# Energy Budget and foraging behaviour of the Cape gannet *Morus capensis* during the breeding season

René Alfredo Navarro-Cañas

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Universidad Austral de Chile

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Supervised by:

Professor L.G. Underhill

Co-supervised by:

Dr. R.J.M. Crawford

## Declaration

I hereby declare that all of the work presented in this thesis, titled "Energy Budget and foraging behaviour of the Cape gannet, *Morus capensis,* during the breeding season", is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed in Cape Town in July 2010,

Signed by candidate

René Alfredo Navarro-Cañas

Date of graduation: December 16th, 2010

*To Henk Visser*

Whose vision and enthusiasm
lead to this project,
it's funding and its beginnings.
I am grateful for the trust
and opportunity he gave me
to conduct this piece of
research

*"Supiste que vencer o ser vencido
son caras de un azar indiferente,
que no hay otra virtud que ser valiente."*

Did you know that to win or to be defeated
are faces of an indifferent fate
that there is no other virtue that being brave

*Jorge Luis Borges*

# Contents

# Energetics and foraging behaviour of the Cape gannet *Morus capensis* during the breeding season

René A. Navarro

Animal Demography Unit, Department of Zoology, University of Cape Town

July 2010

## Abstract

This thesis deals with the energy expenditure of free-ranging Cape gannets *Morus capensis* breeding at Malgas Island, South Africa. I sought to determine the energy budget of family units and to extrapolate this to the whole population. Energy expenditure was measured using the doubly labelled water technique on adults and chicks. $CO_2$ production was determined from ratios of isotope turnover, and converted into energy expenditure using a factor suitable for a fish-eating seabird. Chick rearing adults injected with a dose of label were, at the same time, fitted with a data logger that recorded the geographic position of the bird every 10 seconds during a complete foraging trip. I developed two algorithms for the analysis of foraging tracks. One uses changes in speed and turning-rate to partition the track into outgoing-, search-, foraging-, drifting and return-flight. The second introduces the distance-ratio scale (DRS), a new sinuosity based method that allows the direct assessment of the scale at which animals seem to perceive the environment. DRS values were also used to identify sections of the track where birds displayed area-restricted search (ARS) behaviour, which optimal foraging theory predicts for non-random foragers. Analysis of the ARS-zones showed that Cape gannets experienced greater variability in the spatio-temporal patchiness of the shoaling fish prey within breeding seasons than between seasons. The combination of DLW and GPS loggers on the same birds allowed the estimate of cost of various forms of flight during a foraging trip, which were the biggest costs yet reported for any seabird. The energetically expensive foraging mode of Cape gannets means that their efficiency to successfully fledge a chick is reduced and highly susceptible to variations in food availability, as attested by the current population decline in view of reduced food availability. The food consumption of the South African population was estimated at 15% of the annual fisheries catch, suggesting the potential for competition between the purse-seine fisheries and Cape gannets.

# Acknowledgements

When I embarked on this doctoral dissertation I knew quite well the magnitude of the task lying ahead but the lure of working in seabird ecology once again proved stronger than any common sense I may have had. A PhD thesis is a full-time job in its own right and I did this one alongside another full-time job, the one that actually paid the bills. The only way that I managed to accomplish this work was due to the fact that my supervisor, Professor Les Underhill, who is also my boss showed unwavering support both in terms of professional input but also practically by helping me balance all the conflicting demands imposed by the job and the thesis. I am deeply grateful to you, Les, for believing in me, for giving me the opportunity and the space to conduct this research; for the incredible support and understanding throughout the duration of the study; for all the guidance and discussions regarding the analysis and interpretation of the complex data sets that this project generated; for all your input, comments and for making sure that my written English was intelligible! My gratitude also for making it possible for me attend conferences to present parts of the work reported here, and for the opportunity to visit the Centre for Isotope Research at the University of Groningen, Netherlands. Thank you for opening your home where we could meet and discuss this thesis, and my gratitude to your wife, Jane, for her warm hospitality.

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I did all my field work at Malgas Island in Saldanha Bay, but even working on a relatively accessible island still required navigating a great deal of logistical problems - coming on and off the island was always a bit of a challenge. For the first season I tagged along with past and present Marine and Coastal Management staff: Rob Crawford, Bruce Dyer, Leshia Upfold and Linda Staverees; my gratitude for all the logistical help to get to Malgas Island. To the crew of the "Sardinops" for the occasional lift to the island. For the second season I relied on the weekly trips by the West Coast National Park to relieve the ranger on duty on the island; my gratitude to Piérre Nel and his team for their help and support with transport to the island. Those reliable boat trips came to and abrupt end one night when a fierce storm took the boat from its berth and smashed it against the rocks! For the third season, after many desperate phone calls I contacted Keith Davidson in Saldanha who always managed to provide some form of transport to the island, usually in his own boat, the aging and slow "Lappop" with the equally aging and slow skipper Hugo Lambreg at the helm. Hugo had spent a year working on a fishing vessel in Chile and as soon as he found out that I was Chilean, our friendship was securely established. His Spanish command was limited to "sopa de peascado" (fish soup) which he repeated whenever the opportunity arose! Thanks Hugo for taking us safely to and from Malgas. A couple of times I was stranded on the island and my thanks go to cell-phone technology, Meredith Thorton and to the SA Navy (Saldanha) for coming to retrieve me from Malgas. To Max Starcke, thanks for fetching me from Saldanha and for all the music that kept me sane when I was all on my own on the island. Thank you to Peter Ryan, who supplied me with desperately needed glass micro-capillaries when there were none to be had; and to Nigel Adams who collected growth data for the season 1988/1989.

