foraging ecology, with consequential implications on further energy expenditure (Stienen *et al.* 2015), which highlights the importance of studying this interaction. Lastly, energetic needs were assessed only during the breeding season, which is generally the most demanding period of the year for seabirds (Shaffer 2004). However, a more comprehensive assessment should include the non-breeding season, enabling fisheries management and conservation plans to accurately and flexibly account for seabird energetic needs and consumption in space and time.

Conclusions

The time-energy budget model for breeding greater crested terns illustrated a steady increase of foraging effort and consequent increase in total estimated DEE and DFI from incubation to late provisioning. This study provides evidence for the relatively low energy requirements of these terns at both the individual and population level, when compared to other Benguela breeding seabirds that rely on the same resources. A comprehensive assessment of the impact of human activities on seabird populations requires more detailed estimates, including the proportion of prey biomass consumed in a defined area. Further studies implementing detailed knowledge of energetics, prey demand and demographic variables of Benguela endemic seabirds are thus vital to understand factors, which affect the population dynamics of threatened species breeding in this system.

Chapter 5

The costs of kleptoparasitism in mixed-species breeding colonies of greater crested terns and Hartlaub's gulls

Abstract

Mixed-species assemblages are common in nature, providing numerous benefits to associating species. However, associating with other species may also impose costs due to kleptoparasitism. This is especially common in mixed seabird breeding colonies, where offspring provisioning may be reduced both directly by kleptoparasitism and indirectly through modification of adult behaviour to avoid kleptoparasitism. Identification of the costs induced by kleptoparasitism and how these vary when species breed alongside one another versus with conspecifics alone is therefore essential to understand the potential benefit associated with living in mixed-species assemblages.

Here, I explore the costs of kleptoparasitism for greater crested terns *Thalasseus bergii* provisioning their offspring at a colony consist only of terns (single-species), where individuals suffer intraspecific kleptoparasitism from other terns, and a colony where terns breed alongside Hartlaub's gulls *Chroicocephalus hartlaubii* (mixed) where they are vulnerable to both intra- and interspecific kleptoparasitism. Observations of kleptoparasitic interactions during offspring provisioning showed that the presence of gulls at the mixed colony increased kleptoparasitic attacks and the proportion of prey lost or stolen, as compared with the single-species colony. Additionally, provisioning adults suffered behavioural costs, requiring more attempts to provision young, taking longer to do so and ultimately swallowing (to the detriment of the offspring) more returned prey in response to kleptoparasitism at the mixed colony. Furthermore, the presence of gulls increased the duration of vulnerability to kleptoparasitism, because gulls continued to steal food from adults and chicks when precocial chicks had left the nest, a time when intraspecific kleptoparasitism became negligible.

These results show that terns breeding in a mixed colony suffer direct and indirect costs through decreased provisioning and increased provisioning effort. This could potentially impact reproductive success, resulting in colony decline where kleptoparasitism is frequent. This study highlights the fact that forming mixed assemblages, despite potentially been beneficial, can entail a cost, potentially resulting either parasitic or mutualistic relationships.

Introduction

Many species form associations with others, termed mixed-species assemblages (Wood *et al.* 2015). Typically, such assemblages provide net benefits to the species associating with one another and are thus considered to be mutualistic (Broinstein 2001, Leigh 2010). However, many species also impose costs on associating species, and the relationships may tend towards parasitic when these costs are high (Rathcke 1992, Baigrie *et al.* 2014). In particular, mixed-species breeding colonies, typical among many seabird species, are commonly considered to provide mutual anti-predation species or to facilitate access to the same favourable local environmental resources (e.g. Wittenberger & Hunt 1985, Siegel-Causey & Kharitonov 1990, Danchin *et al.* 1998, Broinsten 2001). However, food theft, or kleptoparasitism, is also common in some seabird colonies, where breeders returning to provision their young with prey are particularly vulnerable to attack, both by conspecifics (intraspecific kleptoparasitism) and other species (interspecific kleptoparasitism) (Brockmann & Barnard 1979, Iyengar 2008). Interspecific kleptoparasitism could represent a significant cost of associating with other species, both through food lost and through changes to adult provisioning behaviour to reduce being parasited, that result in increased energy expenditure (Nettleship 1972, Stienen *et al.* 2001). Consequently, there is a need to identify the costs arising from kleptoparasitism and to assess how these differ when species breed alongside one another versus with conspecifics alone.

Prey stealing is likely to be particularly acute where kleptoparasitic species breed alongside other species in mixed-breeding colonies, potentially resulting in decreased individual survival and breeding success (Fuchs 1977, Furness 1987). For example, in mixed-colonies of breeding sandwich terns *Thalasseus sandvicensis* and black-headed gulls *Chroicocephalus ridibundus* in the Netherlands, kleptoparasitism by gulls decreased food provisioned to tern' chicks and overall productivity (Stienen *et al.* 2006). Interspecific kleptoparasitism may also diminish feeding rates due to a greater time spent airborne in order to evade kleptoparasitism (Le Corre 1997, Stienen *et al.* 2001, Blackburn *et al.* 2009). Direct comparison of kleptoparasitism rates between breeding colonies of puffins *Fratercula arctica*, with or without gulls, illustrated that chick feeding rates were higher in gull-free colonies (Finney *et al.* 2001). However, this study did not consider whether the presence of gulls increased provisioning costs for adults, nor whether other factors, such as chick development, specifically affect vulnerability to kleptoparasitism in mixed versus single-species colonies.

To better understand the costs imposed by kleptoparasitism, further comparisons of colonies that differ only in the presence of a kleptoparasitic species are needed. Key factors to investigate include the total amount of food stolen and the costs of attempting to feed offspring under the threat of kleptoparasitism. In addition, detailed information on what is stolen and when, is necessary to determine which factors make birds vulnerable to parasitism and therefore more likely to be the targets of kleptoparasitic attacks. Specifically, direct comparison of inter- versus intraspecific kleptoparasitism is crucial to determine the relative costs they impose, how they differentially affect behaviour and whether they interact to affect the outcome of kleptoparasitism (Ens *et al.* 1990). For example, where provisioning adults are vulnerable to intra and interspecific kleptoparasitism in different contexts, this has the potential to drive different behaviour in single-species versus mixed colonies. Such investigations would help to elucidate the dynamics underlying interactions within mixed-species aggregations and shed light on the evolution of these relationships, particularly when there are potential shifts between mutualism and parasitism.

In southern Africa, greater crested terns *Thalasseus bergii* often breed in mixed-colonies with Hartlaub's gull *Chroicocephalus hartlaubii* (Uys 1978). Greater crested terns generally lay one egg (Crawford *et al.* 2005). For the first 2–4 days after hatching parents feed their immobile chick in the nest cup, thereafter feeding occurs out of the nest cup as the precocial chicks become mobile. Mobile chicks remain flightless until fledging and frequently gather in crèches (Heydorn & Williams 1993). Recent observations indicate that terns returning to provision offspring are often victims of kleptoparasitism by other terns, but also by Hartlaub's gulls (Gaglio & Sherley 2014). However, the impact of kleptoparasitism on these terns by gulls, and also by other terns, has not been explored. In this chapter, I first aim to investigate the direct costs of kleptoparasitism by comparing the frequency of kleptoparasitism attempts, and the amount of food stolen between a single-species tern colony, and mixed colony where terns breed in association with Hartlaub's gulls. Exploring whether patterns of intraspecific kleptoparasitism vary between these colonies will enable me to establish whether any differences are driven by the presence of gulls. I will then investigate the relative costs of intra versus interspecific kleptoparasitism within a mixed colony, specifically considering the factors affecting when terns are vulnerable to kleptoparasitism. Finally, I will investigate the indirect costs borne by terns to prevent loss of prey, and whether this differs between inter- and intraspecific kleptoparasitism.

Methods

Study system

Data were collected on Robben Island, from February to May during three breeding seasons (2013, 2014 and 2015). Two colonies with different sizes occurred in the first two breeding seasons (2013-2014) and only one large colony was settled in 2015, as described in Chapter 1. At the mixed colonies, located within the Robben Island human settlement, greater crested terns were observed to breed in association with ca 50 and 30 Hartlaub's gull in 2013 and 2014, respectively and ca 100 gull nests were observed in 2015. The two colonies were similar in terms of substratum, vegetation (Chapter 1) and nesting density (ca 7.0 ± 2.5 nests m^{-2}; Gaglio *et al.* 2015a) and assumed to be under similar environmental conditions (Chapter 1).

Throughout the study period, greater crested tern's activity (hereafter 'tern') at the mixed colony was monitored daily, with the number of breeding pairs of terns and Hartlaubs' gulls (hereafter 'gull') recorded from the moment the colony was settled. These terns occupy an area for several days before laying eggs and establishing a colony, see (Gaglio *et al*. 2015a).

Rates of kleptoparasitism on nestling and mobile chicks

Feeding and kleptoparasitism rates during the tern chick's nestling phase were assessed using video recordings. Filming took place from February to March in 2013, 2014 and 2015 at all observed colonies, using video cameras as described in Chapter 4. A total of 229 nests were monitored during 35 days of video-recording. In this study, chicks within the nest-cup were termed "nestlings" and chicks out of the nest-cup were termed "mobile chicks". Each individual was given a nest or chick ID code. As chicks became mobile, video-recording was not possible. Instead, feeding frequencies and rates of kleptoparasitism were gathered from a hide, using focal observations on individual chicks (distance 10 – 30 m) that were banded with metal and engraved colour rings (Chapter 4) and followed for at least two consecutive feeds. Ringing by DEA was only performed on mobile chicks, hence analyses comparing nestling and mobile chick data could potentially include individual chicks recorded both within the nest and when mobile, but with different ID codes. However, the probability that individuals were repeatedly sampled within different chick stages was low due to recruitment frequencies and the large number of chicks monitored (during all three years of study 229 nestlings were monitored out of a total of ca 26,700 nestlings at both colonies and 149 mobile chicks were monitored out of a total of ca 11,200 mobile chicks observed and ca 1,250 chicks were banded at the mixed colony). Hence, age classes were compared directly in the same analysis. Breeding by greater crested terns is highly synchronous within the same colony (Crawford *et al.* 2005), and most chicks were already out of their nest-cup when visual observations of mobile chicks took place (25 days of observations), so there was little temporal overlap in data collected for nestlings and mobile chicks.

Video recordings were analysed using VLC media player (VideoLAN project). The fate of prey and kleptoparasitism events were documented as follows: (1) delivered (when the prey was successfully delivered to a chick); (2) tern kleptoparasitism (intra-specific, when the prey was stolen by another tern); (3) gull kleptoparasitism (inter-specific, when the prey was stolen by a gull); (4) focal adult consumed the prey (typically, but not always, when the prey was swallowed by an adult undergoing a kleptoparasitic attack); (5) prey given to the partner (courtship or display) and (6) prey lost or stolen outside the screen/or observer view (when the provisioning adult under attack was forced to fly away from the nest and returned without its prey; in these cases the outcome of the kleptoparasitic attack was unknown). Generally, adults that lost their prey came back to the nest and interacted with their partner or chick, before departing on a new foraging trip or switching with the partner. In the rare event the adult was not observed coming back, the prey was considered lost after 10 minutes, as this duration corresponds to a short foraging trip for greater crested terns (McLeay *et al*. 2010).

An attempted kleptoparasitism was defined as a movement by an individual bird toward a tern holding a prey (either an adult or chick), and aiming to seize the prey item, or the aerial pursuit of an adult tern carrying prey (following Finney *et al.* 2001). No aerial chases were observed on terns not carrying prey. Tern kleptoparasitism typically occurred on the ground between neighbours at the nest, usually when chicks were handling prey items, which often fell to the ground. Conversely, kleptoparasitism by gulls occurred in the air as well as on the ground and adults with prey were targeted as they approached their nest or while transferring prey to chicks. These attempts were differentiated from attacks that did not target prey. For example, attacks over territory were observed largely by incubating terns, which use their beaks to chase away intruders and defend their nest. I also recorded the number of feeding passes per food item by adults attempting to deliver prey. A feeding pass occurred when an adult approached its chick with a food item at a distance of ≤ 1 m, but then flew away. Finally, for a subset of successful feeding passes, where there was, or was not a kleptoparasitism attempt, I recorded the time elapsed (in seconds) between the moment the tern landed near the nest with a prey item in the bill until the moment the prey was ultimately swallowed by the chick (termed ‘handling time’).

The type of prey items returned to chicks were identified as 'silver' or 'other' prey. Silver prey included fish such as anchovy, sardine, redeye round-herring, Atlantic saury and other less common silver fish. Other prey included other fish (e.g. long-snout pipefish), and non-fish prey (e.g. crickets, squid, etc.; see Chapter 3). Prey size was estimated relative to the adult tern's bill length, and categorized as "small" (prey ≤ 1.5 times the adult's culmen, ≤ 90 mm) and "large" (prey > 1.5 of the tern's bill culmen, > 90 mm). While adults were incubating eggs, their partners occasionally returned with prey for courtship. The number of prey recorded in this period (during 400 hours of video-recording) was very low (n = 13/1150 return visits), and only on one occasion was a kleptoparasitic attack attempted (by another tern). Hence, kleptoparasitism of incubating birds was unlikely to be important and was therefore excluded from analyses.

Statistical analyses

Fewer data were available on prey type and size per feeding attempt at the single-species colony. Consequently, proportion tests (non-parametric 2-sample test for equality of proportions) were used to determine whether prey sizes and types provisioned at the two colonies were comparable. The handling time during a feeding attempt, from when adults landed at a nest to when a chick received prey, with and without a kleptoparasitic attack, was compared using a two-sample t-test with data $\log_{10}$ transformed to fulfil assumptions of normality.

To further investigate the outcome and consequences of kleptoparasitism, generalised linear mixed models (GLMMs) were undertaken using the R package lme4 (Bates & Maechler 2009, R Core Team 2016) allowing for the inclusion of both fixed and random terms. ID code (nestling or mobile chick identity) nested within year, was used to fit random intercepts in all models to account for repeated measures. I used a hypothetico-deductive approach and created maximal models from which terms were sequentially dropped in order of significance and retained in the model only when log-likelihood ratio tests indicated that their removal significantly reduced the model's explanatory power. The residuals for each model were checked for over-dispersion and visually for homogeneity of variances.

Kleptoparasitism at mixed versus single-species breeding colonies

To investigate whether terns suffered increased kleptoparasitism pressure in the presence of gulls, I first used a GLMM (binomial error, logit link) to determine: (i) the overall likelihood of a kleptoparasitism attempt and (ii) whether food was stolen or lost following kleptoparasitism (tern and gull kleptoparasitism combined), at the two colonies. I then used a GLMM (binomial error, logit link) to determine the likelihood of (iii) a tern kleptoparasitism attempt only and (iv) whether food was stolen following the attempt, at the two colonies. It was not possible to investigate colony differences in gull kleptoparasitism alone, because this was not observed at the single-species site. Explanatory variables were colony (single-species, mixed) and prey item size (small, large). I first undertook an analysis with the subset of feeding attempts where prey size was known, to determine whether prey size affected kleptoparasitism. Where this did not significantly improve model fit (likelihood-ratio test), I removed prey size and then analysed the full dataset. Similar methods were used in all subsequent analyses where prey size was included as an explanatory variable.

Comparison of intraspecific and interspecific kleptoparasitism at the mixed colony

For the mixed colony only, I first used GLMMs (binomial error, logit link) to test whether terns or gulls more frequently kleptoparasitise food. For this, I investigated the proportion of parental feeding passes per nestling or mobile chick on which there were (i) kleptoparasitism attempts by either terns or gulls and (ii) the proportion of occasions when food was stolen or lost. Explanatory variables were kleptoparasitism type (tern, gull), chick stage (nestling, mobile) and their interaction. I then used GLMMs (binomial error, logit link) to further investigate the factors affecting the likelihood of (iii) a tern or (iv) gull kleptoparasitism attempt, and whether food was stolen or lost following (v) a tern or (vii) gull kleptoparasitism attempt at the mixed-species colony. Explanatory variables included prey size and chick stage.

Finally, to explore when gull versus tern kleptoparasitism attempts are successful, and therefore why they may target specific provisioning contexts, I used a GLMM (binomial error, logit link) to determine (viii) what factors affect the likelihood that a kleptoparasitism attempt is successful. Explanatory and random terms were the same as above, with the inclusion of the species attempting kleptoparasitism (gull, tern, both) and their interaction.

Parental costs due to kleptoparasitism avoidance tactics

I used GLMMs to investigate (i) whether kleptoparasitism attempts increased the number of feeding passes adults took to deliver food to their young at the two colonies. The number of feeding passes was fitted as the response variable in a GLMM (Poisson error, log link). Explanatory terms included prey size and chick stage, with the addition of whether or not there was a kleptoparasitism attempt (attempt, no attempt).I then additionally used a GLMM (Poisson error, log link) to investigate the effect of chick stage and food item size on number of delivery passes using data for the mixed colony (ii). Finally, I used a

GLMM (binomial error, logit link) to investigate the factors (colony, kleptoparasitism attempt and prey size) affecting whether adults ate food themselves (iii).

All analyses were conducted using R (v. 3.3.1) (R Core Team 2016), and the significance level set at $P < 0.05$ for all tests.

Results

The development of the mixed-species colony followed the same steps in each year. Initially, a group of terns laid eggs in one area, while in the vicinity many other pairs of terns were observed courting and copulating (17–23 February 2013; 22–28 February 2014; 22–28 February 2015). Hartlaub's gulls were present, but none had laid eggs. Few days later (2–4 days), while the colony of terns was still growing, the first gull's nests were recorded in close proximity to incubating terns.

Among all prey returned to the mixed colony, 22% were scored as 'large' (> 1.5 times adult bill length) and 78% 'small', with similar proportions when compared to the single-species colony (16% large and 84% small; prop.test $\chi^2 = 1.16$ d.f. = 1, p = 0.28). There was a marginal difference in the proportion of prey types returned between the colonies, with silver fish accounting for 92% of prey at the mixed colony and 99% at the single-species colony (prop.test $\chi^2 = 5.70$ d.f. = 1, p = 0.02).

The impact of gulls at mixed versus single-species tern breeding colonies

Terns suffered increased kleptoparasitism pressure in the presence of gulls at the mixed colony, compared to the single-species colony (Table 5.1). Overall, the likelihood that a prey item returned to the colony was subject to a kleptoparasitic attempt was greater at the mixed 44.1 ± (4.42%) than at the single-species colony 7.5 ± (1.91%) ($Z = -5.05$, p = <0.001, n = 682, Table C.1, Figure 5.1a). Similarly, significantly more prey returned were stolen or lost at the mixed (22.6 ± 2.72%) than at the single-species colony (4.1 ± 1.11%) ($Z = -6.13$, p = <0.001, n = 682, Table C.1, Figure 5.1b). When considering kleptoparasitism by terns, there was no significant difference between the two colonies in the likelihood of a kleptoparasitism attempt by a tern, but prey returned were more often lost or stolen as a result of tern kleptoparasitism at the mixed colony, which cannot be accounted for by the terns increase only (mixed 8.0 ± 3.83%, single-species 3.1 ± 1.84%) (attempts: $Z = -1.25$, $p = 0.21$, n = 682; stolen: $Z = -2.54$, $P = 0.010$; n = 682; Table C.1, Figure 5.1c,d).