After some trial-by-fire I was able to do all the field work on my own, including fitting loggers and taking blood samples, but it was always easier and more fun with someone to help. My dearest daughter Nathania, who was only 12 years old when she joined me for the first time, was my assistant on many occasions, thank you Nats! I also enjoyed the company and assistance of Anna Rousseau, Robert Makin-Taylor, and Maria Mateos. Maria travelled from Cadiz, Spain, especially to spend some time helping with my work at Malgas.

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Over the course of these years I had the fortune of working with many people who helped me with this work and to whom I feel deeply indebted. I hope that I have acknowledged all of you in the preceding paragraphs but please accept my sincere apologies should I unwittingly have omitted anyone.

# Layout and contribution of co-authors

This thesis comprises eight chapters, six of which have been written as self contained papers ready for submission to a journal. As a result, some repetition of the methods and references was unavoidable; where appropriate I describe a method in a chapter and referred to this elsewhere in the thesis. Tables, figures and appendices follow the text for each chapter. Each chapter includes its own list of references rather than collecting all references in a single list, this simplified enormously the task of correctly referencing each chapter.

I was responsible for the data collection, analysis and writing of each chapter, with the following exception. Chapter 2 was written by R.H.E. Mullers, I contributed most of the growth data used in it; I also contributed to the data analysis and made extensive comments on the text; the chapter was published in *ICES Journal of Marine Science,* 2009, **66**:2244–2252.

L.G. Underhill commented on all chapters and suggested the 'distance-ratio scale' method, which I developed and implemented in Chapter 5, and use for the analyses in Chapter 6. L.G. Underhill developed and implemented the growth index used in Chapter 2 (see appendix 2.1). R.J.M. Crawford contributed the diet data and made suggestions to Chapter 2. H.A.J. Meijer commented on the use and application of the doubly labelled water technique (Chapter 3). R.H.E. Mullers contributed the track data for Ichaboe Island and complemented my own track data for Malgas Island (Chapter 6); he also contributed DLW data for Chapter 7.

# CHAPTER 1

# CHAPTER 1

# GENERAL INTRODUCTION

## Motivation and Rationale

Most seabird species are colonial and generally they are long-lived birds with small clutches, deferred maturity and low adult mortality rates (Ashmole 1971). These characteristics set them apart from most other birds. Whether of coastal or pelagic habits, seabirds are central place foragers, at least during the breeding season, because parents need to return regularly to brood and feed chicks. An additional disadvantage for pelagic seabirds is in their need to travel long distances to their feeding grounds, and to find enough food in huge expanses of open-ocean. Tropical seabirds are specially affected because they utilize pelagic resources in low productivity waters. Because of these constraints, seabirds have less energy available for reproduction per unit of energy consumed than terrestrial birds (Visser 2001). This results in strong selection pressures for a suite of adaptations to compensate for the low levels of energy availability; examples are small clutch size, brood reduction strategies, slow grow rate of chicks, specialized digestion (as in albatrosses that concentrate food into stomach oils), etc.

During the breeding season parents have to obtain sufficient food to cover their own needs and those of the chick(s). Typically, food requirements of the entire family tend to peak during the second half of the nestling period, when chicks are large and growth rate is high. If parents fail to meet the maximal energy requirements of their families, chicks will receive less food, and this will impact their growth, rate of maturation, and eventually their chances of survival. Even adult survival is threatened when food levels are too low and mass desertion may occur, leaving abandoned young to starve to death when the adults desert them and go in search of food elsewhere (Schreiber & Schreiber 1989). Adult mortality and total nest failure due to food shortage occasionally take dramatic proportions; seabirds off Peru die by the million during strong El Niño Southern Oscillation (ENSO) events (Jordan & Fuentes 1966, Duffy 1983). ENSO events in waters off South Africa have moderate effects on seabirds, mostly resulting in shifts in diet, local breeding failures and perhaps increased mortality of young birds. Out of three species analysed, Cape gannets were the least affected during the 1982–1983 ENSO event (Duffy *et al.* 1984).

Cape gannets *Morus capensis*, like most seabirds, are central place foragers, having to fly long distances from their breeding colonies to obtain food and bring it back to their brood. GPS tracking data indicate that Cape gannets breeding at Malgas Island fly between 85 and 956 km (mean = 293 km) per foraging trip (Grémillet *et al.* 2004). Once a school of fish has been located, they feed by circling over prey and plunge diving. The mean maximum diving depth of Cape gannets breeding at Malgas Island is 5.9 m, ranging from 1.2 to 12.6 m (Adams & Walter 1993). The deepest dives most probably require of active underwater swimming in pursuit of fish. Sulids use their partly out-stretched wings for underwater “flight” (Nelson 1978). This is a particularly energetically expensive mode of foraging. At-sea energy expenditure of Cape gannets has been estimated at about 6.5 times basal metabolic rate (Adams *et al.* 1991); an even higher value (8.1×BMR) was found for its North Atlantic congeneric *Morus bassanus* (Birt-Friesen *et al.* 1989). However, both values are considerably higher than 4×BMR, which has been suggested as a maximum sustainable metabolic rate for birds (Drent & Daan 1980).

In the context of the breeding season, parental foraging efficiency is expressed as the total food intake of the family divided by total parental energy spent (Visser 2001). In general, parental foraging efficiencies of seabirds are smaller than in land birds (Visser 2001). This is probably the result of relatively low food densities in pelagic ecosystems. Therefore, to collect sufficient food birds have to fly vast distances, which is energetically expensive. Moreover, Cape gannets have a higher absolute at-sea metabolic rate than other seabirds, 143% more than those using gliding and 34% more than those using non-gliding flight (Adams *et al.* 1991). Given these considerations, it is not surprising that many seabird species, including the Cape gannet, manage to rear only one chick per season (Jarvis 1971). However, in years of good feeding productivity, Cape gannets are able to increase their foraging efforts and can rear two chicks successfully (Navarro 1991).