Factors affecting the likelihood of kleptoparasitism

Gulls and terns were similarly likely to attempt kleptoparasitism on nestlings, but terns were significantly less likely 1.1 ± (0.52%) to attempt kleptoparasitism on feeding attempts to mobile young than gulls 6.5 ± (1.31%) (interaction: $Z = 2.59$, $p = 0.009$, $n = 578$, Figure 5.2), while these factors did not influenced the likelihood of prey returned being stolen or lost (Table C.2).

Prey size was an important determinant of kleptoparasitism by terns at the mixed colony, which were more likely to attempt to steal larger prey (large = 36.5 ± 11.14% small = 23.2 ± 7.90%) and more large prey were stolen or lost as a result of tern kleptoparasitism (large = 9.5 ± 3.76% small = 3.1 ± 1.41%) (attempted: $Z = -2.56$, $p = 0.010$, $n = 582$; stolen or lost: $Z = -3.03$, $p = 0.002$, $n = 582$, Table C.2, Figure 5.3 a,b). Conversely, prey size did not affect the likelihood that gulls attempted to kleptoparasitise food ($Z = -1.84$, $p = 0.064$, $n = 582$)**,** nor whether prey were stolen or lost following such attempts ($Z = 1.38$, $p = 0.167$, $n = 582$). However, there was a greater likelihood (two-fold for terns and five-fold for gulls) that provisioning attempts to nestlings resulted in prey being stolen or lost, than in provisioning attempts to mobile chicks, following either tern ($Z = 4.13$, $p < 0.001$, $n = 1,158$) or gull kleptoparasitism ($Z = 2.49$, $p = 0.012$, $n = 1,158$, Table C.3, Figure 5.3 c,d), presumably because larger chicks are more efficient at handling prey, making it harder to steal from them.

Consideration of when gulls and terns were successful in their kleptoparasitism attempts revealed that large prey were nearly twice as likely to be stolen as small prey ($Z = -2.89$, $p = 0.003$, $n = 289$), Table C.4, Fig 5.4a). Furthermore, kleptoparasitism attempts by terns or both terns and gulls were more often successful on nestlings than on mobile young, while kleptoparasitism success by gulls alone was unaffected by chick age and was higher on mobile chicks than by terns or both species together (Nestling: gulls = 22.4 ± 7.91%, terns = 38.7 ± 7.94%, both = 55.8 ± 12.23%; Mobile: gulls = 21.0 ± 7.75%, terns = 5.1 ± 3.73%, both = 6.3 ± 4.55%; both species on nestling: $Z = 2.44$, $p = 0.014$, $n = 468$, Table C.4, Figure 5.4b).

Table 5.1: Number (and proportions) of different fates of prey returned to greater crested tern chicks during nestling and mobile stages at single-species and mixed-species colonies on Robben Island (2013–2015).

Colony & Chick stage	Fate of prey	2013	2013 (%)	2014	2014 (%)	2015	2015 (%)	Total	Total (%)
Single-sp.	Delivered	114	65%	104	61%	-	-	218	63%
Nestling	Success tern (attempted)	11 (16)	6% (9%)	4 (18)	2% (11%)	-	-	15 (34)	4% (10%)
	Lost	28	16%	26	15%	-	-	54	16%
	Swallowed	19	11%	31	18%	-	-	50	14%
	Given partner	4	2%	5	3%	-	-	9	3%
	Total	176		170				346	
Mixed-sp.	Delivered	31	42%	169	64%	236	57%	436	58%
Nestling	Success tern (attempted)	12 (19)	16% (26%)	10 (24)	4% (9%)	28 (158)	7% (38%)	50 (201)	7% (27%)
	Success gull (attempted)	5 (13)	7% (18%)	20 (114)	8% (43%)	11 (85)	3% (20%)	36 (212)	5% (28%)
	Lost	14	19%	40	15%	86	21%	140	19%
	Swallowed	9	12%	21	8%	39	9%	69	9%
	Given partner	2	3%	6	2%	16	4%	24	3%
	Total	73		266		416		755	
Mixed	Delivered	66	85%	179	86%	119	98%	364	90%
Mobile	Success tern (attempted)	2 (10)	3% (13%)	4 (56)	2% (27%)	1 (35)	1% (29%)	7(101)	2% (25%)
	Success gull (attempted)	8 (33)	10% (42%)	19 (81)	9% (39%)	0 (16)	0% (13%)	27 (130)	7% (32%)
	Lost	2	3%	5	2%	1	1%	8	2%
	Total	78		207		121		406	

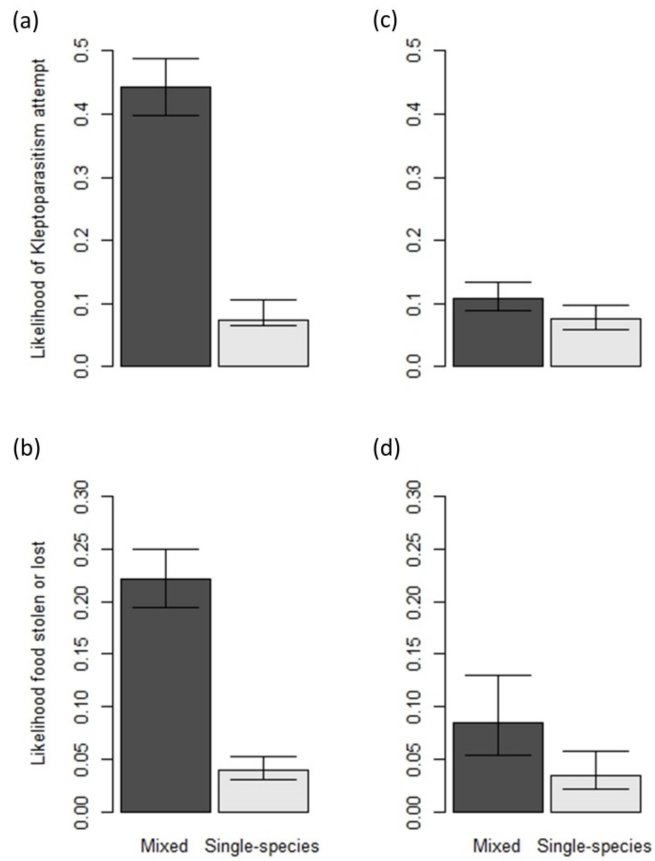


Figure 5.1: The likelihood: (a) that a kleptoparasitism attempt was made on terns returning prey to chicks at a single-species and mixed colony, (b) that a returned prey item was lost or stolen, (c) that a kleptoparasitism attempt was made by terns only, at the two colonies, and (d) that a returned prey item was lost or stolen as a result of kleptoparasitism by a tern only. Predicted means from models ± 1 SE are shown for all figures.

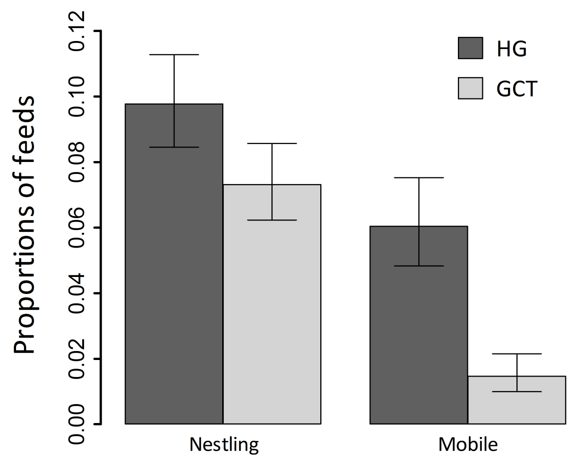


Figure 5.2: Overall proportion of parental feeds by greater-crested terns to their nestling and mobile chicks on which terns or Hartlaub's gulls attempted a kleptoparasitic attack. HG = Hartlaub's gull; GCT = greater-crested tern. Predicted means from models ± 1 SE are shown.

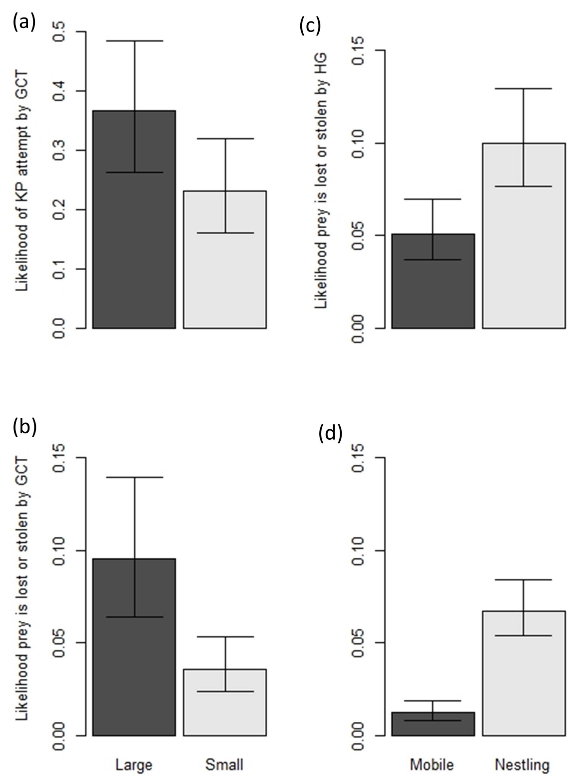


Figure 5.3: (a) Likelihood that greater-crested terns (GCT) attempted to kleptoparasitise prey from terns and (b) the likelihood that prey were stolen or lost following a tern kleptoparasitism attempt, according to prey size. Likelihood prey were stolen or lost following (c) Hartlaub's gull (HG), or (d) tern kleptoparasitism attempt, according to chick stage. Predicted means from models ± 1 SE are shown for all figures.

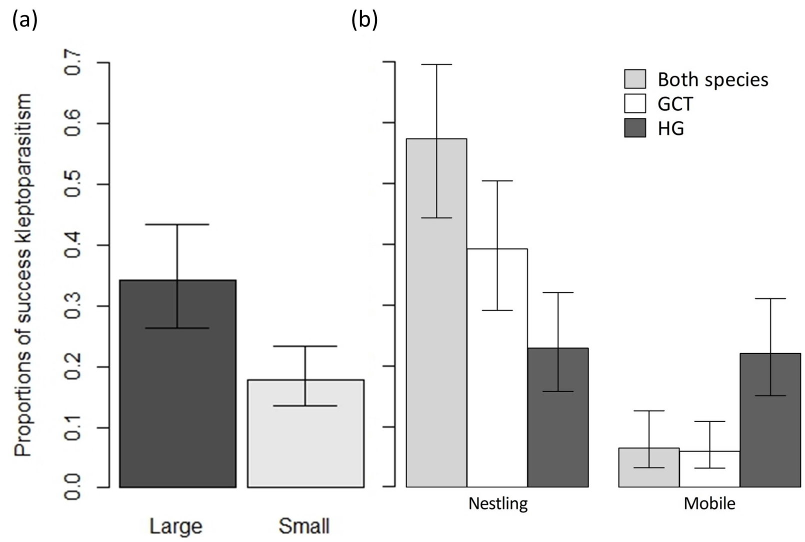


Figure 5.4: Likelihood that a food item was successfully stolen, when a kleptoparasitic attack was performed according to prey size (a). Likelihood of successful kleptoparasitism by species (GCT = greater crested tern; HG = Hartlaub's gull or both) when an attack was performed on a nestling or a mobile chick (b).

Parental costs due to kleptoparasitism avoidance tactics

Adults performed more feeding passes per prey item returned to a chick at the mixed (1.8 ± 0.14) than at the single-species colony (1.5 ± 0.13) (Z = -2.10, p = 0.035, n = 682) and when under a kleptoparasitic attack (attack: 2.1 ± 0.19, no attack: 1.2 ± 0.10; Z = -7.18, p < 0.001, n = 682; Table C.5, Figure 5.5a,b). Investigation of feeding passes at the mixed colony, similarly revealed that significantly more feeding passes were made when under attack (attack: 2.4 ± 0.11, no attack: 1.2 ± 0.06), (Z = 14.9, p < 0.001, n = 582). Typically, adults required one feeding pass to provision chicks when not under attack, yet this doubled when there was a kleptoparasitism attempt. Additionally this analysis showed that marginally more feeding passes were made when provisioning nestlings versus mobile chicks (Z = 3.15, p = 0.001, n = 582; Table C.6, Figure 5.5c,d).

Adult terns were approximately three times more likely to swallow prey that they were trying to provision to chicks (n = 560) at the mixed (14.2 ± 4.49) than the single-species colony (5.9 ± 2.14) (Z = 2.14, p = 0.031, n = 560, Table C.7, Figure 5.6a) and when attacked than when not under attack, both when the data from both colonies were combined (attack: 15.1 ± 4.92%, , no attack: 5.2 ± 1.63%, p = 0.001, Table C.7, Figure 5.6c) and at only the mixed colony (attack: 3.3 ± 1.70%, , no attack: 1.2 ± 0.71%, Z = 2.6, p = 0.007, n = 560, Table C.7, Figure 5.6b;). Finally, successful delivery of prey without any interference was significantly shorter compared to the mean handling time when adults were under a kleptoparasitic attack (two-sample t-test p < 0.001; Figure 5.7).

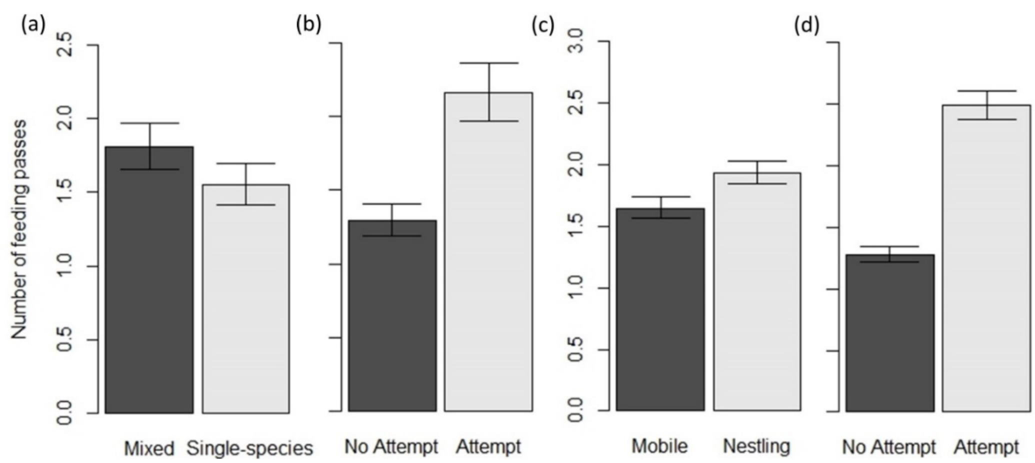


Figure 5.5: Overall number of feeding passes performed by adult greater crested terns, (a) between the two colonies and (b) when a kleptoparasitism attempt was observed or not. Numbers of feeding passes performed by adult greater crested terns according to (c) chick stage and (d) when a kleptoparasitism attempt was observed or not. Predicted means from models ± 1 SE are shown for both figures.

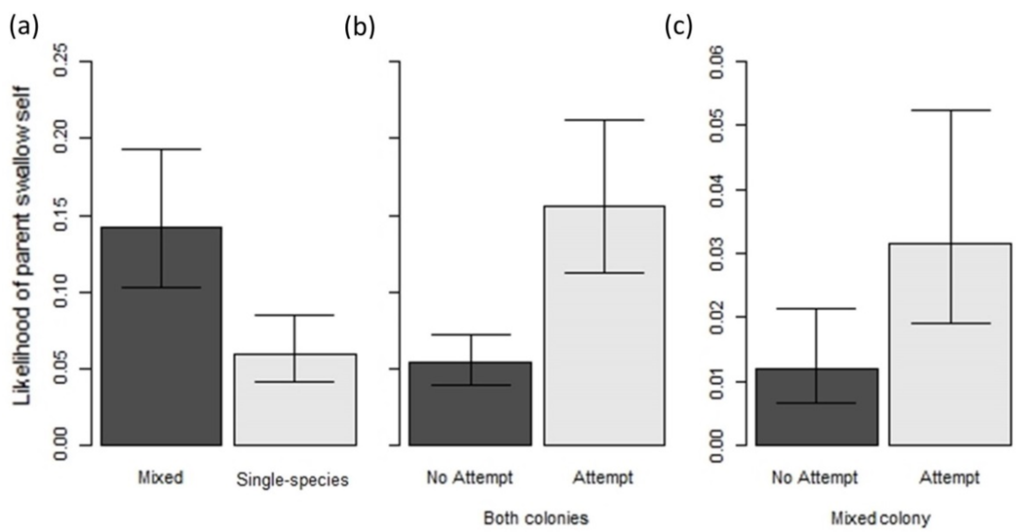


Figure 5.6: (a) Likelihood that adults swallowed a prey item returned to the nest (a) at the mixed or single-species colony, and when a kleptoparasitic attempt occurred (Attempt) or not (No Attempt) for data from (b) both colonies or (c) the mixed colony only. Predicted means from models ± 1 SE are shown.

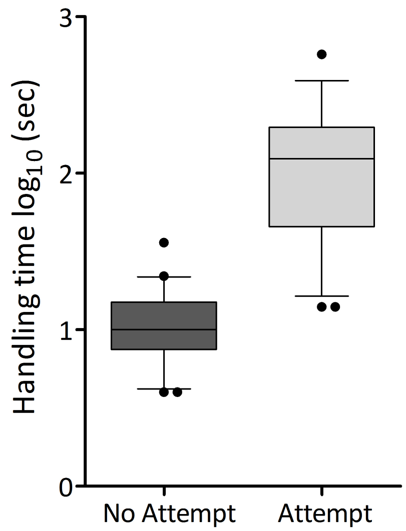


Figure 5.7: Comparison of time taken to deliver a prey item (handling time, $\log_{10}$ seconds; box-plot whiskers 10th and 90th percentile) when no kleptoparasitism was observed (No attempt) and when at least one kleptoparasitic attempt was performed by terns and/or gulls (Attempt).

Discussion

This study compares patterns of kleptoparasitism between a single-species breeding colony of greater crested terns and one breeding in association with Hartlaub's gulls. Results show that breeding with gulls increases the rate of kleptoparasitism and the amount of food terns lose, due to parasitism by gulls. In fact, kleptoparasitism was more than four times greater when terns bred in association with gulls and this increase could not be accounted for by the small difference in intraspecific kleptoparasitism between the colonies. The presence of gulls also increased behavioural costs through greater time and presumably energy expenditure when attempting to deliver prey in the face of kleptoparasitic attacks. Such attacks further reduced chick provisioning because parents were often forced to eat prey themselves. In addition, the presence of gulls expanded the period when chicks were sensitive to kleptoparasitism, because unlike other terns, gulls continued to engage in kleptoparasitism when terns were provisioning mobile chicks that had left the nest. Together, these findings illustrate that in a mixed-species colony, terns suffer direct costs to chick provisioning rates and indirect costs through energy expenditure, which together might impact reproductive success. Consequently, breeding assemblages could shift towards parasitism when food theft is common and the costs of associating with other species may outweigh the benefits in terms of predator defense.