This study aims to unravel, during the breeding period of the annual cycle, relationships between parental foraging decisions, parental energy expenditure, chick growth and reproductive success. To this end, I have used GPS-tracking of individual birds with simultaneous measurement of their energy expenditure with stable isotope methods (doubly labelled water). Moreover, because of validations of the doubly labelled water method in growing birds (Visser & Schekkerman 1999, Visser *et al.* 2000), it is now possible to determine reliable energy budgets of free-living chicks.

All methods used for studying and handling gannets during this study were approved by the Animal Use and Care Committee of South African National Parks (SANParks) and the research permit was issued by SANParks.

**Key Questions**

1. What are the detailed routines and foraging activities of individual Cape gannets?
2. By using doubly labelled water methods simultaneously with data loggers, what is the daily energy expenditure of the individuals in relation to activity, particularly distance travelled?
3. By using doubly labelled water methods, what is the relationship between chick growth rate and the energy budget of free-living chicks from hatching until fledging?
4. What are the overall energy budgets of breeding per family units, including the contributions of both chicks and adults?
5. What is the population energy budget during a yearly cycle?

## Natural history of the Cape gannet

The Cape gannet is a member of the family Sulidae, which comprises three species of gannets (genus *Morus*), and seven species of boobies (genus *Sula*) now that a subspecies of the masked booby has been recognized as a full species (Pittman & Jehl 1998).

The Cape gannet is a fairly large seabird with a mean weight of *ca* 2800 g and measuring *ca* 84–94 cm long, with a wing span of *ca* 171–185 cm (Nelson 1978). Like other sulids, it is essentially a fish-eating bird, travelling on the wing in search for food and catching its prey by plunge diving into the water from the air (Ashmole 1971). The Cape gannet is restricted to the coast of Africa, from the Western Sahara on the west coast to Mozambique (rarely to Kenya) on the east coast (Nelson 1978). However, its breeding range is extremely restricted in comparison with other sulids; only the Abbot's booby *Sula abbotti* that breeds at a single locality, Christmas Island, Indian Ocean, has a smaller number of breeding colonies (Nelson 1978). Cape gannets breed at six offshore islands, five of them located on the west coast of South Africa and Namibia, within the influence of the cold Benguela Upwelling System, and one on the east coast, in the warmer waters of the Indian Ocean (Crawford *et al.* 1983). Furthermore, at least two colonies of Cape gannets have become extinct during historical times.

With the exception of Mercury Island that has few level areas Cape gannets breed in dense colonies on flat islands (Duffy & La Cock 1985). Nest densities vary between 2.3–2.8 nests $m^{-2}$ (Rand 1963, Jarvis 1971). The nest is a hollow-topped mound made entirely of guano plus detritus such as feathers and sticks. Occupancy of the colony is throughout the year, including the non-breeding period. Nest building and egg lying sometimes begin as early as June (pers. obs), but the peak laying takes place between September to mid-October at Malgas Island (Berruti 1987) However, this varies with locality and year. The clutch is typically a single egg, very rarely two (Jarvis 1974). The bluish egg is relatively small, weighting *ca* 98 g, which is about 3.5% of the adult mass (pers. obs). Incubation typically lasts for *ca* 42–46 days, and the nestling period for *ca* 93–105 days. Both, male and female incubate, care for and feed the young until fledging (Jarvis 1971). There is no post-fledging care of the young in any of the gannet species; such care is, however, characteristic of boobies (Nelson 1978). Although there are no adequate estimates, mortality of Cape gannets during the first two or three years is high and is thought to be similar to that of North Atlantic gannets (70–80%, Nelson 1978). Annual adult survival has been estimated at 87.8% (se = 2%) and 89.6% (se = 1.53%) for the Malgas Island and Lambert's Bay populations respectively (Altwegg *et al.* 2008).

Numbers of Cape gannets breeding at islands off the Namibian coast (Mercury, Ichaboe and Possession) have declined between 1956 and present (2005/2006 season) from 114 633 to 10 433 breeding pairs respectively, a 91% decrease in 50 years. This contrasts with the trends at the islands of South Africa where Cape gannets have increased by *ca* 270% in the period 1956–2006, from 50 047 to 134 575 breeding pairs. However, the total population showed a decrease: from 253 817 breeding pairs in 1956–1957 to 145 008 in 2005/2006, a 42.9% decrease in 50 years (Crawford *et al.* 2007). The sharp decrease in Namibia has been attributed primarily to a greatly diminished food supply following the collapse of the sardine *Sardinops sagax* stock off the Namibian coast during the late 1960s (Crawford & Shelton 1981). Birds emigrating from the Namibian islands and the intrinsic population growth are attributed to the increase in the South African populations (Crawford *et al.* 2007). The increase is most likely linked to an increase in the abundance of sardine and anchovy *Engraulis encrasicolus* since the early 1970s (Crawford & Shelton 1981). Because of its dependence on so few colonies and the overall decreasing trend in population size, the Cape gannet is considered as "Vulnerable" (BirdLife International 2000).

Adams & Navarro (2005) studied the foraging behaviour of Cape gannets using radio-tagged birds during three breeding seasons (1987/1988, 1988/1989, and 1989/1990), they found that flight directions of birds departing from and returning to the colony were non-random and were strongly influenced by the dominant winds; with most birds returning with a tail wind that could represent energy savings of 26% to 48% for tail winds of 4 and 9 m $s^{-1}$ respectively. Grémillet *et al.* 2004 were the first to use Global Positioning System loggers to study the foraging behaviour of Cape gannets from two neighbouring colonies, Malgas Island and Bird Island—Lamberts Bay. They found that birds from Malgas Island foraged more intensively; their foraging trips lasted longer (22.6 vs 8.5 h), involving longer total flight time (7.8 vs 5.9 h), longer foraging path length (293 vs 228 km), and greater maximum distance from the breeding site (104 vs 67 km). They also travelled faster (50 vs 44 km h–1), and had a larger number of foraging locations during each trip (252 vs 121), with more sinuous foraging paths (1.4 vs 1.1). However, there were no significant differences in the number of dives per foraging trip (68 vs 66), the average maximum depth attained (3.4 vs 3.6 m), nor the average or total dive duration per foraging trip (4.3 vs 4.3 s and 5.7 vs 4.3 min, respectively). They concluded that gannets from these two colonies were spatially segregated and experienced different foraging conditions, most likely mediated by the pattern of prevailing winds. Lewis *et al.* (2006)

compared per capita growth rates of five of the six extant Cape gannet colonies with foraging range (using GPS-loggers), foraging work rate, food delivery rates and body condition of breeding adults; they found significant associations between the rate of population change, individual behaviour, energetic gain and body condition that indicate that recent population changes are associated with extrinsic effects. However, Mullers & Navarro (2010) in a more intensive study (also using GPS-loggers, but over several breeding seasons), found evidence that contradicts Lewis *et al.* (2006) finding. Pichegru *et al.* (2007) studied the foraging behaviour of Cape gannets from two colonies with contrasting diet and population trends: Malgas Island (declining population) and Bird Island–Nelson Mandela Bay (increasing population; feeding exclusively on natural prey). They found that birds from Malgas Island foraged in areas containing very low abundances of pelagic fish; fed mostly on low-energy fishery discards; increased their foraging effort and exploited a greater area than birds from the growing colony, which took advantage of abundant pelagic fish stocks in their foraging range. They conclude that the marked eastward shift of pelagic fish initiated in the late 1990s has resulted in the shortage of natural prey to Cape gannets on the west coast, strongly suggesting that the local population trend is driven by food availability during the breeding season. Grémillet *et al.* (2008) found evidence supporting the junk-food hypothesis for Cape gannets; they show that non-breeding birds can survive when complementing their diet with fishery wastes, but that they struggle to reproduce if the preferred prey is scarce. Chapter 2 of this thesis provides ample support to the junk-food hypothesis.

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# CHAPTER 2

## CHAPTER 2

# THE GROWTH OF CAPE GANNET CHICKS: INTRA- AND INTER-SEASONAL COMPARISONS IN RELATION TO ADULTS FORAGING EFFORT AND PREY AVAILABILITY

## Abstract

From 1996/1997 to 2006/2007 the population of Cape gannets *Morus capensis* breeding at the west coast of South Africa has been declining, and such decline coincided with decreased availability of lipid-rich fish prey anchovies *Engraulis encrasicolus* and sardines *Sardinops sagax.* Seabirds can use fishery discards as an alternative, but the quality of this “junk-food” in the Benguela ecosystem is lower than that of natural prey species. In this paper I consider whether chick growth and survival co-vary with periods of high and low availability of their lipid-rich prey species and whether fishery discards would be an alternative food source. The proportion of anchovy and sardine in the diet was between 66–84% in 1986–1988 and decreased to 16–35% in 2004–2006. Months with large proportions of anchovy and sardine in the diet were associated with faster chick growth. No association between the proportions of fishery discards in the diet and chick growth was found. These patterns are consistent with the idea that a distributional shift of anchovy and sardine decreased their contribution to the diet of Cape gannets and lowered chick growth and survival in the breeding colony. The reduced chick survival may partially explain the decline in numbers of Cape gannets breeding in the southern Benguela.

# Introduction

The Benguela Upwelling System off the south-western African coast is one of the most productive oceanic environments in the world (Shannon & O'Toole 2003). Large biomasses of the pelagic fish species anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* exploit these productive waters. Their high energetic value (Batchelor & Ross 1984), high lipid content (FAO 1989) and inshore distribution (Hampton 1987) make anchovy and sardine profitable food sources, providing enough energy to sustain large communities of predatory fish, marine mammals and seabirds (Shannon 1985). The availability of both forage fish species is important for several endemic seabird species breeding in the Benguela ecosystem. The abundance of anchovies is associated with the numbers of Cape cormorants *Phalacrocorax capensis* and swift terns *Sterna bergii* attempting to breed and the number of African penguin *Spheniscus demersus* chicks that fledge (Crawford & Dyer 1995). Numbers of Cape gannets *Morus capensis*, breeding in both Namibia and South Africa, are strongly related to the biomass of sardines (Crawford *et al.* 2007). These pelagic fish are also targeted by human fisheries (Griffiths *et al.* 2005). Besides competing with seabirds and marine mammals for the same fish, the fisheries produce considerable amounts of fishery discards, providing an alternative food source for seals and seabirds (Ryan & Moloney 1988). If the availability of their natural prey decreases, seabirds could compensate by feeding on discards, which can be beneficial to seabird populations (Tasker *et al.* 2000, Montevecchi 2002). The South African hake fisheries discarded about 7000 tonnes of hake annually off the west coast of South Africa at the end of the 1990s (Walmsley *et al.* 2007).