Results also showed that overall, nestling chicks suffered greater costs of kleptoparasitism than mobile chicks that had left the nest to join crèches. The greater proportion of prey stolen or lost at this breeding stage was driven by kleptoparasitism by both terns and gulls, with terns attempting to steal less food from mobile young, likely because they were less successful when they targeted mobile chicks. Nestlings may be particularly vulnerable to other terns because they are restricted to the nest cup and in close proximity to other breeding terns. Their predictable location may also allow kleptoparasitic individuals to accurately predict where the prey will be returned, increasing their probability of success (pers. obs., Stienen 2006). However, the high rate of prey loss to both terns and gulls observed when feeding nestling chicks is probably because nestlings are clumsy when handling prey items. Small chicks struggle to swallow larger prey items, increasing the handling time and consequentially the risk kleptoparasitism (*sensu* Garcia *et al.* 2014). The dispersal of the tern chicks away from other nesting tern adults during the mobile stage, combined with the greater age and size of mobile chicks may be responsible for the lower success of kleptoparasitism during this stage. The precocial behaviour of chicks has been proposed to be an anti-kleptoparasitism tactic in sandwich terns breeding in a mixed-species colony (Stienen & Brenninkmeijer 1999). In greater crested terns precocial behaviour significantly reduced kleptoparasitism attempts by other terns, and not gulls, suggesting a potential function to reduce intraspecific kleptoparasitism in this species.

The size of the prey returned to the colony also influenced the rates of kleptoparasitism by terns which tried to steal larger prey more often. Similar increases in kleptoparasitism on larger food items have been observed in other studies (Steele & Hockey 1995, Ratcliffe *et al.* 1997, Garcia *et al.* 2010). The selectivity for larger prey items by terns may be driven by the fact that large prey have a greater energetic reward, are more conspicuous and generally easier to steal, especially due to the inability of nestlings to handle large prey. Conversely, gulls did not target larger prey items more often than small prey, despite the fact that, like terns, they were more successful when they did so. This could perhaps result from gulls targeting provisioning adults more often than terns, when kleptoparasitism success might be unrelated to prey item size. Additionally, terns and gulls may differ in the net payoffs available from kleptoparasitism of small prey because competition costs likely differ, as does the value of the prey resource to these species (Huntingford and Turner 1987). Consequently, small prey may offer insufficient benefits to counter competition costs for terns, but not gulls (Morand-Ferron *et al.* 2006, Stienen 2006, García *et al.* 2010). Provisioning terns likely suffer indirect costs from kleptoparasitism through energy invested in evading food theft attempts (Hulsman 1984, Stienen & Brenninkmeijer 1999, Stienen *et al*. 2001). Adults typically required one attempt to deliver prey to their nestlings, but when pursued by other terns or gulls, adults flew off and made subsequent delivery attempts, or swallowed prey themselves**.** The increased delivery passes (32%) and longer handling times (85%) to deliver prey to nestlings when under a kleptoparasitic attack illustrate how terns expend considerable time and energy avoiding kleptoparasitism. Furthermore, adults increase the proportion of prey swallowed (particularly at the mixed-species colony) in response to kleptoparasitism. Although swallowing prey themselves likely redeems some of the adult's investment in provisioning attempts, offspring provisioning will decline and adults will still pay a cost for the time and energy expended in the round trip to capture and return with prey. Nevertheless, these behavioural tactics likely mitigate the overall impact of kleptoparasitism. In addition to evasive behaviours during kleptoparasitic attacks, individuals may further reduce kleptoparasitism costs by adjusting provisioning**.** For example, by provisioning prey less vulnerable to kleptoparasitism as proposed by Finney *et* al (2001). Recently there has been extensive consideration of how breeders adjust provisioning in response to predation pressure (Zanette *et al.* 2011) and future work exploring adjustments in response to kleptoparasitism could further illustrate the counter tactics employed by breeders and the indirect costs imposed by these.

Contrary to the expectation that terns derive benefits from seeking association with gulls, at Robben Island, gulls appeared to seek association with tern colonies. Several reports suggest that terns may seek associations with gulls, because the gulls are more aggressive to predators, thereby providing protection during the early stages of the terns' breeding season (Fuchs 1977, Veen 1977, Urban *et al.* 1986, Stienen 2006). However, in this study, gulls laid their eggs after the tern colony had settled, and the tern colonies were often surrounded by nesting gulls, a pattern also observed in other studies ((Stienen & Brenninkmeijer 1999, Stienen *et al.* 2001, Garcia *et al.* 2010). Thus, a more plausible interpretation may be that terns begin the colony first and only thereafter do gulls build nests around the tern colony (Fuchs 1977, Veen 1977, Stienen 2006). Hartlaub's gulls generally target different prey from terns (Ryan 1987) and therefore may benefit by exploiting terns when payoffs from self-foraging decline (Brockmann & Barnard 1979, Ens *et al.* 1990, Flower *et al.* 2013). Previous studies describing interactions between gulls and terns at mixed colonies have only illustrated the direct costs imposed by kleptoparasitism (Fuchs 1977, Quintana and Yorio 1999, Dies and Dies 2005, Stienen 2006). In particular, research on sandwich terns showed higher mortality of tern chicks in the presence of gulls in some years (Stienen & Brenninkmeijer 1999). By comparing a single-species and mixed colony my results demonstrate that breeding in association with gulls carried a cost for terns. The relationship, may therefore be parasitic rather than mutualistic, as described in other systems (e.g. Groom 1992, Baigrie *et al.* 2014), or more correctly payoffs may fluctuate from providing net benefits to net costs depending upon prevailing conditions. Further studies which explore productivity (fledging success, survival and chick growth rates) with or without kleptoparasitism are needed to better determine the mutualistic or parasitic nature of mixed-species associations (Finney *et al*. 2001).

The costs and benefits of breeding in association with kleptoparasitic species is likely related to variation in the anti-predator benefits (Stienen 2006), or costs of kleptoparasitism (Wood *et al* 2015). For greater crested terns, Hartlaub's gull may repel predators such as kelp gulls *Larus dominacanus* which steal eggs or chicks, thereby compensating for kleptoparasitism costs when such nest predation risk is high. Conversely, associating with other species may incur greater costs when the ratio of kleptoparasitic individuals to hosts increases (Wood *et al* 2015), or individuals more frequently resort to kleptoparasitism, owing to limitations on self-foraging (Flower *et al* 2013). Increasing nest failure, or nest abandonment under such circumstances might aggravate per capita kleptoparasitism on remaining breeders, potentially threatening colony persistence (Oro *et al.* 1996, St. Clair *et al.* 2001, Blackburn *et al.* 2009, Wood *et al.* 2015), with profound consequences at the population level. This appears to be an unlikely threat to greater crested terns at present, whose breeding numbers have increased over the last few decades in this region (Crawford 2009), implying that the current impact of kleptoparasitic gulls did not influence the terns' demography negatively. Nevertheless, it is important to monitor food availability and the ratio of terns and gulls breeding in association, to see how kleptoparasitism varies in response to changing environmental conditions (especially in an exploited environment such as the Benguela system). Ideally, more long-term data on variation in kleptoparasitism and nest predation are required to explore parasitism/mutualism costs and benefits from associating with other species and effects on population viability.

Conclusion

To conclude, this study provides evidence that when breeding in association with Hartlaub's gulls, greater crested terns suffer higher kleptoparasitism costs than when breeding alone. In general, the greater occurrence of kleptoparasitism was associated with a larger proportion of prey stolen, lost or swallowed by the adult, resulting in adult terns spending more time and energy avoiding attacking gulls. These impacts likely lead to reductions in food delivered to chicks and increased energetic cost of prey provisioning, with a potential negative effect on tern reproductive success. Whether this cost is greater than any benefits derived from associating with gulls remains unclear. Nevertheless, the costs of kleptoparasitism and observations of gulls nesting after terns, suggest that this assemblage of gulls and terns may be a form of parasitism instead of mutualism, with a core colony member exploited by the other species through kleptoparasitism. Further studies are needed to assess variation in the costs and benefits of associating with other species and whether kleptoparasitism may even threaten colonies under extreme conditions.

Appendix C

Table C.1: GLMM (Binomial) of the factors affecting the (I) overall likelihood of a kleptoparasitic attempt, (ii) Overall likelihood that a prey was stolen, (iii) Overall likelihood of a tern kleptoparasitic attempt; (iv) Overall likelihood that a prey was stolen by a tern. Two sets of models are shown, which included a first analysis with a subset of feeding attempts where prey size was known (prey size in left set of columns), to determine whether prey size affected the outcome, and analysis of the larger dataset including where prey size was not known. Similar methods were used in all subsequent analyses where prey size was included as an explanatory term. The minimal model used 682 feeding attempts to 129 nests containing nestlings in 2013 and 2014 breeding season; for sub-analysis of prey size data was available to 348 feeding attempts to 112 nests containing nestlings in 2013 and 2014 breeding seasons. Significant terms are highlighted in bold.

Model term		**Effect ± S.E.**	***Z***	***P***	**Effect ± S.E.**	***Z***	***P***
(i)		*Overall likelihood of a KP attempt (prey size)*			*Overall likelihood of a KP attempt*		
Intercept		-0.25 ± 0.34	0.71	0.475	0.00 ± 0.25	0.001	0.999
Colony (mixed)	single-species	-2.14 ± 0.43	-4.93	**<0.001**	-2.19 ± 0.43	-5.05	**<0.001**
Prey size (large)	small	-0.36 ± 0.34	-1.06	0.287	-	-	-
(ii)		*Overall likelihood that prey was stolen (prey size)*			*Overall likelihood that prey was stolen*		
Intercept		-0.84 ± 0.27	-3.12	**0.001**	-1.25 ± 1.16	-7.84	**<0.001**
Colony (mixed)	single-species	-1.07 ± 0.33	-3.19	**0.001**	-1.92 ± 0.31	-6.13	**<0.001**
Prey size (large)	small	-0.59 ± 0.32	-1.82	0.068	-	-	-
(iii)		*Likelihood of a tern KP attempt (prey size)*			*Likelihood of a tern KP attempt*		
Intercept		-1.47 ± 0.32	-4.53	**<0.001**	-2.10 ± 0.23	-8.93	**<0.001**
Colony (mixed)	single-species	-	-	-	-0.39 ± 0.31	-1.25	0.210
Prey size (large)	small	-0.57 ± 0.35	-1.64	0.090	-	-	-
(iv)		*Likelihood that prey was stolen following tern KP (prey size)*			*Likelihood that prey was stolen following tern KP*		
Intercept		-1.99 ± 0.49	-3.99	**<0.001**	-2.37 ± 0.48	-4.95	**<0.001**
Colony (mixed)	single-species	-0.18 ± 0.43	-0.42	0.673	-0.93 ± 0.36	-2.54	**0.010**
Prey size (large)	small	-0.40 ± 0.43	-0.94	0.345	-	-	-

Table C.2: GLMM (Binomial) of the factors affecting the (v) proportion of parental feeding attempts to a nestling or mobile chick on which there were kleptoparasitic attempts by either terns or gulls and (vi) the proportion of feeding attempts was stolen or lost. Data were available for 578 feeding attempts to 289 nests or mobile chicks at the mixed-species colony between 2013 and 2015. Significant terms are highlighted in bold.

Model term		**Effect ± S.E.**	***Z***	***P***		**Effect ± S.E.**	***Z***	***P***
(v)		*Proportion of feeds with kleptoparasitism attempts*			(vi)	*Proportion of feeds when food was stolen or lost*		
Intercept		-2.74 ± 0.23	-11.65	**< 0.001**		-0.90 ± 0.11	-7.80	**<0.001**
Species (tern)	gull	-1.46 ± 0.41	-3.58	**< 0.001**		-0.18 ± 0.09	-1.89	0.058
Stage (mobile)	nestling	0.52 ± 0.26	1.99	**0.045**		-0.07 ± 0.13	-0.54	0.584
Species * Stage		1.14 ± 0.44	2.59	**0.009**		-	-	-

Table C.3: GLMMs (Binomial) of the (vii) Factors affecting the likelihood of a kleptoparasitic attempt by a tern, (viii) by a gull. (ix)Factors affecting the likelihood that a prey item was stolen or lost following a tern or (x) gull attack. Data were available from 1158 kleptoparasitic attempts on 289 chicks from 2013 to 2015 at the mixed-species colony (when including prey size data were available from 582 kleptoparasitism attempts on 243 chicks at the mixed colony in all years). Explanatory terms included prey size (small, large) and chick stage (mobile, nestling).

Model term		**Effect ± S.E.**	***Z***	***P***	**Effect ± S.E.**	***Z***	***P***
(vii)		*Factors affect the likelihood of a tern kleptoparasitism attempt*			*Factors affect the likelihood of a tern kleptoparasitism attempt (prey size)*		
Intercept		-1.24 ± 0.33	-3.70	**<0.001**	-0.54 ± 0.48	-1.12	0.260
Stage (mobile)	nestling	-0.16 ± 0.20	-0.79	0.428	-	-	-
Prey size (large)	small	-	-	-	-0.65 ± 0.25	-2.56	**0.010**
(viii)		*Factors affect the likelihood of a gull kleptoparasitism attempt*			*Factors affect the likelihood of a gull Kleptoparasitism attempt (prey size)*		
Intercept		-0.96 ± 0.30	-3.12	**0.001**	-0.33 ± 0.29	-1.14	0.253
Stage (mobile)	nestling	-0.10 ± 0.21	-0.49	0.620	-	-	-
Prey size (large)	small	-	-	-	0.45 ± 0.25	-1.84	0.064
(ix)		*Factors affecting the likelihood of food stolen or lost following a tern attack*			*Factors affecting the likelihood of food stolen or lost following a tern attack (prey size)*		
Intercept		-4.39 ± 0.44	-9.79	**<0.001**	-3.09 ± 0.60	-5.22	**<0.001**
Stage (mobile)	nestling	1.76 ± 0.42	4.13	**<0.001**	-1.70 ± 0.52	3.25	**0.001**
Prey size (large)		-	-	-	-1.04 ± 0.34	-3.03	**0.002**
(x)		*Factors affecting the likelihood of food stolen or lost following an gull attack*			*Factors affecting the likelihood of food stolen or lost following an tern attack (prey size)*		
Intercept		-2.92 ± 0.33	-8.70	**<0.001**	-2.07 ± 0.39	-5.22	**<0.001**
Stage (mobile)	nestling	-0.72 ± 0.29	2.49	**0.012**	-0.55 ± 0.30	-1.82	0.680
Prey size (large)		-	-	-	0.44 ± 0.32	1.38	0.167

Table C.4: GLMM (xi) (Binomial) of the factors affecting successful kleptoparasitism (data were available for 468 kleptoparasitic attempts on feeding attempts to 211 chicks/nests colony (when including prey size data were available from 289 kleptoparasitism attempts on feeding attempts on 169 nest/chicks at the mixed colony in all years).

Model term		**Effect ± S.E.**	***Z***	***P***
Intercept		-0.33 ± 0.45	-0.72	0.467
Prey size (large)	small	-0.87 ± 0.30	-2.89	**0.003**
Species (both)	tern/gull	-2.08 ± 1.07	-1.93	0.052
Stage (mobile) * Species (both)	nestling	2.87 ± 1.17	2.44	**0.014**
Stage (mobile) * Species (tern)	nestling	1.74 ± 0.80	2.18	**0.029**

Table C.5: GLMM (Poisson) (xii) of the factors affecting the number of passes adults took to feed food at the two colonies and the effects of kleptoparasitic attempts. Data were available for 682 feeding attempts to 129 chicks/nests colony (when including prey size data were available from 348 feeding attempts to 112 nest/chicks in 2013 and 2014).

Model term		**Effect ± S.E.**	**Z**	**P**	**Effect ± S.E.**	**Z**	**P**
		Number of feeding passes			*Number of feeding passes (prey size)*		
Intercept		0.84 ± 0.09	9.30	**<0.001**	0.45 ± 0.09	5.14	**< 0.001**
Colony (mixed)	single-species	-0.15 ± 0.07	-2.10	**0.035**	-	-	-
KP attempt (yes)	no	-0.50 ± 0.07	-7.18	**<0.001**	-	-	-
Prey size (large)	small	-	-	-	-0.07 ± 0.10	-0.69	0.488

Table C.6**:** GLMM (Poisson) (xiii) of the factors affecting the number of feeding attempts according to whether there was kleptoparasitism attempt or not and by chick stage (1158 feeding attempts to 289 nests containing nestlings in 2013-2014 breeding season; for sub-analysis of prey size 582 feeding attempts to 243nest/chicks in 2013 and 2014).

Model term		**Effect ± S.E.**	***Z***	***P***
Intercept		1.16 ± 0.06	2.73	**0.006**
Stage (mobile)	nestling	1.16 ± 0.05	3.15	**0.001**
KP attempt (yes)	no	0.67 ± 0.04	14.98	**<0.001**

Table C.7**:** GLMM (Binomial) (xiv) of the factors affecting the likelihood that adults swallow prey returned for their chicks when a kleptoparasitic attempt occurred or not at both colonies (data available for 560 feeding attempts to 126 nests containing nestlings in 2013 and 2014; for sub-analysis of prey size data available from 299 feeding attempts to 107nest/chicks at the mixed colony in all years).

Model term		**Effect ± S.E.**	***Z***	***P***	**Effect ± S.E.**	***Z***	***P***
Intercept		-3.34 ± 0.43	-7.70	**<0.001**	-1.84 ± 0.45	-4.04	**<0.001**
KP attempts (yes)	no	1.17 ± 0.36	3.23	**0.001**	-	-	-
Colony (mixed)	single-species	0.96 ± 0.45	2.14	**0.031**	-	-	-
Prey size (large)	small	-	-	**-**	-0.47 ± 0.44	-1.06	0.290
Intercept		-2.8 2 ± 0.33	-8.49	**<0.001**	-1.99 ± 0.48	-4.11	**<0.001**
KP attempts (yes)	no	0.90 ± 0.33	2.68	**0.007**	0.39 ± 0.41	0.95	0.341
Prey size (large)	small	-	-	**-**	-0.43 ± 0.45	0.96	0.337

Chapter 6

Synthesis

Introduction

The overall objective of this thesis was to investigate the possible factors contributing to the recent increase in the southern African population of greater crested terns. Prior to my study, relatively little was known about the biology of greater crested terns in southern Africa, and was limited to counts, elementary life history traits or relationships between food availability and number of breeding pairs (Cooper *et al.* 1990, Crawford *et al.* 2002, Crawford 2003, 2009). In the last three decades, the diet of the southern African population was assessed on only two occasions, with no data available from 1994 to 2012 (Walter *et al.* 1987a, Crawford & Dyer 1995). My study provides several novel findings and a more in-depth knowledge of foraging ecology, energetic requirements and cost of kleptoparasitism for breeding greater crested terns. By comparing the diet and energetics of the greater crested tern to those of other seabirds breeding in the region that rely on the same food resources, my study provides a greater understanding of the species-specific demographic responses to natural and human-induced ecosystem variation.

This final chapter aims to synthesize the major findings of this thesis and discuss the implications of the investigations carried out in previous chapters in the broader context of population responses to natural and anthropogenic environmental changes in the Benguela system. In addition, it outlines how future research could augment this study to enhance conservation and management plans for fish stocks and seabird populations in the southern Benguela region.

A non-invasive method for dietary study of seabirds

Fluctuations in populations of marine top predators, such as seabirds, can be indicative of conditions over large spatial and temporal scales, making them effective indicators of environmental change (Piatt *et al.* 2007, Parsons *et al.* 2008). Availability of prey is a major factor influencing seabird population dynamics, particularly for colonial species and therefore dietary investigations of seabirds provide vital knowledge on how species respond to prey availability and environmental change (e.g. Suryan *et al.* 2002; Parsons *et al*. 2008). In Chapter 2, I developed a non-invasive, photographic method to study the diet of breeding greater crested terns by identification of prey items carried in their bills. Application of this method in Chapter 3, demonstrated digital photography as a comprehensive tool to identify and estimate the size of tern prey. I identified > 24,000 prey items from at least 51 different prey taxa, and added 34 new prey species to the greater crested tern's diet. These results confirm the efficacy of this approach compared to more traditional (and more invasive) diet sampling methods, previously used to estimate the diet of this species (Walter *et al.* 1987a, Crawford & Dyer 1995). The comparison of photo-inferred diet obtained by two observers of equal photographic experience in the same conditions provided similar results, indicating the versatility of the method. Further investigation is needed to assess whether similar outcomes would also be obtained from photo-samples taken by photographers with different experience. Photo-sampling typically is limited to individuals returning prey to a predictable location (e.g. breeding colony/nest) and it does not necessarily always reflect what adults eat at sea. Hence, the use of photo-sampling together with other indirect methods (e.g. measuring stable isotope ratios in blood and feather tissues of adults and of prey; Inger & Bearhop 2008) may be beneficial to explore adult prey choice, or diet outside the breeding season.

The photo-sampling method developed in Chapter 2 can be implemented in seabird monitoring programs as a standard and effective tool to study the diet of greater crested terns or other prey loader species that return prey to known locations (e.g. Department of Environmental Affairs seabird long-term monitoring program). The large number of samples collected, allowed the estimation of a sampling regime, which can be used for a regular monitoring program. Despite the variability in the number of prey species captured by greater crested terns, results of Chapter 3 illustrated that just 7 prey species account for 90% of the total prey consumed by chicks. From the findings of this study, I am able to propose an optimal sampling regime with the minimum sample-size required for each breeding stage to detect the maximum variability of prey possible. This was done by taking a random sample of 3,000 images for each breeding stage and generating species accumulation curves (Figure 6.1). These results show that the optimal number of samples is breeding stage dependent, ranging from 200 - 450 samples with significantly fewer species being accumulated with increased sampling effort beyond these inflection points. This optimal sampling regime incorporated between 8 and 25 prey species depending on the breeding stage, which is expected to be representative of the majority of the prey returned to the colony. Further to this, I deduced the optimal number of days needed to spread this effort by randomly sub-sampling consecutive days of monitoring based on 3 and 6 day runs with the equivalent total number of samples taken in 1 day. Results could only be generated for early and late provisioning stages (Figure 6.2). In both stages 3 days of sampling performed optimally with more effort in terms of days sampled showing no appreciable benefit in terms of numbers of species accumulated (Figure 6.2). In summary, the proposed sampling regimes should consist of the collection of approximately 450 identifiable images per breeding stage distributed over 3 days of sampling each.

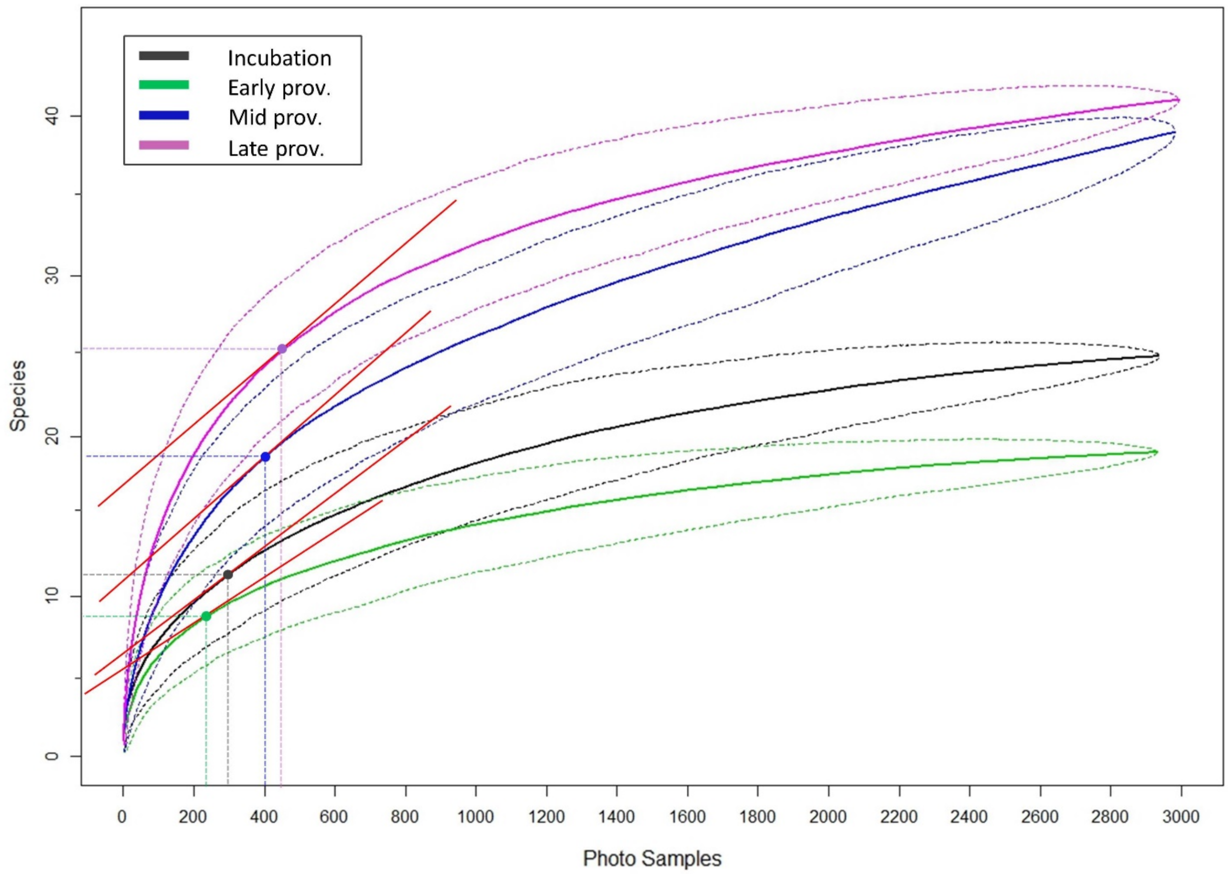


Figure 6.1: Species accumulation curves for greater crested tern diet at Robben Island according to breeding stages. Accumulation curves present the observed species accumulation from 3,000 random photo-samples collected during incubation (black line), early provisioning (green line), mid-provisioning (blue line) and late provisioning (purple line). Filled circles indicate the point of inflection of the curve. Vertical dotted lines indicate minimum recommended photo-sample size according to breeding stage and horizontal dotted lines indicate the number of species detected with that sample size.

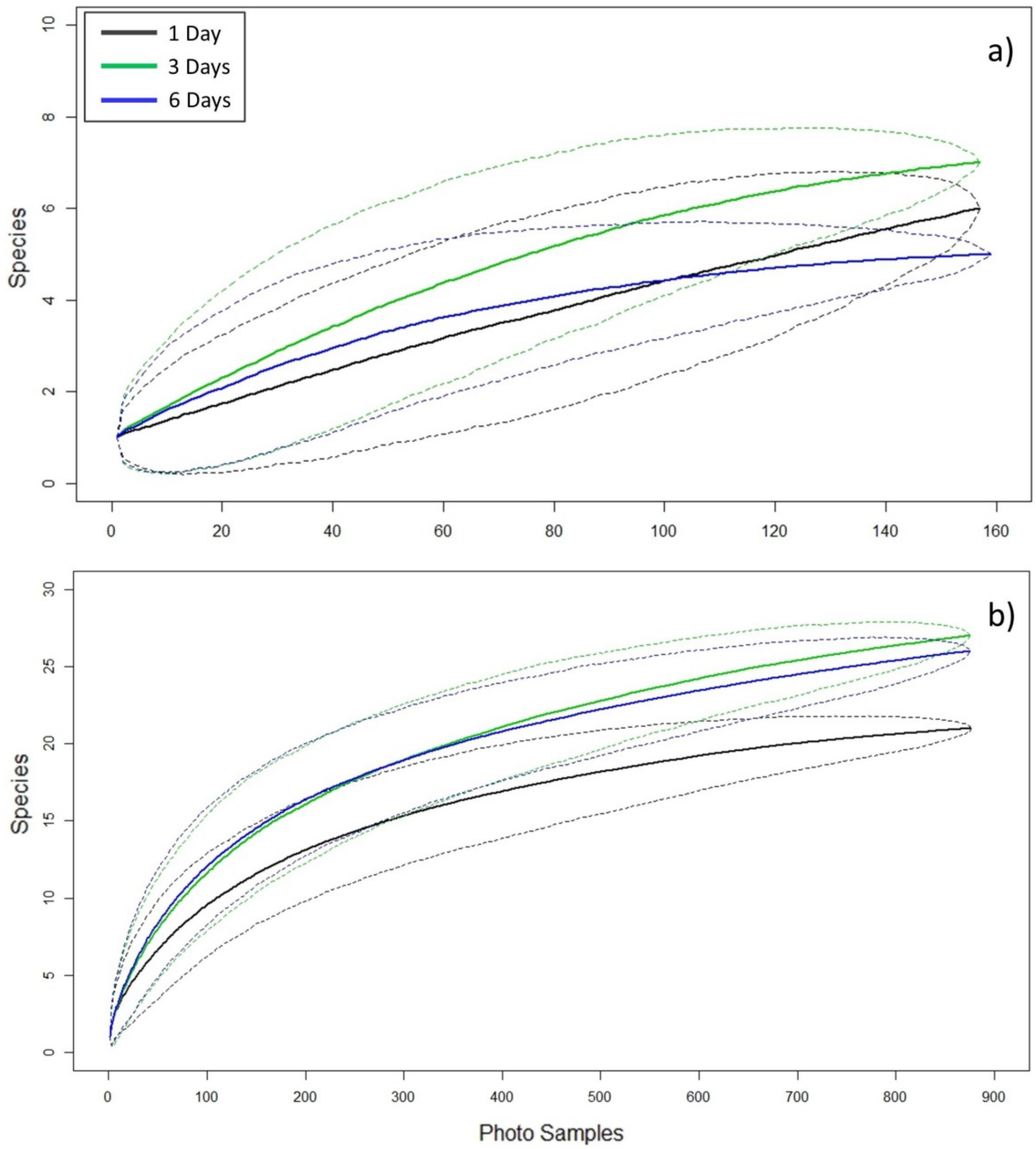


Figure 6.2: Species accumulation curves for greater crested tern diet at Robben Island according to number of days of sampling (1 day black line, 3 days green line, 6 days blue line). Results are shown for early provisioning (a) (maximum sample size in one day = 160) and late provisioning (b) (maximum sample size in one day = 860).

Further expansion of the approach developed in Chapter 2 may be to employ time-lapse photography. The recent development of programmable digital cameras with timers incorporated (e.g. camera-traps) may allow for automation of this photographic approach, without the need for the researcher's presence in the colony (e.g. Lorentzen *et al.* 2012, Huffeldt & Merkel 2013, García-Salgado *et al.* 2015 Lynch *et al.* 2015, Merkel 2016). Camera-traps located within the colony can collect numerous images of provisioning parents holding a prey in their bill, providing potential for a fully-automated, non-invasive, longitudinal dietary investigation for colonial species. However, this is less efficient than targetted photography (most images will not contain prey items), and image quality will need to be exceptional in order to give comparable results to targetted photographs. The low proportion of prey in camera-trap images makes their analysis extremely time-consuming, ideally requiring the implementation of an image-analysis software. This approach offers exceptional potential for computer-automated prey identification, but to be fully functional, this branch of technology (computer-aided) needs further developments (e.g. van Tienhoven *et al.* 2007, Sherley *et al.* 2010, Chabot & Francis 2016). An automated approach would be most useful in very remote locations and/or for species that are particularly sensitive to disturbance (e.g. threatened species).

Foraging plasticity and lower energy requirements as coping mechanisms

Although seabirds are able to buffer reduced food availability to some extent (Wendeln & Becker 1999, Takahashi *et al.* 2003), in highly variable marine ecosystems, variations in food supply and localized environmental factors are more likely to affect the foraging ecology of breeding seabirds and consequentially their reproductive output (Burger & Piatt 1990, Monaghan *et al.* 1992, McLeay *et al.* 2009b, Labbé *et al.* 2013). In contrast to greater crested terns, breeding African penguins, Cape cormorant and Cape gannets show different population trends and thus appear to be at greater risk from environmental and human induced variations (Pichegru *et al.* 2010b, Crawford *et al.* 2014, Sherley *et al.* 2017). Results from the diet (Chapter 3) and the foraging behaviour (Chapter 4) and energy requirements (Chapter 5) of greater crested terns investigated in this study provided some insights into the mechanisms underlying their success.

Breeding greater crested terns were found to mostly target small schooling Clupeiformes, with anchovy being the main prey. These Clupeiformes have high nutritional value for the regulation of physiological processes, which are beneficial to chick growth and may reduce chick fledging periods (Batchelor & Ross 1984, Pichegru *et al.* 2007). During breeding the delivery of high quality prey to chicks maximises the provisioning effort per unit time of foraging, as predicted by central place foraging models for single prey loaders (Orians & Pearson 1979, Davoren & Burger 1999) and can influence breeding success in many seabirds. For example, breeding failure among common guillemots *Uria aalge* was associated with the provisioning of lower quality prey or 'junk food' in the North Sea (Wanless *et al.* 2005). Similarly, Cape gannets breeding in the Benguela system frequently forage on fishery discards, which are of a much lower nutritional value than their natural food (sardine and anchovy) and have had negative consequences for chick growth (Grémillet *et al.* 2008).

The temporal variability in prey composition and anchovy size during the breeding season could possibly be reflective of the constraints on parents, which vary during the different breeding stages. During early provisioning, the adults are limited to delivering prey, which are small enough for their chicks to ingest, while during late provisioning they need to balance their own energetic needs, as well as increase high energy delivery rates for their chick, when its energy demand peaks (Takahashi *et al.* 2003, Shaffer 2004, Lyons *et al.* 2005, Burke & Montevecchi 2009). However, prey choice may be concurrently influenced by the spatio-temporal availability of prey (e.g., Montevecchi *et al.* 1988; Garthe *et al.* 1999) and localised environmental factors in the vicinity of their colony (e.g. wind, fog). In Chapter 3, anchovies were highly abundant in tern's diet at the start of the breeding season and became less frequent as the season progressed (from February to May) (Chapter 3). This does not correlate with the predicted abundance of young-of-the-year anchovy nearby the colony, as anchovy recruits only reach Robben Island after May (Hutchings *et al*. 1998, van der Lingen & Huggett 2003, Hutchings *et al.* 2009, 2014). The abundance of anchovy recruits in the diet of greater crested tern in this period may be beneficial for fledglings and may contribute to sustain the exceptional high adult and first-year survival assumed for this species (Payo payo *et al.* unpubl. data). Additionally, a peak in anchovy larvae abundance was detected at the onset of the terns' breeding season (January and February) ca 30 km south of Robben Island (Van der Lingen & Huggett 2003; data from 1995 – 2001), hence the abundance on small anchovy and larvae during the early stages of the season may be related to this seasonal occurrence, and in theory may influence the breeding phenology of the greater crested terns breeding in Robben Island.

A core understanding of the functional relationships between local prey availability and tern foraging ecology may be gained by the concurrent use of fine-scale recording of at-sea prey abundance coupled with greater crested tern diet and detailed foraging behaviour. Development of small scale fish surveys are currently under development and recent studies have shown that inexpensive recreational fish-finders can quantify fish abundance at fine-scales (McInnes *et al.* 2015), with the potential to be implemented into managements plans. In addition with the aforementioned opportunity to gather a large amount of diet samples, the recent development of miniature data-loggers suitable for small seabirds such as terns (Soanes *et al.* 2015, Maxwell *et al.* 2016) will help to determine to what extent temporal changes in foraging behaviour and prey choice are linked to changes in the availability of their main prey in the system. In addition, it will shows in greater detail the habitats used by individuals and the magnitude of their foraging range during the breeding season.

The foraging range of greater crested terns breeding in southern Africa is, in fact, currently unknown; however, is assumed to be <10 km (Walter *et al.* 1987b). Breeding pairs are known to carry fish across the Cape Flats, suggesting that they commute to foraging grounds in False Bay (at least 40 km), suggesting a larger foraging range similar to the Australian population (< 40 km; McLeay *et al.* 2010). The presumed short foraging range combined with their characteristic foraging plasticity is advantageous for single prey loaders, not only because they are limited to the amount of food that can be transported to the colony and by their shallow diving ability, but also because it reduces the need to fly long distances compared to some other species breeding in the same system (e.g. Cape gannets travel up to 200-300 km when provisioning chicks Pichegru *et al.* 2010a). Foraging plasticity may be an evolutionary adaptation to buffer the unpredictable spatio-temporal abundance and distribution of their main prey. In addition, greater crested terns may take advantage of social facilitation detecting foraging flocks of which terns are partially dependent as it is assumed that underwater predators (e.g. African penguins, dolphins and predatory fish) bring prey to the surface making them available for hunting terns (Haney *et al.* 1992, Ryan *et al.* 2012). The low proportion of anchovy returned to the colony on foggy days highlighted in Chapter 3, confirms the importance of such facilitations. Therefore, to better understand the social facilitation effect on this inshore forager, the implementation of miniaturized video cameras and GPS tracking recorders simultaneously, would reveal important detailed knowledge on the origins of terns movement patterns (Tremblay *et al.* 2014), although currently unrealistic due to terns small size.

This foraging plasticity (Chapters 2 and 3), combined with the greater crested tern's low energetic requirements (Chapter 4), may be crucial in allowing the terns to cope in a changing and highly exploited environment. In the northern Benguela for example, the population of foraging fish (sardine) has been depleted since the early 1970s, and species such as African penguins decreased due to the consumption of a more abundant but low quality prey (pelagic goby; Ludynia *et al.* 2010). In the same region, despite the fact greater crested terns are also relying on pelagic goby (J.-P. Roux pers. comm.), their populations have remained stable, suggesting that they do not appear to suffer when switching to an alternative low quality prey (Kemper 2007). In this context, the terns' low energy requirements are an advantage, as their chicks need less food than penguins (Chapter 4), highlighting the apparent species-specific responses to shifting foraging conditions, which seem to favour breeding greater crested terns.

The other life history characteristics of greater crested terns, the typical one-egg clutch (Crawford *et al.* 2002, 2005), together with their small body size (both adults and chick) and apparent low mass-specific flight costs (two times less than gannets or cormorants; Flint & Nagy 1984) may also contribute to the lower energy requirements compared to other breeding seabirds relying on pelagic fish (Chapter 4). In addition, their short fledgling period (almost half the fledging period of Cape gannets; Crawford *et al.* 2005), combined with their extended post-fledging care, (which doesn't occur in Cape gannets or African penguins, and is limited in Cape cormorants; Hockey *et al.* 2005) also help to lower energy requirements. During post fledging care (of up to four months; Crawford *et al.* 2005), juvenile terns follow their parents away from their breeding localities to foraging grounds and continue to receive food, which is more energetically efficient than central place foraging (Orians & Pearson 1979, Le Roux 2004). In addition, the relatively long period of support after fledging allows juveniles to fine-tune their hunting skills and for dispersal to areas where food is more abundant.