Since 1997 distributions of both anchovy and sardine have moved eastward along the western and southern coasts of South Africa (van der Lingen *et al.* 2005). This shift reduced the availability of these prey species to Cape gannets at the two west coast breeding colonies, Lambert's Bay and Malgas Island. Cape gannets from Malgas Island have increased the proportion of fishery discards in their diet, and have since shown an increased foraging effort compared to birds from a colony where sardines were readily available (Pichegru *et al.* 2007). Feeding on fishery waste was considered unsustainable for Cape gannets during the breeding season (Pichegru *et al.* 2007, Grémillet *et al.* 2008) due to the low energy content of the waste (Batchelor & Ross 1984). Cape gannet chicks hand-raised on hake (*Merluccius capensis* and *M. paradoxus)* fishery discards are almost exclusively hakes) have reduced growth rates and lower fledging weights compared to chicks fed anchovy and/or sardine (Batchelor & Ross 1984). However, until now no data have been collected on how this "junk-food" affected chick growth rates on a colony scale.

The Cape gannet is a seabird species endemic to southern Africa, which breeds on only six islands in the Benguela ecosystem. The number of breeding pairs on the west coast decreased from 50 000 to 36 000 pairs between 1997 and 2005 (Crawford *et al.* 2007), coinciding with the decreased availability of anchovy and sardine. The Cape gannet is listed as 'Vulnerable' (BirdLife International 2000). In this study I consider the effects of decreased availability of lipid-rich fish prey on chick growth and survival of Cape gannets and I investigated the suitability of fishery discards as an alternative to natural prey. I use two extensive datasets on chick growth during contrasting periods; 1986/1987–1988/1989, when anchovy and sardine were readily available near the breeding colony of Malgas Island and 2003/2004–2006/2007 when this availability decreased drastically. I present a detailed assessment of the impact of natural versus discard diet on chick growth in this seabird species and study these effects between, but also within years. I predict that Cape gannet chicks will show increased growth in periods that coincide with increased proportions of anchovy and sardine in the diet.

## Methods

Data presented here were collected during the breeding seasons 1986/1987–1988/1989 and 2003/2004–2006/2007 at Malgas Island (33°03'S 17°55'E), Saldanha Bay, South Africa, the largest of the five Cape gannet colonies off the west coast of Namibia and South Africa (Crawford *et al.* 2007). The Cape gannet breeding season at Malgas Island lasts eight to nine months. Individual pairs incubate the single egg for *ca.* 44 days (Jarvis 1974) and raise the chick to fledging in *ca.* 97 days (Jarvis 1974). The onset of egg-laying varies between individuals from August through early November (Staverees *et al.* 2008). In this chapter, I use 2003, for example, to indicate the breeding season from August 2003 until April 2004.

### Diet samples

Diet data were collected by Marine and Coastal Management. In each study year, diet samples were collected monthly from adult gannets over 1–3 consecutive days. Gannets were captured with a 2-m hooked pole (Kemper 2007) upon arrival from a foraging trip and inverted over a bucket in which they regurgitated (Berruti *et al.* 1993). During the study period, 2321 diet samples were collected (annual mean 332 samples, SD 220), which were analysed by weighing the mass of individual fish species in each sample. The percentage contribution (wet mass) of each fish species was calculated for each month. The diet was categorised into five groups: anchovy, sardine, saury *Scomberesox saurus*, fishery discards (hake) and other species. Anchovy and sardine were combined for further analyses as in Crawford *et al.* (2007).

### Chick growth

Human access to the interior of the colony involved unacceptable levels of disturbance. For this reason chicks were selected at different sites near the periphery of the colony (3 m) to measure growth. Chicks were taken from the nest with a hooked pole, measured and put back within three minutes. Bill length (to nearest 0.1 mm), length of flattened wing chord (to nearest 1 mm) and body mass (<1000 g to nearest 10 g, >1000 g to nearest 25 g) were measured. Chicks were measured at approximately the same time of each measuring day and in the same order. Chicks were identified either by nest location or by individually coded colour rings.

To test whether chicks growing at the periphery represented chick growth for the whole colony, I measured chicks in the interior of the colony in the first year (1986). Differences in parental condition (Coulson 1968, Gibbs *et al.* 2000) or predation pressure (Tenaza 1971) within and at the edge of a colony could affect chick growth rates. Nests were at least 3 m from the edge of the colony, surrounded by other nests on all sides.

I combined several datasets on Cape gannet chick growth and therefore the measuring protocols differed between years. However, all growth increments were analysed in the same way and variation in intervals between measurements did not affect growth results (Multilevel model: interval $F_{1,3222} = 1.5$, $p = 0.218$). I aimed to measure a sample of chicks of all ages and from different parts of the colony throughout each breeding season. During the 1986/1987 breeding season chicks were measured at 3–4-day intervals until they either died or fledged (see Navarro 1991 for details). In 1987 and 1988, different samples of chicks were measured over four days at each month (mean sample size 53 ± 28, $n = 635$). In addition, in 1988 another sample of chicks was measured twice per month at a four-day interval, but repeated until they died or fledged. In the years 2003 to 2006 I selected a sample of chicks at each of four sites and measured the same chicks at weekly intervals until they died or fledged. Newly hatched chicks were added into the sample in order to collect data on the growth of young chicks throughout the breeding season.

Chick age was estimated from the first measurement of each chick, using algorithms derived from data of 103 known aged chicks (R. Navarro & N. Klagen, unpublished data). When wing length was less than 40 mm, age $d$ (days) was computed by

$$d = -\log_e((89.78 - c)/(6.15c))/0.086, \qquad (2.1)$$

where $c$ is bill length (mm). For chicks with wing length greater than 40 mm, age was computed as

$$d = (1.395 - \log_e(\log_e(588.8/w)))/0.0264, \qquad (2.2)$$

where $w$ is the wing length (mm). The biological motivation for this dual system is that the bill grows rapidly when the chick is small while the wing shows little growth, and subsequently this pattern is reversed.