After breeding in the Western Cape, many terns (both immatures and adults), disperse northeast as far as Richards Bay (KwaZulu-Natal) and north as far as Walvis Bay (Namibia) (Underhill *et al.* 1999, Gaglio unpublished data), where nursery areas may be available to terns in the non-breeding periods (Underhill *et al.* 1999, Le Roux 2004). The nomadic behaviour during the non-breeding period, combined to their low fidelity to breeding sites, may benefit this species all-year round and may had contribute to maintain the high adult and juvenile survival assumed for this species (Payo payo *et al.* unpubl. data). Individuals may have the capability to choose breeding locations in relations to oceanic cues (e.g. abundance of forage fish), although they may be constrained by the absence of islands in suitable locations. Generally, species that are able to modify their distributional range seem to be more likely to cope with rapid natural or human induced environmental changes (Oro *et al.* 2004), hence the opportunity for greater crested terns to move where food is more abundant year-round is potentially of great benefit for their reproductive output and survival.

In contrast, the high fidelity to breeding localities coupled with the restricted foraging range of African penguins during breeding is suggested as one of the possible reasons for their decrease, particularly when local foraging resources are depleted (Pichegru *et al.* 2010b, 2012). The high mortality of juvenile penguins from west coast colonies is suspected to be linked to their maladaptive selection of foraging ground, being dramatically depleted by fishing and climate change (Sherley *et al.* 2017). Cape gannets, which have a larger foraging range than African penguins but also show high fidelity to breeding localities (Lewis *et al.* 2006), showed decreased reproductive output possibly resulting from the exploitation of fishery discards, while breeding due to reduction of their local natural prey (Grémillet *et al.* 2008, Cohen et al. 2014). Notably, the recent displacement of sardine and anchovy toward east seems to have played a crucial role to the recent collapse of Cape gannet west of Cape Agulhas and the concurrent increase of pairs breeding on Bird Island, Algoa Bay, off the southeastern coast of South Africa (e.g., Berruti *et al.* 1993, Pichegru *et al.* 2007, Grémillet *et al.* 2008, Crawford *et al.* 2014). Cape cormorants are another breeding seabird in the Benguela, which relies on pelagic fish. Like the greater crested terns, they show greater flexibility in terms of moving between breeding localities than penguins or gannets, and also have some post-fledging care (Berry 1976**,** Hockey *et al.* 2005). They are also flexible in terms of the timing of breeding, and can breed all year-round, although peak activity in the Western Cape is usually between September and February (Hockey *et al.* 2005), thus showing more flexibility than greater crested terns (70% of breeding occurs between February and March; Crawford *et al.* 2005). The cormorants' foraging range while breeding (up to 40 km, Hamann *et al.* 2012, Cook *et al.* 2012) is less than that of the Cape gannet, but similar to that of African penguins and perhaps greater than greater crested terns. However, between the 1990 and 2000s, in periods of prey scarcity off western South Africa, adult Cape cormorants suffered high mortality. Reasons for the recent decrease of Cape cormorant have not been fully investigated, but disease outbreaks have played a role in at least some breeding colonies (Crawford *et al.* 1992).

Benguela endemic seabirds, which rely on pelagic fish seems to have been strongly affected by prey scarcity in terms of reproductive performance and population sizes, but contrasting behaviour and life history characteristics have determined species-specific responses to changing foraging conditions. Dietary shifts, dispersal capability and low fidelity to breeding sites have allowed greater crested terns to weather the changes better than the other Benguela breeding seabirds that rely on the same human-exploited food resources.

Time activity budgets coupled with detailed information of greater crested tern diet (Chapters 2 & 3) allowed, for the first time in this species, the development of energetic models during breeding (Chapter 4). Additionally, investigations of energy requirements during the greater crested tern's non-breeding season would be valuable. The elaboration of more comprehensive energy budgets using foraging behaviour data collected with data-loggers (coupled with chick growth data) may help to improve quantification of energetic requirements for breeding greater crested terns and understand how feeding rates and energy content of different prey species influence chick growth, body condition and their survival and hence breeding success, i.e. the number of chicks raised successfully by the end of the breeding season (Le Bohec *et al.* 2008, Durant *et al.* 2010), survival of immature birds and adults (Le Bohec *et al.* 2008), and the decision of adults whether to breed depending on their body condition (Danchin & Cam 2002). These investigations can also be implemented to compute the energetic costs due to kleptoparasitism when, breeding in association to others species.

Costs of kleptoparasitism when breeding in association with Hartlaubs' gulls

In Chapter 5, the cost of intra- and interspecific kleptoparasitism for greater crested tern breeding on Robben Island by comparing two separate colonies, which differed for the presence of breeding Hartlaub's gulls was explored. Although mixed seabird colonies are typically thought be beneficial for their occupants by providing enhanced protection from predators (Stienen 2006), results from this investigation show that breeding in association with Hartlaub's gulls increases costs of kleptoparasitism through food lost and changes to adult provisioning behaviour to reduce food theft. In greater crested terns, precocial behaviour contributes to reduce intraspecific kleptoparasitism, a pattern that was not evident for gull kleptoparasitism, suggesting an anti-kleptoparasitism strategy aimed to reduce robberies primarily from conspecifics. The cost of kleptoparasitism implies that this breeding assemblage is more representative of a parasitic relationship, where the costs of associating with other species outweigh the benefits, rather than of a mutualistic relationship (Fuchs 1977, Veen 1977, Stienen 2006). However, as the costs and benefits of these mixed-species associations are poorly defined, more studies are required to elucidate the full nature of these relationships and the impact which kleptoparasitism may have on colonies under extreme conditions. In particular, the findings of this study do not discount the hypothesis that, in a small colony, breeding in association with Hartlaub's gulls could be an advantage when kelp gulls, which predate eggs or chicks, breed nearby. In such conditions, the anti-predator behaviour of Hartlaub's gulls may deter kelp gulls and thus compensate for the cost of interspecific kleptoparasitism. Further studies can address this question at Robben Island by recording rates of anti-predatory behaviour according to breeding species in response to potential predators. For example, rates of kleptoparasitism, coupled with intrusion rates of kelp gulls within the tern colony and the response of greater crested terns and Hartlaub's gulls to these intrusions (greater crested terns only, greater crested terns and Hartlaub's gulls or Hartlaub's gulls only). Rates of predation (attempt or successful) and durations of kelp Gull incursions would be recorded and coupled with colony size, minimum distance to kelp gull nests and presence/absence of Hartlaub's gulls in the breeding colony.

In this breeding association, understanding how kleptoparasitism varies in response to changing environmental conditions (especially in an exploited environment such as the Benguela system) will necessitate a comprehensive monitoring of the ratio of terns to gulls breeding together, coupled with detailed information on local food availability. In addition, even though the impact of kleptoparasitic gulls does not seem to negatively influence the recent terns' demography, more longitudinal data on patterns of kleptoparasitism and nest predation are required to explore the costs and benefits from associating with other species. Alternatively, a modelling approach could be applied to investigate whether the energetic costs imposed by interspecific kleptoparasitism may affect growth rate, survival and hence reproductive output of greater crested terns. Variables of this model including colony size, breeding stage and availability of prey will be compared in colonies, which differ in the presence/absence of gulls. Outcomes from the model will inform the cost of decreased provisioning to breeding pairs, allowing the examination of the transitions from parasitic to mutualistic relations and the potential effect kleptoparasitism may have on tern population dynamics or on other colonial seabirds. A modelling approach could also be used to predict how variation in kleptoparasitism frequency affects offspring provisioning and the potential for colony collapse at a high ratio of gulls to terns.

Concluding remarks

My thesis shows that it is possible to study the diet and time-budget of single prey loaders with minimal disturbance using digital photography and assisted by focal observations. In particular, photo-sampling provided a large sample size and detailed information on the type and sizes of the main prey consumed. The application of this non-invasive method revealed a degree of plasticity in greater crested tern foraging ecology, which probably helps to buffer temporal variation of preferred (and most abundant) prey, providing the potential for provisioning parents to find alternative prey, when their main prey is scarce. Prey composition and foraging behaviour varied according to breeding stage, suggesting that parents are constrained by variations in chick requirements and local oceanic environmental conditions, although different availability of anchovy may influence prey composition and should be investigated in future studies. Foraging plasticity combined to the low energy requirements of breeding greater crested terns may help this species to buffer food scarcity in the system, as they can switch to a lower energy content prey, which is more abundant in the system. The smaller amount of food required for greater crested terns to raise a chick compared to the other Benguela breeding seabirds that rely on pelagic fish, both at an individual and population level, are likely associated with their morphological features (e.g. small body size) combined with several characteristics, which are dissimilar to those of other species, such as small clutch size, short foraging range and extended post-fledging care. These species-specific characteristics have most likely helped the greater crested tern cope with anthropogenic changes in the Benguela. Although a cost was determined for terns breeding in association with Hartlaubs' gulls, the recent increase of greater crested terns in the Western Cape, suggests that the current influence of kleptoparasitic gulls does not impact the terns' demography negatively and further studies are needed to reveal the true nature of this association. Long-term studies of foraging ecology and energetic requirements of this species are needed to assess their influence on survival (both adult and juvenile) to drive population changes. Results will provide important ecological information to comprehend the mechanisms driving seabird populations in the Benguela region and provide crucial knowledge for conservation plans and key inputs for ecosystem approach fisheries management.

References

Adams, N. J., Abrams, R. W., Siegfried, W. R., Nagy, K. A., & Kaplan, I. R. (1991) Energy expenditure and food consumption by breeding Cape gannets *Morus capensis. Marine Ecology Progress Series,* **70**, 1–9.

Anderson, H. B., Evans, P. G., Potts, J. M., Harris, M. P., & Wanless, S. (2014) The diet of Common Guillemot *Uria aalge* chicks provides evidence of changing prey communities in the North Sea. *Ibis*, **156**, 23–34.

Arthur, K. E., & Balazs, G. H. (2008) A Comparison of Immature Green Turtle (*Chelonia mydas*) Diets among Seven Sites in the Main Hawaiian Islands 1. *Pacific Science*, **62**, 205–217.

Baigrie, B. D., Thompson, A. M., & Flower, T. P. (2014). Interspecific signalling between mutualists: food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. *Proceedings of the Royal Society of London B: Biological Sciences,* **281**, 20141232.

Baird, P. H. (1990) Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. *Ornis Scandinavica,* **21**, 224–235.

Balmelli, W., & Wickens, P. A. (1994) Estimates of daily ration for the South African (Cape) fur seal. *African Journal of Marine Science,* **14**, 151–157.

Baptist, M. J., & Leopold, M. F. (2010) Prey capture success of Sandwich Terns *Sterna sandvicensis* varies non-linearly with water transparency. *Ibis,* **152,** 815–825.

Barnes, K. N. (1998) The Important Bird Areas of Southern Africa. BirdLife South Africa, Johannesburg.

Barrett, R. T. (2002) Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. *Marine Ecology Progress Series*, **230**, 275–287.

Barrett, R. T., Camphuysen, C. J., Anker-Nilssen, T., Chardine, J. W., Furness, R. W., Garthe, S., Huppop, O., Leopold, M. F., Montevecchi, W. A., & Veit, R. R. (2007). Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science*, **64**, 1675–1691.

Bart, J. (1977) Impact of human visitations on avian nesting success. *Living Bird*, **16**, 187–192.

Batchelor, A. L., & Ross, G. J. B. (1984) The diet and implications of dietary change of Cape Gannets on Bird Island, Nelson Mandela Bay. *Ostrich,* **55**, 45–63.

Bates, D., & Maechler, M. (2009) lme4: Linear mixed-effects models using S4 classes. http://www.R-project.org.

Begon M., Harper J., & Townsend, C. (1996) Ecology: Individuals, Populations and Communities. Blackwell Science, Oxford.

Bennett, L. J. (1938) The blue-winged teal: its ecology and management. Ames, IA: Collegiate Press.

Berg, M. P., Kiers, E. T., Driessen, G., Van Der Heijden, M., Kooi, B. W., Kuenen, F., Liefting, M., Verhoef, H. A., & Ellers, J. (2010) Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, **16**, 587–598.

Berruti, A., Underhill, L. G., Shelton, P. A., Moloney, C., & Crawford R. J. M. (1993) Seasonal and inter-annual variation in the diet of two colonies of the Cape Gannet (*Morus capensis*) between 1977–78 and 1989. *Colonial Waterbirds,* **16**, 158–175.

Berry, H. H. (1976) Physiological and behavioural ecology of the Cape cormorant *Phalacrocorax capensis*. *Madoqua*, **9**, 5–30.

Blaber, S. J. M., Milton, D. A., Smith, G. C., & Farmer, M. J. (1995) Trawl discards in the diets of tropical seabirds of the northern Great Barrier Reef, Australia. *Marine Ecology Progress Series*, **127**, 1–13.

Blackburn, G. S., Hipfner, J. M., & Ydenberg, R. C. (2009) Evidence that tufted puffins *Fratercula cirrhata* use colony overflights to reduce kleptoparasitism risk. *Journal of Avian Biology*, **40**, 412-418.

Blamey, L. K., Howard, J. A., Agenbag, J., & Jarre, A. (2012) Regime-shifts in the southern Benguela shelf and inshore region. *Progress in Oceanography*, **106**, 80–95.

Blamey, L. K., Shannon, L. J., Bolton, J. J., Crawford, R. J. M., Dufois, D., Evers- King, H., Griffiths, C. L., Hutchings, L., Jarre, A., Rouault, M., Watermeyer, K. E., & Winker H. (2015) Ecosystem changes in the southern Benguela and the underlying processes. *Journal of Marine Systems* **144**, 9–29.

Botsford, L. W., Castilla, J. C., & Peterson, C. H. (1997) The management of fisheries and marine ecosystems. *Science*, **277**, 509–515.

Bouwhuis, S., Visser, G. H., & Underhill, L. G. (2007) Energy budget of African penguin *Spheniscus demersus* chicks. In Kirkman SP (ed.) 2007. Final report of BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME. Avian Demography Unit, Cape Town: 125–127.

Boyd, I. L., & Murray, A. W. A. (2001) Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology,* **70**, 747–760.

Braby, J. (2011) The Biology and conservation of the Damara Tern in Namibia. PhD dissertation, University of Cape Town, Cape Town.

Branch, G.M., Griffiths, C.L., Branch, M.L. & Beckley, L.E. (2010) Two Oceans: A Guide to the Marine Life of Southern Africa. Randomhouse/Struik, Cape Town.

Brander, K. M. (2007) Global fish production and climate change. *Proceedings of the National Academy of Sciences USA*, **104**, 19709–19714.

Britten, G. L., Dowd, M., Minto, C., Ferretti, F., Boero, F., & Lotze, H. K. (2014) Predator decline leads to decreased stability in a coastal fish community. *Ecology Letters*, **17**, 1518–25.

Brockmann, H. J., & Barnard C. J. (1979) Kleptoparasitism in birds. *Animal Behaviour,* **27**, 487–514.

Bronstein, J. L. (2001) The exploitation of mutualisms. *Ecology Letters*, **4**, 277–287.

Brown, M. T., & Ulgiati, S. (2004) Energy quality, energy, and transformity: HT Odum's contributions to quantifying and understanding systems. *Ecological Modelling*, **178**, 201–213.

Bugge, J., Barret, R. T., & Pedersen, T. (2011) Optimal foraging in chick-raising Common Guillemots *Uria aalge*. *Journal of Ornithology,* **152**, 253–259.

Bunce, A. (2001) Prey consumption of Australasian gannets (*Morus serrator*) breeding in Port Phillip Bay, southeast Australia, and potential overlap with commercial fisheries. *ICES Journal of Marine Science: Journal du Conseil,* **58**, 904–915.

Burger, A. E., & Piatt, J. F. (1990) Flexible time budgets in breeding Common Murres: Buffers against variable prey availability. *Studies in Avian Biology*, **14**, 71–83.

Burke, C. M., & Montevecchi, W. A. (2009) The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*, **278**, 354–361.

Campbell, K. (2016) Factors influencing the foraging behaviour of African Penguins (*Spheniscus demersus*) provisioning chicks at Robben Island, South Africa (Doctoral dissertation, University of Cape Town, Cape Town).

Carey, M. J. (2009) The effects of investigator disturbance on procellariiform seabirds: a review. *New Zealand Journal of Zoology,* **36**, 367–377.

Carney, K. M., & Sydeman, W. J. (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, **22**, 68–79.

Cezilly, F. & Wallace, J. (1988) The determination of prey captured by birds through direct field observations: a test of the method. *Colonial Waterbirds*, **11**, 110–112.

Chabot, D., & Francis, C. M. (2016) Computer-automated bird detection and counts in high-resolution aerial images: a review. *Journal of Field Ornithology,* **87**, 343–359.

Cherel, Y., Le Corre, M., Jaquemet, S., Ménard, F., Richard, P., & Weimerskirch, H. (2008) Resource partitioning within a tropical seabird community: new information from stable isotopes. *Marine Ecology Progress Series*, **366**, 281–291.

Chiaradia, A., Dann, P., Jessop, R., & Collins, P. (2002) The diet of crested tern (*Sterna bergii*) chicks on Phillip Island, Victoria, Australia. *Emu,* **102**, 367–371.

Clarke, M.R. (1986) A Handbook for the Identification of Cephalopod Beaks. Clarendon Press, Oxford.

Coetzee, J. C., van der Lingen, C. D., Hutchings, L., & Fairweather, T. P. (2008) Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science,* **65**, 1676–1688.

Cohen, L. A., Pichegru, L., Grémillet, D., Coetzee, J., Upfold, L., & Ryan, P. G. (2014) Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade. *Marine Ecology Progress Series*, **505**, 281–293.

Collins, P. M., Halsey, L. G., Arnould, J. P., Shaw, P. J., Dodd, S., & Green, J. A. (2016) Energetic consequences of time-activity budgets for a breeding seabird. *Journal of Zoology*, **300**, 153–162.

Cook, T. R., Hamann, M., Pichegru, L., Bonadonna, F., Grémillet, D., & Ryan, P. G. (2012) GPS and time-depth loggers reveal underwater foraging plasticity in a flying diver, the Cape Cormorant. *Marine Biology,* **159**, 379–387.

Cooper, J. (1977) Energetic requirements for growth of the jackass penguin. *Zoologica Africana*, **12**, 201–213.

Cooper, J., Crawford, R. J. M., Suter, W., & Williams, A. J. (1990) Distribution, population size and conservation of the Swift Tern *Sterna bergii* in southern Africa. *Ostrich* **61**, 56–65.

Costello, C., Ovando, D., Clavelle, T., Strauss, C.K., Hilborn, R., Melnychuk, M. C., Branch, T. A., Gaines, S.D., Szuwalski, C. S., Cabral, R. B. & Rader, D. N., (2016) Global fishery prospects under contrasting management regimes. *Proceedings of the National Academy of Sciences USA*, 201520420.

Cram, D. L., Schülein, F. H. (1974) Observations on surface-shoaling Cape hake off South West Africa*.* *Journal du Conseil,* **35**, 272–275.