### Growth index

Growth rates were analysed using a non-parametric approach (see Appendix 2.1 for full description of method), because standard parametric families of growth models such as the Gompertz, logistic or Richard's growth curves do not have the flexibility to fit the data adequately (see also Brown *et al.* 2007). The growth index measures deviations from "average" growth, and is independent of whether growth is measured at an early age when the absolute growth rates (g $d^{-1}$) are small, at the maximum growth spurt, or late in development when growth rates decrease. The growth index is scaled so that it represents the number of standard deviations above or below average growth rate; with this standardization it is appropriately denoted $z$. For analyses data were pooled across years, growth indices were calculated and then tested for between and within year variation. Only chicks up to the age of 85 days were used for analyses, because the average mass of chick tended to decrease after this age (visual inspection of this dataset).

### Chick survival

In 2003 and 2004, 10 sites were randomly selected to monitor chick survival: five sites at the periphery and five sites in the interior of the colony (at least 3 m from the edge and surrounded by other nests). Disturbance was kept to a minimum as sites that could be approached by stepping on large rocks or rocky ridges were selected to monitor chick survival. At each site I marked one position from which I checked the contents of all nests within a 2 m radius. Contents of nests were monitored by lifting birds gently when they were sitting on the nest to check for eggs or small chicks. When chicks were larger and clearly visible, nests were not disturbed. Presence and approximate age of the chicks (based on plumage) were monitored every two weeks. Survival was analysed for chicks until 12 weeks of age, because after this age I could not determine whether they had died or fledged when not observed at the nest. Survival of chicks is defined as the proportion of chicks that survived between two nest checks, relative to the number of chicks of the first of the two checks.

### Statistical analyses

Results are presented as mean ± standard deviation. Variables were selected using multiple regression models in which the potential explanatory effects of predictive variables were tested using a backwards deletion method. The residuals of models were tested for normality.

In order to correct for a possible effect of individual on repeated growth measurements, growth indices were tested with multilevel mixed-modelling procedures in MLWin 2.02 with individual and observation as levels. Further included in the models were explanatory variables such as location (periphery or interior), year, month, hatching date and diet. The growth index was independent of chick age and therefore chick age was not included in the models. Significance levels were calculated with restricted iterative generalized least squares (RIGLS). Chick age was only included in the models testing the relationship between chick growth and diet, to correct for differences in average age between the months. To study effects on survival a multilevel mixed-modelling procedure was used with plot (site in colony, $n = 10$), plot per year (two years times 10 plots, $n = 20$), individual identity and observation (each observation) as levels. The binomial logit link model included year (2003 and 2004), location of nest (interior or periphery), age of chicks (<4 weeks; 4–8 weeks and >8 weeks) and date (days after 30 September), as well as their interactions. Growth indices were calculated using GenStat 8 and statistical analyses were done with the SPSS 13.0 and MLWin 2.02 packages.

## Results

### Diet

The proportions of anchovy and sardine in the diet varied from 66 to 84% between 1986 and 1988, and decreased from 59% to 17% between 2003 and 2005 (Fig. 2.1). The contribution of fishery discards was around

5% during the 1980s. This proportion increased to 45% in 2005, after which it decreased again to 20% and concomitantly the proportion of anchovy and sardine increased to 35% in 2006. The main seasonal trend was that the proportion of anchovy and sardine decreased as the breeding season progressed, whereas the proportion of saury increased (Fig. 2.2). The proportion of hake was relatively large from October till December between 2003 and 2006.

### Chick growth

During seven breeding seasons 1256 gannet chicks were measured (Fig. 2.3a), from which 3375 growth indices could be calculated.

The non-parametric growth curve derived from plotting growth (g $d^{-1}$) against mass (Fig. 2.3b) showed an initial increase in growth with increasing mass. The point of inflection was at a mass of 839 g (23 days) with a growth rate of 49.5 g $d^{-1}$. From that point onwards the growth rate decreased towards 14.0 g $d^{-1}$ for chicks with a mass of 3250 g (slope = –0.014), but much more gradually than the initial increase (slope = 0.047). The overall mean of the growth indices was –0.015 (± 0.98, $n$ = 3375) and did not differ from zero (one sample t-test: $t = -0.887$, $df = 3374$, $p = 0.376$).

### Periphery versus interior

To check whether growth of chicks at the periphery represented overall growth of the colony, I also measured chicks in the interior of the colony: 291 growth increments in 14 chicks were measured in the interior of the colony and compared with 138 growth increments in nine chicks at the periphery (within 1 m from the edge) in 1986. Growth of chicks at the periphery of the colony did not differ significantly from growth of chicks in the interior (Multilevel model: location $F_{1,427} = 2.2$, $p = 0.140$). All measured chicks hatched between 2 and 6 November 1986. Including hatching date and survival of chicks in the model, the location was still not associated with chick growth (Multilevel model: hatch date $F_{4,422} = 1.0$, $p = 0.306$; survival $F_{1,422} = 3.8$, $p = 0.052$; location $F_{1,422} = 0.7$, $p = 0.413$).

## Chick growth between and within years

The mean growth indices per year were largest in 1986 and 1987 and smallest in 2003–2006 (Fig. 2.4a). Within each year the growth indices showed considerable fluctuations. Average growth per month combined for all years was generally higher at the beginning of the year (October till December) than at the end (January till March) (Fig. 2.4b). For each month, except February/March, chick growth was faster in 1986–1988 than in 2003–2006.

The growth indices differed significantly between the seven years (Multilevel model: year $F_{6,3368} = 84.6$, $p < 0.001$) and between months during the seven years (Multilevel model: month $F_{4,3369} = 39.9$, $p < 0.001$). The growth indices were higher in 1986–1988 compared to 2003–2006 (Multilevel model: period $F_{1,3373} = 59.0$, $p < 0.001$).

From October until January the growth indices were higher in the 1986–1988, but in February/March growth was faster in 2003–2006 (Fig 2.4b). Seasonality was analysed in a model that tested for the interaction between year and months (GLM: year $F_{6,3346} = 11.1$, $p < 0.001$; month $F_{4,3346} = 8.2$, $p < 0.001$; years × month $F_{18,3346} = 3.8$, $p < 0.001$). The model showed that growth did not follow the same seasonal pattern in different years. The model explained 5.9% of the variation in chick growth.

## Chick growth and diet

Growth indices were averaged for each calendar month and correlated to the proportion of the different prey species in the diet. Average growth indices were positively correlated with the contribution of anchovy and sardine to the diet ($r = 0.554$, $n = 32$, $p = 0.001$, Fig. 2.5). For six of the seven years these correlations were also positive between the months within years, in two years significantly (1989: $r = 0.850$, $n = 6$, $p = 0.032$; 2006: $r = 0.998$, $n = 3$, $p = 0.042$). The proportion of fishery discards in the diet was not correlated to growth ($r = 0.011$, $p = 0.952$).

The combined proportion of anchovy and sardine in the diet had a positive effect on chick growth. In periods when chicks were older, growth was marginally faster with a larger proportion of anchovy and sardine in the diet than in periods when chicks were younger (GLM: anchovy and sardine $B = 0.013$, $F_{1,28} = 9.8$, $p = 0.004$; age $F_{1,28} = 1.9$, $p = 0.182$; (anchovy and sardine) × age $F_{1,28} = 5.4$, $p = 0.028$). The model explained 46.9% of the variance in growth.

**Chick survival**

During the 2003 and 2004 breeding seasons, 303 and 396 nests respectively were monitored for chick survival at both the interior and the periphery of the colony. Nests were monitored for at least four months. In 2003, chicks hatched at 233 nests; in 2004 at 242 nests. Chick survival until 12 weeks was higher in 2003 (60.9%) compared to 2004 (55.4%) and survival was higher in the interior than the periphery (Table 2.1).

Results from the model are presented in Table 2.2. Until day 80 (19 December) chick survival was lower in 2004 than in 2003. Survival decreased in both years as the breeding season progressed (Fig. 2.6a). This decrease was less steep in 2004 than in 2003. Survival increased with the age of chicks. This effect was stronger in 2003 than in 2004 (Fig. 2.6b). Chicks at the interior of the colony had higher survival compared to chicks reared at the periphery, but the difference decreased as the season progressed (Table 2.2).

## Discussion

Although Cape gannets are opportunistic feeders with large variability in their diet (Berruti *et al.* 1993) and foraging behaviour (Lewis *et al.* 2006, Pichegru *et al.* 2007), the availability of anchovy and sardine appears to have a considerable influence on their reproductive performance. At Malgas Island, a decreased availability of anchovies and sardines (van der Lingen *et al.* 2005) was associated with an increase in foraging effort (Pichegru *et al.* 2007) and a decrease in numbers of gannets breeding (Crawford *et al.* 2007). Our results demonstrate that the growth of Cape gannet chicks is also associated with the proportion of these lipid-rich prey species in the diet and that fishery discards are an inadequate substitute for natural prey. This confirms earlier observations on captive birds that chicks fed anchovy and sardine exhibit better growth than those fed hake (Batchelor & Ross 1984).

### Growth measurements

Birds breeding in the interior of a colony are expected to be more experienced or in a better condition than birds at the periphery (Coulson 1968, Gibbs *et al.* 2000). At the periphery, predation pressure is also thought to be larger (Tenaza 1971). This might result in differences of chick growth rates or survival. In this study I found that chick survival was lower at the periphery compared with the interior. This was most likely due to higher predation pressure at the periphery by kelp gulls *Larus dominicanus* (pers. obs). Growth rates did not differ between chicks from the interior and periphery, so the growth of chicks at the periphery of the colony was representative for the whole colony. Although I have combined two datasets collected 20 years apart, I collected the data during both study periods, which minimises biases introduced by measurement errors from different observers.

### The impact of natural versus discards diet on chick growth

Fishery discards can be a potential alternative food source for seabirds (Montevecchi 2002) and increases of several seabird populations have been attributed to opportunities to scavenge fishery waste (Mitchell *et al.* 2004, Oro *et al.* 2004). Seabirds seem to select discards from fishing vessels that are of good digestibility and high caloric content (Furness *et al.* 2007). However, the energy content of hake (4.07 kJ $g^{-1}$), the main fishery waste in the Benguela ecosystem, is half that of anchovy or sardine (6.74 and 8.59 kJ $g^{-1}$ respectively, Batchelor & Ross 1984), the Cape gannet's natural prey. Hake is also poor in lipid content (average fat content: Cape hake 2.5%, southern African anchovy 4.2%, southern African sardine 7.9%, FAO 1989). The hake diet samples regurgitated by Cape gannets mainly consisted of bony heads or body portions with large bones. Nevertheless, the proportion of fishery discards (almost exclusively hake) increased from about 5% in the 1980s to 45% in 2005 in the diet of breeding Cape gannets.

Average growth of Cape gannet chicks reared at Malgas Island was positively associated with the proportion of lipid-rich prey species in the diet. In years with good availability of anchovy and sardine (1986–88), chicks were growing faster than in the years with reduced availability of these species (2003–06). The importance of lipid-rich species for chick growth was also evident within years. Chicks had faster growth rates in months with more anchovy and sardine in their diet. Moreover, there was no relationship between chick growth and the proportion of fishery discards in the diet, suggesting partial compensation by adult gannets returning more discards to the chick as found by Pichegru *et al.* (2007). Although the fishery discards were of poor quality, both in terms of caloric content and digestibility, Cape gannets seemed to have no other suitable alternatives prey to anchovy and sardine and had to feed on this junk-food, at least during parts of the breeding season.