Crawford, R. J. M. (1980) Seasonal patterns in South Africa's Western Cape purse-seine fishery. *Journal of Fish Biology*, **16**, 649–664.

Crawford, R. J. M. (2003) Influence of food on numbers breeding, colony size and fidelity to localities of Swift Terns in South Africa's Western Cape, 1987-2000. *Waterbirds,* **26**, 44–53.

Crawford, R. J. (2007) Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology*, **148**, 253–260.

Crawford, R. J. M. (2009) A recent increase of Swift Terns *Thalasseus bergii* off South Africa: the possible influence of an altered abundance and distribution of prey. *Progress in Oceanography,* **83**, 398–403.

Crawford, R. J. M., Ryan, P. G., & Williams, A. J. (1991) Seabird consumption and production in the Benguela and western Agulhas ecosystems. *South African Journal of Marine Science*, **11**, 357–375.

Crawford, R. J. M., Allwright, D. M., & He, C. W. (1992) High mortality of Cape Cormorants (*Phalacrocorax capensis*) off western South Africa in 1991 caused by *Pasteurella multocida*. *Colonial Waterbirds*, **15**, 236-238.

Crawford, R. J. M., Dyer, B. M., & Brooke, R. K. (1994) Breeding nomadism in southern African seabirds: constraints, causes and conservation. *Ostrich,* **65,** 231–246.

Crawford, R. J. M., & Dyer, B. M., (1995) Responses by four seabirds to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis,* **137**, 329–339.

Crawford, R. J. M., & Dyer, B. M., (2000) Swift Terns *Sterna bergii* breeding on roofs and at other new localities in southern Africa. *Marine Ornithology*, **28,** 123–124.

Crawford, R. J. M., Cooper, J., Dyer, B.M., Upfold, L., Venter, A.D., Whittington, P.A., & Wolfaardt, A.C., (2002) Longevity, inter-colony movements and breeding of Crested Terns in South Africa. *Emu*, **102,** 1–9.

Crawford, R. J. M., Hockey, P. A. R., & Tree, A. J. (2005) In: Hockey, P. A. R., Dean, W. R. J. & Ryan, P. G. Roberts Birds of Southern Africa, 7th ed. John Voelcker Bird Book Fund, Cape Town: 453-455.

Crawford, R. J. M, Barham, P. J., Underhill, L. G., Shannon, L. J., Coetzee, J. C., Dyer, B. M., Leshoro, T. M., & Upfold, L. (2006) The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation*, **132**, 119–125.

Crawford, R. J. M., Sabarros, P. S., Fairweather, T., Underhill, L. G., & Wolfaardt, A. C. (2008) Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science*, **30**, 177–184.

Crawford, R. J. M., Altwegg, R., Barham, B. J., Barham, P. J., Durant, J. M., Dyer, B. M., Geldenhuys, D., Makhado, A. B., Pichegru, L., Ryan, P. G. & Underhill, L. G., (2011) Collapse of South Africa's penguins in the early 21st century. *African Journal of Marine Science*, **33**, 139–156.

Crawford, R. J. M., Makhado, A. B., Waller, L. J., & Whittington, P. A. (2014) Winners and losers responses to recent environmental change by South African seabirds that compete with purse-seine fisheries for food. *Ostrich*, **85**, 111–117.

Crawford, R. J., Makhado, A. B., Whittington, P. A., Randall, R. M., Oosthuizen, W. H., & Waller, L. J. (2016) A changing distribution of seabirds in South Africa: the possible impact of climate and its consequences. *Climate Change and Marine Top Predators*, **3**, 1–11.

Croxall, J. P., & Briggs,D. R. (1991) Foraging economics and performance of polar and subpolar Atlantic seabirds. *Polar Research,* **10**, 561–578.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, **22**, 1–34.

Cury, P., Bakun, A., Crawford, R. J., Jarre, A., Quinones, R. A., Shannon, L. J., & Verheye, H. M. (2000) Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, **57**, 603−618.

Cury, P., & Shannon, L. J. (2004) Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography,* **60**, 223–243.

Cury P. M., Boyd I. L., Bonhommeau S., & Anker-Nilssen T. (2011) Global seabird response to forage fish depletion: one-third for the birds. *Science*, **334**, 1703−1706.

Dahdul, W. M., Horn, M. H. (2003) Energy allocation and postnatal growth in captive Elegant Tern (*Sterna elegans*) chicks: response to high- versus low- energy diets. *Auk,* **120**, 1069–1081.

Danchin, E., & Wagner, R. H. (1997) The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, **12**, 342−347.

Danchin, E., Boulinier, T., & Massot, M. (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology,* **79**, 2415–2428.

Danchin, E., & Cam, E. (2002) Can non-breeding be a cost of breeding dispersal?. *Behavioral Ecology and Sociobiology*, **51**, 153–163.

Davis, M. B., Shaw, R. G., & Etterson, J. R. (2005) Evolutionary responses to changing climate. *Ecology*, **86**, 1704–1714.

Davoren, G. K., & Burger, A. E. (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, **58**, 853–863.

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003) Distributional patterns of a marine bird and its prey: habitat selection based on prey and conspecific behaviour. *Marine Ecology Progress Series* **256**, 229–242.

de Villiers, S. A. (1971) Robben Island: Out of Reach, Out of Mind. A History of Robben Island. Struik, Cape Town.

Diamond, A. W. (1984) Feeding overlap in some tropical and temperate seabird communities. *Studies in Avian Biology*, **8**, 24–46.

Dies, J. I., & Dies, B. (2005) Kleptoparasitism and host responses in a Sandwich Tern Colony of eastern Spain. *Waterbirds*, **28**, 167–171.

Distiller, G., Altwegg, R., Crawford, R. J. M., Klages, N. T. W., & Barham, B. (2012) Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape gannet. *Marine Ecology Progress Series,* **461**, 245–255.

Doucette, J. L., Wissel, B. & Somers, C. M. (2011) Cormorant-fisheries conflicts: stable isotopes reveal a consistent niche for avian piscivores in diverse food webs. *Ecological Applications*, **21**, 2987–3001.

Drent, R. H., & Daan S. (1980) The prudent parents: energetic adjustments in avian breeding. *Ardea* **68**, 225–252.

Duffy, D. C. (1987) Multiple fish carrying in Swift Terns *Sterna bergii. Cormorant,* **14**, 46–49.

Duffy, D. C. & Jackson, S. (1986) Diet studies of seabirds: a review of methods. *Colonial Waterbirds*, **9**, 1–17.

Dunn, E. K. (1973) Changes in fishing ability of terns associated with wind speed and sea surface conditions. *Nature,* **244**, 520–521.

Durant, J. M., Crawford, R. J., Wolfaardt, A. C., Agenbag, K., Visagie, J., Upfold, L., & Stenseth, N. C. (2010) Influence of feeding conditions on breeding of African penguins: importance of adequate local food supplies. *Marine Ecology Progress Series*, **420**, 263–271.

Einoder, L. D. (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research*, **95**, 6–13.

Ellenberg, U., Mattern, T., Seddon, P.J. & Jorquera, G.L. (2006) Physiological and reproductive consequences of human disturbance in Humboldt Penguins: the need for species-specific visitor management. *Biological Conservation*, **133**, 95–106.

Elliott, K. H. & Gaston, A. J. (2015) Diel vertical migration of prey and light availability constrain foraging in an Arctic seabird. *Marine Biology*, **162**, 1739–1748.

Ellis, H. I. (1980) Metabolism and evaporative water loss in three seabirds (Laridae). *Federation Proceedings,* **39**, 1165.

Ellis, H. I. & Gabrielsen, G. W. (2002) Energetics of free-ranging seabirds. In Biology of Marine Birds (eds: Schreiber EA, Burger J). CRC Press, Boca Raton, 359–407.

Ens, B. J., Esselink, P., & Zwarts, L. (1990) Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. *Animal Behaviour*, **39**, 219–230.

Enstipp, M. R., Grémillet, D. & Lorentsen, S. H. (2005) Energetic costs of diving and thermal status in European shags (*Phalacrocorax aristotelis*). *Journal of Experimental Biology*, **208**, 3451–3461.

Enstipp, M. R., Daunt, F., Wanless, S., Humphreys, E. M., Hamer, K. C., Benvenuti, S., & Grémillet, D. (2006) Foraging energetics of North Sea birds confronted with fluctuating prey availability. In: Boyd, S.; Wanless, S., Camphuysen, C. J., (eds.) Top predators in marine ecosystems: their role in monitoring and management. Cambridge University Press, Cambridge UK, 191–210.

Erwin, R. M. (1977) Foraging and breeding adaptations to different food regimes in three seabirds: the common tern *Sterna hirundo*, royal tern *Sterna maxima* and black skimmer *Rynchops niger. Ecology,* **58**, 389–397

Fairweather, T. P., van der Lingen, C. D., Booth, A. J., Drapeau, L., van der Westhuizen, J. J., & Town, C. (2006) Indicators of sustainable fishing for South African sardine *Sardinops sagax* and *anchovy Engraulis encrasicolus*. *African Journal of Marine Science,* **28**, 661–680.

Fauchald, P. (2009) Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series,* **391,** 139–151.

Fijn, R. C., van Franeker, J. A., & Trathan, P. N. (2012) Dietary variation in chick-feeding and self-provisioning Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea* at Signy Island, South Orkney Islands, Antarctica. *Marine Ornithology,* **40,** 81–87.

Fijn, R. C., de Jong, J., Courtens, W., Verstraete, H., Stienen, E. W. M., & Poot, M. J. M. (2016) GPS-tracking and colony observations reveal variation in offshore habitat use and foraging ecology of breeding Sandwich Terns. *Journal of Sea Research*.

Finney, S. K., Wanless, S., Harris, M. P., & Monaghan, P. (2001) The impact of gulls on puffin reproductive performance: an experimental test of two management strategies. *Biological Conservation*, **98**, 159–165.

Fischer, B., Taborsky, B., & Kokko, H. (2011) How to balance the offspring quality–quantity trade off when environmental cues are unreliable. *Oikos*, **120**, 258–270.

Flint, E. N. & Nagy, K. A. (1984) Flight energetics of free-living Sooty Terns. *Auk,* **101**, 288–294.

Flower, T. P., Child, M. F., & Ridley, A. R. (2013) The ecological economics of kleptoparasitism: pay-offs from self-foraging versus kleptoparasitism. *Journal of Animal Ecology*, **82**, 245–255.

Fort J., Porter W. P., & Gremillet D. (2011) Energetic modelling: a comparison of the different approaches used in seabirds. *Molecular & Integrative Physiology,* **158**, 358–365.

Frederiksen, M., Wanless, S., Harris, M. P., Rothery, P., & Wilson, L. J. (2004) The role of industrial fisheries and oceanographic change in the decline of North Sea Black-legged Kittiwakes. *Journal of Applied Ecology,* **41**, 1129–1139.

Fuchs, E. (1977) Predation and anti-predator behaviour in a mixed colony of terns Sterna sp. and black-headed gulls *Larus ridibundus* with special reference to the sandwich tern *Sterna sandvicensis. Ornis Scandinavica*, **8**, 17–32.

Furness, R. W. (1978) Energy requirements of seabird communities: a bioenergetics model. *Journal of Animal Ecology,* **47**, 39–53.

Furness R. W. (1987) Kleptoparasitism in seabirds. In: Croxall J.P. (ed) Seabirds: feeding ecology and role in marine ecosystems: 77–100. Cambridge, UK: Cambridge University Press.

Furness, R. W. (2003) Impacts of fisheries on seabird communities. *Scientia Marina,* **67**, 33–45.

Furness, R.W. & Cooper, J. (1982) Interactions between breeding seabird and pelagic fish populations in the Southern Benguela region. *Marine Ecology Progress Series*, **8**, 243–250.

Furness, R. W., & Camphuysen, K. C. J. (1997) Seabirds as monitors of the marine environment. *ICES Journal of Marine Science*, **54**, 726–737.

Furness, R. W., & Tasker, M. L. (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series,* **202,** 253–264.

Furness, R. W., & Ratcliffe, N. (2004) Great Skua (*Stercorarius skua*). In Mitchel, P.I., S.F. Newton, N. Ratcliffe, & T.E. Dunn (eds.), Seabird populations of Britain and Ireland. T & A D Poyser, London: 173–186.

Fyhn, M., Gabrielsen, G. W., Nordøy, E. S., Moe, B., Langseth, I. & Bech, C. (2001) Individual variation in field metabolic rate of kittiwakes (*Rissa tridactyla*) during the chick-rearing period. *Physiological and Biochemical Zoology*, **74**, 343–355.

Gagliardi, A., Martinoli, A., Preatoni, D., Wauters, L.A., & Tosi, G. (2007) From mass to body elements to fish biomass: a direct method to quantify food intake of fish eating birds. *Hydrobiologia,* **583**, 213–222.

Gaglio, D., & Sherley, R. B. (2014) Nasty neighbourhood: kleptoparasitism and egg predation of Swift Terns by Hartlaub's Gulls. *Ornithological Observations*, **5**, 131–134.

Gaglio, D., Cook, T. R., & Sherley, R. B. (2015a) Egg morphology of Swift Terns in South Africa. *Ostrich*, **86**, 287–289.

Gaglio, D., Sherley, R. B., & Cook, T. R. (2015b) Insects in the diet of the Greater Crested Tern *Thalasseus bergii bergii* in southern Africa. *Marine Ornithology*, **43**, 131–132.

Gaglio, D., Cook T. R., Connan M., Ryan P. G., & Sherley R. B. (2016) Data from: Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. *Methods in Ecology and Evolution.* **8**, 214–222.

García, G. O., Favero, M., & Vassallo, A. I. (2010) Factors affecting kleptoparasitism by gulls in a multi-species seabird colony. *Condor*, **112**, 521–529.

García, G. O., Becker, P. H., & Favero, M. (2011) Kleptoparasitism during courtship in *Sterna hirundo* and its relationship with female reproductive performance. *Journal of Ornithology* **152**, 103–110.

García, G. O., Riechert, J., Favero, M., & Becker, P. H. (2014) Stealing food from conspecifics: spatial behavior of kleptoparasitic Common Terns Sterna hirundo within the colony site. *Journal of Ornithology*, **155**, 777–783.

García-Salgado, G., Rebollo, S., Pérez-Camacho, L., Martínez-Hesterkamp, S., Navarro, A. & Fernández-Pereira, J.-M. (2015) Evaluation of trail-cameras for analyzing the diet of nesting raptors using the Northern Goshawk as a model. *PLoS One*, **10**, e0127585.

Garthe, S., Grémillet, D., & Furness, R.W. (1999) At-sea activity and foraging efficiency in chick-rearing northern gannets (*Sula bassana*): a case study in Shetland. *Marine Ecology Progress Series,* **185**, 93–99.

Gaston, A. J., & Elliott, K. H. (2014) Seabird diet changes in northern Hudson Bay, 1981-2013, reflect the availability of schooling prey. *Marine Ecology Progress Series*, **513**, 211–223.

Gilchrist, H. G., Gaston, A. J., & Smith, J. N. M. (1998) Wind and prey nest sites as foraging constraints on an avian predator, the glaucous gull. *Ecology,* **79,** 2403–2414.

Gladics, A.J., Suryan, R.M., Parrish, J.K., Horton, C.A., Daly, E.A. & Peterson, W.T. (2015) Environmental drivers and reproductive consequences of variation in the diet of a marine predator. *Journal of Marine Systems*, **146**, 72–81.

Gleiss, A. C., Wilson, R. P., & Shepard, E. L. (2011) Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution*, **2**, 23–33.

Goldstein, D. L. (1988) Estimates of daily energy expenditure in birds: the time-energy budget as an integrator of laboratory and field studies. *American Zoologist*, **28**, 829–844.

Golet, G. H., Kuletz, K. J., Roby, D. D., & Irons, D. B. (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *Auk*, **117**, 82–91.

González-Solís, J., Oro, D., Pedrocchi, V., Jover, L. & Ruiz, X. (1997) Bias associated with diet samples in Audouin's Gulls. *Condor*, **99**, 773–779.

González-Solís, J., Smyrli, M., Militão, T., Gremillet, D., Tveraa, T., Phillips, R. A. & Boulinier, T. (2011) Combining stable isotope analyses and geolocation to reveal kittiwake migration. *Marine Ecology Progress Series*, **435**, 251–261.

Gordon, M. S., & Bartol, S. M. (2004) Experimental approaches to conservation biology. University of California Press, Berkeley and Los Angeles.

Gotelli, N. J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Götmark, F. (1990) A test of the information-centre hypothesis in a colony of Sandwich Terns *Sterna sandvicensis*. *Animal Behaviour,* **39,** 487–495

Götmark, F. (1992) The effects of investigator disturbance on nesting birds. In: Power, D. M. ed. *Current Ornithology*, Volume 9. Plenum Press, New York: 63–104.

Götmark, F., & Åhlund, M. (1984) Do field observers attract nest predators and influence nesting success of common eiders?. *The Journal of wildlife management*, **2**, 381-387.

Green, D. B., Klages, N. T. W., Crawford, R. J. M., Coetzee, J. C., Dyer, B. M., Rishworth, G. M. & Pistorius, P. A. (2015) Dietary change in Cape Gannets reflects distributional and demographic shifts in two South African commercial fish stock. *ICES Journal of Marine Science*, **72**, 771–781.

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., & Alonso, A. (2014) Arboreal camera trapping: taking a proven method to new heights. *Methods in Ecology and Evolution*, **5**, 443–451.

Grémillet, D., Storch, S., & Peters, G., (2000) Determining food requirements in marine top predators: a comparison of three independent techniques in great cormorants, *Phalacrocorax carbo carbo*. *Canadian Journal of Zoology*, **78**, 1567–1579.

Grémillet, D., Wright, G., Lauder, A., Carss, D. N. & Wanless, S. (2003) Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. *Journal of Applied Ecology,* **40**, 266–277.

Grémillet, D., Pichegru, L., Kuntz, G., Woakes, A. G., Wilkinson, S., Crawford, R. J., & Ryan, P. G. (2008) A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society of London B: Biological Sciences*, **275**, 1149–1156.

Griffiths, C. L., van Sittert, L., Best, P. B., Brown, A. C., Cook, P. A., Crawford, R. J. M., David, J. H. M., Davies, B. R., Griffiths, M. H., Hutchings, K., Jerardino, A., Kruger, N., Lamberth, S., Leslie, R., Melville-Smith, R., Tarr, R., & van der Lingen, C. D. (2004) Impacts of human activities on marine animal life in the Benguela − a historical overview. *Oceanography and Marine Biology*: *An Annual Review,* **42**, 303–392.

Groom, M. J. (1992) Sand-Colored Nighthawks parasitize the antipredator behavior of three nesting bird species. *Ecology*, **73**, 785–793.

Hall, C. S., Kress, S. W., & Griffin, C. R. (2000) Composition, spatial and temporal variation of Common and Arctic Tern chick diets in the Gulf of Maine. *Waterbirds*, **23**, 430–439.

Hamann, M. H., Grémillet, D., Ryan, P. G., Bonadonna, F., van der Lingen, C. D., & Pichegru, L. (2012) A hard-knock life: the foraging ecology of Cape cormorants amidst shifting prey resources and industrial fishing pressure. *African Journal of Marine Science*, **34**, 233–240.

Hampton, I. (1987) Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. *South African Journal of Marine Science* **5**, 901–917.

Haney, J. C., Fristrup, K. M., & Lee, D.S. (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica,* **23**, 49–62.

Harris, M. P., Beare, D., Toresen, R., Nøttestad, L., Kloppmann, M., Dörner, H., Peach, K., Rushton, D. R., Foster-Smith, J., & Wanless, S. (2007) A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. *Marine Biology,* **151**, 973–983.

Harris, M., Newell, M., Daunt, F., Speakman, J., & Wanless, S. (2008) Snake pipefish *Entelurus aequoreus* are poor food for seabirds. *Ibis*, **150**, 413.

Hebblewhite, M., & Haydon, D. T. (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, **365**, 2303–2312.

Hedd, A., Ryder, J. L., Cowen, L. L., & Bertram, D. F. (2002) Inter-annual variation in the diet, provisioning and growth of Cassin's auklet at Triangle Island, British Columbia: responses to variation in ocean climate. *Marine Ecology Progress Series* **229**, 221–232.

Heydorn, M. J., & Williams A. J. (1993) Swift Terns: observations at Possession Island in 1988. *Bontebok,* **8**, 26–27.

Hobday, A. J., Bell, J. D., Cook, T. R., Gasalla, M. A., & Weng, K. C. (2015) Reconciling conflicts in pelagic fisheries under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography*, **113**, 291–300.

Hockey ,P. A. R., Dean, W. R. J., & Ryan, P. G. (eds) (2005) Roberts – Birds of Southern Africa, VIIth ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

Huffeldt, N. P., & Merkel, F. R. (2013) Remote time-lapse photography as a monitoring tool for colonial breeding seabirds: a case study using thick-billed murres (*Uria lomvia*). *Waterbirds*, **36**, 330–341.

Hull, C. L., Kaiser, G. W., Lougheed, C., Lougheed, L., Boyd, S., & Cooke, F. (2001) Intraspecific variation in commuting distance of marbled murrelets *Brachyramphus marmoratus*: ecological and energetic consequences of nesting further inland. *Auk*, **118**, 1036–1046.

Hulsman, K. (1984) Selection of prey and success of Silver Gulls robbing Crested Terns. *Condor,* **86**, 130–138.

Huntingford, F. A. & Turner, A. K. (1987) Animal Conflict. London: Chapman & Hall, London.

Hutchings, L., Barange, M., Bloomer, S. F., Boyd, A. J., Crawford, R. J. M., Huggett, J. A., Kerstan, M., Korrubel, J. L., De Oliveira, J. A. A., Painting, S. J. & Richardson, A. J., (1998) Multiple factors affecting South African anchovy recruitment in the spawning, transport and nursery areas. *South African Journal of Marine Science*, **19**, 211–225.

Hutchings, L., van der Lingen, C. D., Shannon, L. J., Crawford, R. J. M., Verheye, H. M. S., Bartholomae, C. H., van der Plas, A. K., Louw, D., Kreiner, A., Ostrowski, M., Fidel, Q., Barlow, R. G., Lamont, T., Coetzee, J., Shillington, F., Veitch, J., Currie, J. C., & Monteiro, P. M. S., (2009) The Benguela Current: An ecosystem of four components. *Progress in Oceanography,* **83**, 15–32.

Hutchings, L., Jarre, A., Weller, F. G., Steinfurth, A., Hagen, C., Sherley, R. B., & Wanless, R. M. (2014) Comments on the "River model" (de Moor & Butterworth 2014): Bounding exploitation rate, estimating escapement for critically dependent predators, or understanding the interactions between anchovy and penguin demographics? SARChl internal report, University of Cape Town.

Inchausti, P., Guinet, C., Koudil, M., Durbec, J-P., Barbraud, C., Weimerskirch, H., Cherel, Y., & Jouventin, P. (2003) Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology,* **34**, 170 – 176.

Inger, R. & Bearhop, S. (2008) Applications of stable isotope analyses to avian ecology. *Ibis*, **150**, 447–461.

Iyengar, E. V. (2008) Kleptoparasitic interactions throughout the animal kingdom and a re-evaluation, based on participant mobility, of the con- ditions promoting the evolution of kleptoparasitism. *Biological Journal of the Linnaean Society*, **93**, 745–762.

Jackson, S. (1988) Diets of the White-chinned Petrel and Sooty Shearwater in the southern Benguela region, South Africa. *Condor*, **90**, 20–28.

Jackson, S. & Ryan, P.G. (1986) Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). *Auk*, **103**, 617–619.

Jordan, M. J. R. (2005) Dietary analysis for mammals and birds: a review of field techniques and animal-management applications. *International Zoo Yearbook*, **39**, 108–116.

Kämpf, J., & Chapman, P. (2016) The Benguela Current Upwelling System. In Upwelling Systems of the World. Springer, Berlin: 251–314.

Karnovsky, N. J., Hobson, K. A. & Iverson, S. J. (2012) From lavage to lipids: estimating diets of seabirds. *Marine Ecology Progress Series*, **451**, 263–284.

Keller, T. M., & Visser, G. H. (1999) Daily energy expenditure of great cormorants *Phalacrocorax carbo sinensis* wintering at Lake Chiemsee, southern Germany. *Ardea,* **87**, 61–69.

Kemper, J., Underhill, L. G., Crawford, R. J. M., & Kirkman, S. P. (2007) Revision of the conservation status of seabirds and seals breeding in the Benguela ecosystem. In Kirkman, S. P., editor, Final

Report of the BCLME (Benguela Current Large Marine Ecosystem) Project on Top Predators as Biological Indicators of Ecosystem Change in the BCLME. Avian Demography Unit, Cape Town: 325–342.

Klaassen M., Bech, C., Masman, D. & Slagsvold, G. (1989) Growth and energetics of Arctic Tern chicks (*Sterna paradisaea*). *Auk,* **106**, 240–248.

Klages, N. T. W., Willis, A. B., Ross, G. J. B. (1992) Variability in the diet of the Cape Gannet at Bird Island, Algoa Bay, South Africa. *South African Journal of Marine Science,* **12**, 761–771.

Krebs, J. R., & Davies, N. B. (1993) Economic decisions and the individual. In 'An Introduction to Behavioural Ecology'. (Eds J. R. Krebs & N. B. Davies.) Blackwell Scientific Publications, London, 48–76.

Labbé, A. M., Dunlop, J. N., & Loneragan, N. R. (2013) Central place foraging and feather regrowth rate in bridled terns (*Onychoprion anaethetus*): an insight from stable isotopes. *Marine and Freshwater Research,* **64,** 1184–1191.

Lack, D. L. (1968). Ecological adaptations for breeding in birds. Methuen, London.

Langham, N. P. E., & Hulsman, K. (1986) The breeding biology of the Crested Tern *Sterna bergii*. *Emu,* **86,** 23–32.

Larson, K. & Craig, D. (2006) Digiscoping vouchers for diet studies in bill-load holding birds. *Waterbirds,* **29**, 198–202.

Laugksch, R. C., & Duffy, D. C. (1984) Energetics equations and food consumption of seabirds in two marine upwelling areas: comparisons and the need for standardization. *South African Journal of Marine Science*, **2**, 145–148.

Le Bohec C., Durant, J. M., Gauthier-Clerc, M., Stenseth, N. C., Park, Y. H., Pradel, R., Gremillet, D., Gendner, J. P. & Le Maho, (2008) King penguin population threatened by Southern Ocean warming. *Proceedings of the National Academy of Sciences USA,* **105**, 2493–2497.

Le Corre, M., & Jouventin, P. (1997) Kleptoparasitism in tropical seabirds: vulnerability and avoidance responses of a host species, the red-footed booby. *Condor*, **99**, 162–168.

Lee, N. M. & Hockey, P. A. R. (2001) Biases in the field estimation of shorebird prey sizes. *Journal of Field Ornithology*, **72**, 49–61.

Leigh, J. (2010) The evolution of mutualism. *Journal of Evolutionary Biology*, **23**, 2507–2528.

Leopold, M. F., van Elk, J. F. & van Heezik, Y. M. (1996) Central place foraging in oystercatchers *Haematopus ostralegus*: can parents that transport mussels *Mytilus edulis* to their young profit from size selection? *Ardea,* **84,** 311–325.

Le Roux, J. (2006) The swift tern *Sterna bergii* in southern Africa: growth and movement. Unpubl. MSc dissertation, University of Cape Town, Cape Town.

Lescroël, A., Mathevet, R., Péron, C., Authier, M., Provost, P., Takahashi, A., & Grémillet, D. (2016) Seeing the ocean through the eyes of seabirds: A new path for marine conservation? *Marine Policy*, **68**, 212–220.

Lewis, S., Gremillet, D., Daunt, F., Ryan, P. G., Crawford, R. J., & Wanless, S. (2006) Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia*, **147**, 606–614.

Litzow, M. A., & Piatt, J. F. (2003) Variance in prey abundance influences time budgets of breeding seasbirds: evidence from pigeon guillemots *Cepphus columba*. *Journal of Avian Biology,* **34**, 54–64.

Lorentzen, E., Choquet, R., & Steen, H. (2012) Modelling state uncertainty with photo series data for the estimation of breeding success in a cliff-nesting seabird. *Journal of Ornithology*, **152**, 477–483.

Ludynia K., Roux, J. P., Kemper, J., & Underhill, L. G. (2010) Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009. *African Journal Marine Science*, **32**, 563–572.

Luscier, J. D., Thompson, W. L., Wilson, J. M., Gorham, B. E., & Dragut, L. D. (2006) Using digital photographs and object-based image analysis to estimate percent ground cover in vegetation plots. *Frontiers in Ecology and the Environment* **4**, 408–413.

Lynch, T. P., Alderman, R., & Hobday, A. J. (2015) A high-resolution panorama camera system for monitoring colony-wide seabird nesting behaviour. *Methods in Ecology and Evolution*, **6**, 491–499.

Lyons, D. E., Roby, D. D., & Collis, K. (2005) Foraging ecology of Caspian Terns in the Columbia River estuary, USA. *Waterbirds,* **28**, 280–291.

Makhado, A.B., Dyer, B.M., Fox, R., Geldenhuys, D., Pichegru, L., Randall, R.M., Sherley, R.B., Upfold, L., Visagie, J., Waller, L.J., Whittington, P.A. & Crawford, R.J.M. (2013) Estimates of numbers of twelve seabird species breeding in South Africa, updated to include 2012. *Department of Environmental Affairs, Internal Report,* 1–16.

Marshall, A.D. & Pierce, S.J. (2012) The use and abuse of photographic identification in sharks and rays. *Journal of Fish Biology*, **80**, 1361–1379.

Martins, I., Pereira J. C., Ramos J. A., & Jørgensen, S. E. (2004) Modelling the effects of different quality prey fish species and of food supply reduction on growth performance of Roseate Tern chicks. *Ecological Modelling,* **177**, 95–106.

Maxwell, S. M., Conners, M. G., Sisson, N. B., & Dawson, T. M. (2016) Potential Benefits and Shortcomings of Marine Protected Areas for Small Seabirds Revealed Using Miniature Tags. *Frontiers in Marine Science,* **3**, 264.

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015) Marine defaunation: Animal loss in the global ocean. *Science*, **347**, 1255641.

McInnes, A. M., Khoosal, A., Murrell, B., Merkle, D., Lacerda, M., Nyengera, R., Coetzee, J. C., Edwards, L. C., Ryan, P. G., Rademan, J. & van der Westhuizen, J. J., (2015) Recreational Fish-Finders: An inexpensive alternative to scientific echo-sounders for unravelling the links between marine top predators and their prey. *PloS one*, **10**, 1–18.

McLeay, L. J., Page, B., Goldsworthy, S. D., Ward, T. M., & Paton, D. C. (2009a) Size matters: variation in the diet of chick and adult crested terns. *Marine Biology,* **156,** 1765–1780.

McLeay, L. J., Page, B., Goldsworthy, S. D., Ward, T. M., Paton, D. C., Waterman, M., & Murray, M. D. (2009b) Demographic and morphological responses to prey depletion in a crested tern (*Sterna bergii*) population: can fish mortality events highlight performance indicators for fisheries management? *ICES Journal of Marine Science*, **66**, 237–247.

McLeay, L. J., Page, B., Goldsworthy, S. D., Paton, D. C., Teixeira, C., Burch, P., & Ward, T. (2010) Foraging behaviour and habitat use of a short-ranging seabird, the crested tern. *Marine Ecology Progress Series,* **411**, 271−283.

Mcwilliams, S. R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004) Flying, fasting, and feeding in birds during migration : a nutritional and physiological ecology perspective. *Journal Avian Biology*, **35**, 377–393.

Merkel, F. R., Johansen, K. L., & Kristensen, A. H. (2016) Use of time-lapse photography and digital image analysis to estimate breeding success of a cliff-nesting seabird. *Journal of Field Ornithology*, **87**, 84−95

Minich, L. (2001) Variation in the feeding of four species of seabird on Machias Seal Island, New Brunswick. PhD dissertation, Bowdoin College, Portland.

Monaghan, P., Uttley, J. D., & Burns, M. D. (1992) Effect of changes in food availability on reproductive effort in Arctic terns *Sterna paradisaea. Ardea,* **80**, 71–81.

Monteiro, P. M., & van der Plas, A. K. (2006) 5 Low oxygen water (LOW) variability in the Benguela system: Key processes and forcing scales relevant to forecasting. *Large Marine Ecosystems*, **14**, 71–90.

Montevecchi, W. A., Birt, V. L., & Cairns, D. K., (1988) Dietary changes of seabirds associated with local fisheries failures. *Biological Oceanography,* **5**, 153–161.

Montevecchi, W. A. (2002) Interactions between fisheries and seabirds. In Biology of Marine Birds, pp. 527–557. Eds E. A. Schreiber, J. Burger. CRC Press, Boca Raton, FL.

Morand-Ferron, J., Veillette, M., & Lefebvre, L. (2006) Stealing of dunked food in Carib grackles (*Quiscalus lugubris*). *Behavioural processes*, **73**, 342–347.

Moreby, S. J. & Stoate, C. (2000) A quantitative comparison of neck-collar and faecal analysis to determine passerine nestling diet. *Bird Study*, **47**, 320–331.

Morrison, T. A., Yoshizaki, J., Nichols, J. D. & Bolger, D. T. (2011) Estimating survival in photographic capture–recapture studies: overcoming misidentification error. *Methods in Ecology and Evolution*, **2**, 454–463.

Mullers, R. H. E., Navarro R. A., Crawford, R. J. M., & Underhill, L. G. (2009a) The importance of lipid-rich fish prey for Cape gannet chick growth: are fishery discards an alternative?. *ICES Journal of Marine Science,* **66**, 2244–2252.

Mullers, R. H. E., Navarro R. A., Daan S., Tinbergen J. M. & Meijer H. A. J. (2009b) Energetic costs of foraging in breeding Cape gannets *Morus capensis*. *Marine Ecology Progress Series,* **393,** 161–171.

Nagy, K. A., Siegfried, W. R., & Wilson, R. P. (1984) Energy utilization by free-ranging jackass penguins, *Spheniscus demersus.Ecology*, **65**, 1648–1655.

Navarro, R. A. (2010) Energy Budget and foraging behaviour of the Cape gannet *Morus capensis* during the breeding season. Unpubl. doctoral dissertation, University of Cape Town, Cape Town.

Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S. & Crowston, K. (2012) The future of citizen science: emerging technologies and shifting paradigms. *Frontiers in Ecology and the Environment*, **10**, 298–304.

Newsome, S. D., Bentall, G. B., Tinker, M. T., Oftedal, O. T., Ralis, K., Estes, J. A. & Fogel, M. L. (2010) Variation in $\delta^{13}C$ and $\delta^{15}N$ diet - vibrissae trophic discrimination factors in a wild population of California sea otters. *Ecological Applications*, **20**, 1744-1752.

Nettleship, D. N. (1972) Breeding success of the Common Puffin (*Fratercula arctica L.*) on different habitats at Great Island, Newfoundland. *Ecological Monographs*, **42**, 239–268.

Nicholson, L. (2002) Breeding strategies and community structure in an assemblage of tropical seabirds on the Lowendal Islands, Western Australia. Unpubl. Doctoral dissertation, Murdoch University, Perth.

Oehler, D. A., Pelikan, S., Fry, W. R., Weakley Jr, L., Kusch, A., & Marin, M. (2008) Status of crested penguin (*Eudyptes* spp.) populations on three islands in southern Chile. *Wilson Journal of Ornithology*, **120**, 575–581.

Okes, N. C., Hockey, P. A. R., Pichegru, L., van der Lingen, C. D., Crawford, R. J. M., & Grémillet D. (2009) Competition for shifting resources in the southern Benguela upwelling: Seabirds versus purse-seine fisheries. *Biological Conservation*, **142**, 2361–2368.

Orians, G. H., & Pearson, N. E. (1979) On the theory of central place foraging. In Analyses of ecological systems. Horn, D. J., Mitchell, R. D., & Stairs, G. R. (Eds). Ohio State University Press, Columbus: 154–177.

Oro D. (1996) Gull kleptoparasitism in Audouin's gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. *Ibis,* **138**, 218–221.

Oro, D., Cam, E., Pradel, R., & Martínez-Abraín, A. (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. *Proceedings of the Royal Society of London B: Biological Sciences*, **271**, 387–396.

Paiva, V. H., Ramos, J. A., Catry, T., Pedro, P., Medeiros, R., & Palma, J. (2006) Influence of environmental factors and energetic value of food on little tern *Sterna albifrons* chick growth and food delivery. *Bird Study,* **53**, 1−11.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S., & Reid, J. B. (2008) Seabirds as indicators of the marine environment. *ICES Journal of Marine Science*, **65**, 1520–1526.

Passuni, G., Barbraud, C., Chaigneau, A., Demarcq, H., Ledesma, J., Bertrand, A., Castillo, R., Perea, A., Mori, J., Viblanc, V.A. & Torres ‐ Maita, J. (2016) Seasonality in marine ecosystems: Peruvian seabirds, anchovy, and oceanographic conditions. *Ecology*, **97**, 182−193.

Pennycuick, C. J. (2008) Modelling the flying bird. Academic Press, London.

Péron, C., Delord, K., Phillips, R. A., Charbonnier, Y., Marteau, C., Louzao, M., & Weimerskirch, H. (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels Procellaria aequinoctialis from Kerguelen Island. *Marine Ecology Progress Series*, **416**, 267–284.

Perdeck, A. C. & Cavé A. J. (1992) Laying Date in the Coot: Effects of Age and Mate Choice. *Journal of Animal Ecology,* **61**, 13–19.

Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, **352**, 221–234.

Pichegru, L., Ryan, P. G, van der Lingen, C. D., Coetzee, J., Ropert-Coudert, Y., & Grémillet, D. (2007) Foraging behaviour of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguella upwelling system. *Marine Ecology Progress Series,* **350,** 127–136.

Pichegru, L., Ryan, P. G., Crawford, R. J. M., van der Lingen, C. D. & Grémillet, D. (2010a) Behavioural inertia places a top marine predator at risk from environmental change in the Benguela upwelling system. *Marine Biology,* **157**, 537–544.

Pichegru, L., Grémillet, D., Crawford, R. J. M., & Ryan, P. G. (2010b) Marine no-take zone rapidly benefits Endangered penguin. *Biology Letters*, **6**, 498–501.

Pichegru, L., Cook, T., Handley, J., Voogt, N., Watermeyer, J., Nupen, L., & McQuaid, C. D. (2013) Sex-specific foraging behaviour and a field sexing technique for endangered African Penguins. *Endangered Species Research,* **19**, 255–264.

Ponchon, A., Grémillet, D., Christensen-Dalsgaard, S., Erikstad, K. E., Barrett, R. T., Reiertsen, T. K., McCoy, K. D., Tveraa, T., & Boulinier, T., (2014) When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere*, **5,** 1–19.

Privileggi, N. (2003) Great cormorants *Phalacrocorax carbo sinensis* wintering in Friuli-Venezia Giulia, Northern Adriaic: specific and quantitative diet composition. *Vogelwelt,* **124**, 237–243.

Prosch, R. M. (1986) Early growth in length of the anchovy *Engraulis capensis* Gilchrist off South Africa. *South African Journal of Marine Science,* **4**, 181–191.

Quinn, G. P., & Keough, M. J. (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK.

Quintana, F., & Yorio, P. (1999) Kleptoparasitim by Kelp Gulls on Royal and Cayenne Terns at Punta León, Argentina. *Journal of Field Ornithology,* **70**, 337–342.

R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0. http://www.R-project.org

Ramos, J. A., Encarnacion, S., & Monteiro, L. R. (1998) Prey delivered to roseate tern chicks in the Azores. *Journal of Field Ornithology,* **69,** 419–429.

Ramos, J. A., Maul, A. M., Ayrton, V., Hunter, J., Bowler, J., Bullock, I., Castle, G., Mileto, R., Lidstone-Scott, R., Lidstone-Scott, P., Pacheco, C. (2002) The influence of oceanographic conditions and timing of breeding on tropical Roseate Tern reproductive parameters. *Marine Ecology Progress Series,* **243,** 271–279.

Randall, D., Burggren, W. W., French, K., & Eckert, R. (2002) Eckert animal physiology. Macmillan, New York.

Ratcliffe, A. N., Richardson, D., Scott, R. L., Bond, P. J., Westlake, C., & Stennett, S. (1997) Terns host selection, attack rates and success rates for Black-headed Gull Kleptoparasitism of terns, *Colonial Waterbirds*, **20**, 227–234.

Rathcke B. J. (1992) Nectar distributions, pollinator behavior and plant reproductive success. In: Hunter MD, Ohgushi KT, Price PW, editors. Effects of resource distribution and animal-plant interactions. Academic Press. San Diego, 113–138.

Redpath, S. M., Clarke, R., Madders, M. & Thirgood, S. J. (2001). Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. *Condor*, **103**, 184–188.

Rindorf, A., Wanless, S., & Harris, M. P. (2000) Effects of changes in sandeel availability on the reproductive output of seabirds. *Marine Ecology Progress Series*, **202**, 241-252.

Rishworth, G. M., Tremblay, Y. & Green, D. B. (2014) Drivers of time-activity budget variability during breeding in a pelagic seabird. *PLoS ONE*, **9**, 1–17.

Robinson, J. A., Hamer, K. C., & Chivers, L. S. (2002) Developmental plasticity in Arctic Terns *Sterna paradisaea* and Common Terns *Sterna hirundo* in response to a period of extremely bad weather. *Ibis*, **144**, 344–346.

Robinson, B. G., Franke, A. & Derocher, A. E. (2015) Estimating nestling diet with cameras: quantifying uncertainty from unidentified food items. *Wildlife Biology*, **21**, 277–282.

Roel, B. A., & Armstrong, M. J. (1991) The round herring *Etrumeus whiteheadi*, an abundant, underexploited clupeoid species off the coast of southern Africa. *South African Journal of Marine Science*, 11, 267−287.

Ropert-Coudert, Y., Wilson, R. P., Yoda, K., & Kato, A. (2007) Assessing performance constraints in penguins with externally attached devices. *Marine Ecology Progress Series,* **333**, 281–289

Rossouw, N., Brown R., Morant P., & Deacon H. (2000) Robben Island state of environment: summary report. CSIR Report No. ENV-SC, 99127. Stellenbosch, Cape Town.

Roux, J., van der Lingen, C. D., Gibbons, M. J., Moroff, N. E., Shannon, L. J., Smith, A. D. M., & Cury, P. M. (2013) Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: Lessons from the Benguela. *Bulletin of Marine Science*, **89**, 249–284.

Roy, C., van der Lingen, C. D., Coetzee, J. C., & Lutjeharms, J. R. E. (2007) Abrupt environmental shift associated with changes in the distribution of Cape anchovy Engraulis encrasicolus spawners in the southern Benguela. *African Journal of Marine Science* **29**, 309–319.

Ryan, P. G. (1987) The foraging behaviour and breeding seasonality of Hartlaub's Gull *Larus hartlaubii*. *Cormorant*, **15**, 23–32.

Ryan, P. G. (2014) Moult of flight feathers in darters (Anhingidae). *Ardea*, **101**, 177–180.

Ryan, P. G. (2017) Perch-hunting Swift Terns. *Promerops*, **307**, 19.

Ryan, P. G., & Moloney, C. L. (1988) Effect of trawling on bird and seal distributions in the southern Benguela region. *Marine Ecology Progress Series*, **45**, 1–11.

Ryan, P. G., Pichegru, L., Ropert-Coudert, Y., Grémillet, D., & Kato, A. (2010) On a wing and a prayer: the foraging ecology of breeding Cape cormorants. *Journal of Zoology,* **280**, 25–32.

Ryan, P. G., Edwards, L., & Pichegru, L. (2012) African Penguins *Spheniscus demersus*, bait balls and the Allee effect. *Ardea,* **100,** 89–94.

Sæther, B. E. (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, **12**, 143–149.

Safina, C., Wagner, R. H., Witting, D. A. & Smith, K. J. (1990) Prey delivered to Roseate and Common Tern chicks; composition and temporal variability. *Journal of Field Ornithology*, **61**, 331–338.

Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V.A., Gauthier-Clerc, M., Beaune, D., Park, Y. H., Yoccoz, N. G., Stenseth, N. C. & Le Maho, Y. (2011a) Reliability of flipper-banded penguins as indicators of climate change. *Nature*, **469**, 203–206.

Saraux, C., Robinson-Laverick, S. M., Le Maho, Y. Ropert-Coudert, Y.,& Chiaradia, A. (2011b) Plasticity in foraging strategies of inshore birds: how Little Penguins maintain body reserves while feeding offspring. *Ecology,* **92**, 1919–1916.

Savazzi, E. (2010) Digital photography for science. Lulu.com.

Schmidt-Wellenburg, C. A., Biebach, H., Daan, S. & Visser, G. H. (2007) Energy expenditure and wing beat frequency in relation to body mass in free flying Barn Swallows (*Hirundo rustica*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology,* **177**, 327–337.

Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

Schreiber, E. A., & Burger, J. editors. (2002) Biology of Marine Birds. CRC Press, Boca Raton.

Sergio, F., Newton, I., Marchesi, L., & Pedrini, P. (2006) Ecologically justified charisma: preservation of top predators delivers biodiversity conservation. *Journal of Applied Ecology*, **43**, 1049–1055.

Serventy, D. L., & Curry, P. J. (1984) Observations on colony size, breeding success, recruitment and inter-colony dispersal in a Tasmanian colony of short-tailed shearwaters *Puffinus tenuirostris* over a 30-year period. *Emu,* **84**, 71–79.

Shaffer, S. A. (2004) Annual energy budget and food requirements of breeding wandering albatrosses *Diomedea exulans*. *Polar Biology,* **27**, 253–256.

Shannon, V., Hempel, G., Moloney, C., Woods, J. D., & Malanotte-Rizzoli, P. (Eds.) (2006) Benguela: predicting a large marine ecosystem, **14**, Elsevier, Amsterdam.

Shealer, D. A. (1998) Differences in diet and chick provisioning between adult Roseate and Sandwich Terns in Puerto Rico. *Condor,* **100**, 131–140.

Shealer, D. A. (2002) Foraging behaviour and food of seabirds. In: Schreiber, E. A., Burger, J. (eds) Biology of marine birds. CRC Press, Boca Raton, FL, 137–178.

Shealer, D. A., Spendelow, J. A., Hatfield, J. S., & Nisbet, I. C. T. (2005) The adaptive significance of stealing in a marine bird and its relationship to parental quality. *Behavioural Ecology*, **16**, 371–376.

Sherley, R. B. (2010) Factors influencing the demography of endangered seabirds at Robben Island, South Africa (Doctoral dissertation, University of Bristol).

Sherley, R. B., Burghardt, T., Barham, P. J., Campbell, N., & Cuthill, I. C. (2010) Spotting the difference: towards fully-automated population monitoring of African penguins Spheniscus demersus. *Endangered Species Research*, **11**, 101–111.

Sherley, R. B., Underhill, L. G., Barham, B. J., Barham, P. J., Coetzee, J. C., Crawford, R. J. M., Dyer, B. M., Leshoro, T. M. & Upfold, L. (2013) Influence of local and regional prey availability on breeding performance of African Penguins *Spheniscus demersus*. *Marine Ecology Progress Series*, **473**, 291–301.

Sherley, R. B., Abadi F., Ludynia, K., Barham, B. J., Clark, A. E., & Altwegg, R. (2014) Age-specific survival and movement among major African Penguin *Spheniscus demersus* colonies. *Ibis*, **56**, 716–728.

Sherley, R.B., Ludynia, K., Dyer, B.M., Lamont, T., Makhado, A.B., Roux, J-P., Scales, K.L., Underhill, L.G. & Votier, S.C. (2017) Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Current Biology*, **27**, 1–6.

Sherrill-Mix, S. A., & James, M. C. (2008) Evaluating the potential tagging effects on leatherback sea turtles. Endang Species Res, **4**, 187–193.

Siegel-Causey, D., & Kharitonov, S. P. (1990) The evolution of coloniality. *Current Ornithology*, **7**, 285–330.

Smale, M.J., Watson, G. & Hecht, T. (1995) Otolith atlas of southern African marine fishes. Ichthyological Monographs of the JLB Smith Institute of Ichthyology. Grahamstown

Smith, M. M. & Heemstra, P. C. (2003) *Smiths' Sea Fishes.* Struik Plublishers, Cape Town.

Soanes, L. M., Bright, J. A., Brodin, G., Mukhida, F., & Green, J. A. (2015) Tracking a small seabird: First records of foraging movements in the Sooty tern Onychoprion fuscatus. *Marine Ornithology*, **43**, 235–239.

Sorensen, M. C., Hipfner, J. M., Kyser, T. K., & Norris, D. R. (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *Journal of Animal Ecology*, **78**, 460–467.

St. Clair, C. C., St. Clair, R. C., & Williams, T. D. (2001) Does kleptoparasitism by Glaucous-winged Gulls limit the reproductive success of Tufted Puffins? *Auk*, **118**, 934–943.

Stearns, S. C. (1992) The evolution of life histories, Vol 248. Oxford University Press, Oxford.

Steele, W. K., & Hockey, P. A. (1995) Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). *Auk*, **112**, 847–859.

Stenevik, E. K., Sundby, S., & Cloete, R. (2007) Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. *African Journal of Marine Science,* **29**, 127–136.

Stienen, E. W. M. (2006) Living with gulls: trading off food and predation in the Sandwich Tern Sterna sandvicensis. PhD dissertation, University of Groningen, Groningen.

Stienen, E.W.M. & Brenninkmeijer, A. (1999) Keep the chicks moving: how Sandwich terns can minimize kleptoparasitism by black-headed gulls. *Animal Behaviour*, **57**, 1135–1144.

Stienen, E. W., Van Beers, P. W., Brenninkmeijer, A., Habraken, J. M. P., Raaijmakers, M. H. J., & Van Tienen, P. G. (2000) Reflections of a specialist: patterns in food provisioning and foraging conditions in Sandwich Terns *Sterna sandvicensis*. *Ardea*, **88**, 33–49.

Stienen, E. W. M., Brenninkmeijer, A., & Geschiere, C. E. (2001) Living with gulls: the consequences for Sandwich Terns of breeding in association with Black-headed Gulls. *Waterbirds*, **24**, 68–82.

Stienen, E. W., Brenninkmeijer, A., & Courtens, W. (2015) Intra-specific plasticity in parental investment in a long-lived single-prey loader. *Journal of Ornithology*, **156**, 699–710.

Suryan, R. M., Irons, D. B., & Benson, J., (2000) Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *Condor,* **102**, 374–384.

Suryan, R. M., Irons, D. B., Kaufman, M., Benson, J., Jodice, P. G. R., Roby, D. D. & Brown, E. D. (2002) Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series*, **236**, 273–287.

Takahashi, A., Watanuki, Y., Sato, K., Kato, A., Arai, N., Nishikawa, J., & Naito, Y. (2003) Parental foraging effort and offspring growth in Adélie Penguins: does working hard improve reproductive success*? Functional Ecology,* **17**, 590–597.

Taylor, I. R. (1983) Effect of wind on the foraging behaviour of Common and Sandwich Terns. *Ornis Scandinavia,* **14**, 90–96.

Tella, J. L., Banos-Villalba, A., Hernández-Brito, D., Rojas, A., Pacifico, E., Diaz-Luque, J. A., Carrete, M., Blanco, G. & Hiraldo, F. (2015) Parrots as overlooked seed dispersers. *Frontiers in Ecology and the Environment*, **13**, 338–339.

Thiebault, A., Mullers, R. H., Pistorius, P. A., & Tremblay, Y. (2015) Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, **25**, 1302–1310.

Tornberg, R., & Reif, V. (2007) Assessing the diet of birds of prey: a comparison of prey items found in nests and images. *Ornis Fennica*, **84**, 21.

Tremblay, Y., Thiebault, A., Mullers, R., & Pistorius, P. A. (2014) Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PLoS ONE,* **9**, e88424.

Underhill, L. G., Tree, A. J., Oschadleus, H. D., & V. Parker (1999) Review of ring recoveries of waterbirds in southern Africa. Avian Demography Unit, Cape Town.

Underhill, L. G., Sherley, R. B., Dyer, B. M., & Crawford, R. J. M. (2009) Interactions between snakes and seabirds on Robben, Schaapen and Meeuw Islands, Western Cape province, South Africa. *Ostrich,* **80,** 115–118.

Urban, E. K., Fry, C. H., & Keith, S. (1986) The Birds of Africa, vol. 2. Academic Press, London.

Uys, C. J. (1978) Swift Terns breeding along the Western Cape coast. *Bokmakierie,* **30**, 64–66.

van der Lingen, C. D. (2002) Diet of sardine *Sardinops sagax* in the Southern Benguela upwelling ecosystem. *South African Journal of Marine Science,* **24**, 301–316.

van der Lingen, C. D., Coetzee, J. C., & Hutchings, L. (2002) Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the southern Benguela: implications for recruitment. GLOBEC Report, **16**, 46–48.

van der Lingen, C. D., & Huggett, J. A. (2003) The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In *The big fish bang: proceedings of the 26th annual larval fish conference*. Institute of Marine Research, Bergen: 303–343.

van der Lingen, C. D., Shannon, L. J., Cury, P., Kreiner, A., Moloney, C. L., Roux, J. P., & Vaz-Velho, F. (2006) Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds) Benguela: Predicting a Large Marine Ecosystem. Large Marine Ecosystems 14, Elsevier, Amsterdam: 147–185.

van Tienhoven, A. M., Den Hartog, J. E., Reijns, R. A. & Peddemors, V. M. (2007) A computer-aided program for pattern-matching of naturalmarks on the spotted raggedtooth shark *Carcharias taurus*. *Journal of Applied Ecology*, **44**, 273–280.

Veen, J. (1977) Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna s. sandvicensis* Lath.). *Behaviour*, Supplement, **20**, 1–193.

Vié, J. C., Hilton-Taylor, C., & Stuart, S. N. (2009) Wildlife in a changing world: an analysis of the 2008 IUCN Red List of threatened species. IUCN.

Vieira, B. P., Furness, R. W., & Nager, R. G. (2016) Using field photography to study avian moult. *Ibis*, **159**, 443–448.

Visser, G. H. (2002) Chick growth and developments in seabirds. In Biology of Marine Birds (eds: Schreiber EA, Burger J). CRC Press, Boca Raton, 439–465.

Votier, S. C., Bearhop, S., MacCormick, A., Ratcliffe, N., & Furness, R. W. (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. *Polar Biology,* **26**, 20–26.

Walter, C. B., Cooper, J. & Suter, W. (1987a) Diet of Swift Tern chicks in the Saldanha Bay Region, South Africa. *Ostrich*, **58**, 49–53.

Walter, C. B., Duffy, D. C., Cooper, J., & Suter, W. (1987b) Cape anchovy in swift tern diets and fishery landings in the Benguela upwelling region. *South African Journal of Wildlife Research*, **17**, 139–141.

Wanless, S., Harris, M. P., Redman, P., & Speakman, J. R. (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series*, **294**, 1–8.

Watermeyer, K. E. (2014) Ecosystem implications of the recent southward shift of key components of the southern Benguela. Unpubl. PhD thesis, University of Cape Town, Cape Town.

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993) Foraging strategy of Wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk,* **110**, 325–342.

Weimerskirch, H., Doncaster, C., & Cuenot-Chaillet, F. (1994) Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London B: Biological Sciences*, **255**, 91–9.

Weimerskirch, H., Inchausti, P., Guinet, C., & Barbraud, C. (2003) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, **15**, 249–256.

Wendeln, H., & Becker, P. H. (1999) Effects of parental quality and effort on the reproduction of common terns. *Journal of Animal Ecology,* **68**, 205–214.

Williams, G. C. (1966) Natural selection, the cost of reproduction and a refinement of Lack's principle. *American Naturalist,* **100**, 687–690.

Wilson, R. P. (1984) An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology*, 55, 109–112.

Wilson, R. P., Grant, W. S., & Duffy, D. C. (1986) Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology*, **67**,1091–1093.

Wilson, R. P. & McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment*, **4**, 147–154.

Wittenberger, J. F., & Hunt, G. L. (1985) The adaptive significance of coloniality in birds. *Avian Biology*, **8**, 1–78.

Woehler, E. J., Saviolli, J. Y., Bezerra-Francini, C. L., Neves, T., & Baston-Francini, R. (2013) Insect prey of breeding South American Terns. *Marine Ornithology*, **41**, 199–200.

Wood, S. N. (2006) Generalized additive models: an introduction with R. Chapman & Hall, New York, NY.

Wood, K. A., Stillman, R. A., & Goss-Custard, J. D. (2015) The effect of kleptoparasite and host numbers on the risk of food-stealing in an avian assemblage. *Journal of Avian Biology*, **46**, 589–596.

Worm, B. (2016) Averting a global fisheries disaster. *Proceedings of the National Academy of Sciences USA*, **113**, 4895–4897.

Yoccoz, N. G., Nichols, J. D., & Boulinier, T. (2001) Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution,* **16**, 446–453.

Zanette, L. Y., White, A. F., Allen, M. C. & Clinchy, M., (2011) Perceived predation risk reduces the number of offspring songbirds produce per year. *Science*, **334**, 1398–1401.

Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A., & Ploetz, J. (2008) Seeing the light: depth and time restrictions in the foraging capacity of emperor penguins at Pointe Geologie, Antarctica. *Aquatic Biology*, **3,** 217–226.

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009) Mixed Effects Models and Extentions in Ecology with R. Springer, New York.