There is growing evidence that quality of the diet, in particular the lipid content of fish prey, is crucial for growing seabird chicks (Golet *et al.* 2000, Litzow *et al.* 2002, Wanless *et al.* 2005, Kitaysky *et al.* 2006). Chicks reared on lipid-rich diets can probably increase energy reserves by storing more body fat (Kennedy *et al.* 2007), enhancing the chances of successful fledging of individuals by buffering periods of fluctuating food availability (Ricklefs & Schew 1994). Feeding on fishery discards proved to be an unsuitable alternative for breeding Cape gannets to sustain their own energy requirements and those of their chick (Pichegru *et al.* 2007), but can be an alternative to ensure survival outside the breeding season (Grémillet *et al.* 2008).

## Fluctuations in food availability

In colonial seabirds, chick growth is considered an indicator of local food availability (Ricklefs *et al.* 1984, Shea & Ricklefs 1996, le Corre *et al.* 2003). The diet of Cape gannets breeding at Malgas Island showed a consistent occurrence of saury at the end of the breeding season when anchovy and sardine were less available (Berruti *et al.* 1993, this study). It seems that at the beginning of the breeding season breeding birds do not have this option and can only turn to scavenging behind hake trawlers. The prevalence of saury from December onwards might affect chick growth in different ways. In 1986–88 the lower energy content per gram wet mass of saury (6.20 kJ $g^{-1}$, Batchelor & Ross 1984) may have affected growth negatively at the end of the breeding season. In 2003–06, with higher proportions of lipid-poor fishery discards, the occurrence of better quality saury from January onwards may have increased the growth performance of the chicks at the end of the year (February-March, Figure 2.3b). Indeed, Grémillet *et al.* (2008) showed an increase in the caloric value of the diet in 2005, when the proportion of saury increased in the diet, compared to months with larger proportions of fishery discards.

### Reproductive output

In pigeon guillemots *Cepphus columba* chicks reared on lipid-rich diets showed faster growth and higher fledging success than birds reared on a lean diet (Litzow *et al.* 2002, Golet *et al.* 2000), which may drive population dynamics in this species. Cape gannet chicks with a high fledging mass have higher survival chances than chicks that fledge later or with a lower mass (Jarvis 1974). Chick survival was slightly lower in 2004 than in 2003, coinciding with the reduced availability of anchovy and sardine in 2004 compared to 2003. Increased predation of chicks and fledglings by Cape fur seals *Arctocephalus pusillus pusillus* (Makhado *et al.* 2006) and great white pelicans *Pelicanus onocrotalus* (De Ponte *et al.* 2007) contributed to the decrease in size of the Cape gannet colony at Malgas Island. However, the decreased availability of lipid-rich prey species is likely to have been the main cause of large population decreases of Cape gannets in Namibia (Crawford *et al.* 2007). Demographic data are essential for ongoing discussions about population declines of many different vulnerable species. The finding of this study agrees with that of Grémillet *et al.* (2008) that marine management policies should be careful in assuming that fishery discards is beneficial for seabirds scavenging behind trawlers. This study illustrates the dramatic effects that a decreased availability of lipid rich prey can have on a population scale and that fishery discards do not provide an alternative food source during the breeding season (Wanless *et al.* 2005).

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Table 2.1. Summary statistics of Cape gannet chick survival until 12 weeks of age at Malgas Island. Chick survival is defined as percentage of chicks that survived between consecutive nest checks. Nests at least 3 m from the periphery are defined as reared in the interior of the colony.

| Location | Survival | 2003 | 2004 |
|---|---|---|---|
| Periphery | success | 47 | 47 |
| | | *43.5%* | *45.2%* |
| | failure | 61 | 57 |
| | | *56.5%* | *54.8%* |
| Interior | success | 95 | 87 |
| | | *76.0%* | *63.0%* |
| | failure | 30 | 51 |
| | | *24.0%* | *37.0%* |

Table 2.2. Results for the multi-level binomial logit-link model of survival of Cape gannet chicks at Malgas Island. The model corrected for the levels of plot, year-plot, individual and observation. Year, location, and age were included as categories and date included as covariate. For further model details see results.

| | | B ± S.E. | *d.f.* | $X^2$ | *P* |
|---|---|---|---|---|---|
| Intercept | | 6.1 ± 0.85 | 1 | | |
| Year* | | | 1 | 19.7 | < 0.001 |
| | *2004* | -4.3 ± 0.98 | | | |
| Age[#] | | | 2 | 84.3 | < 0.001 |
| | *< 4 weeks* | -1.6 ± 0.29 | | | |
| | *> 8 weeks* | 2.9 ± 0.43 | | | |
| Location[‡] | | | 1 | 19.0 | < 0.001 |
| | *interior* | 3.4 ± 0.78 | | | |
| Date | | -0.06 ± 0.01 | 1 | 53.5 | < 0.001 |
| Year × date | | | 1 | 29.3 | < 0.001 |
| | *2004 × date* | 0.05 ± 0.01 | | | |
| Year × age | | | 2 | 11.0 | 0.004 |
| | *2004 × < 4 weeks* | 0.3 ± 0.38 | | | |
| | *2004 × > 8 weeks* | -1.6 ± 0.53 | | | |
| Location × date | | -0.03 ± 0.01 | 1 | 12.1 | < 0.001 |
| | *interior × date* | | | | |

* reference category is 2003

[#] reference category is 4 - 8 weeks

[‡] reference category is periphery

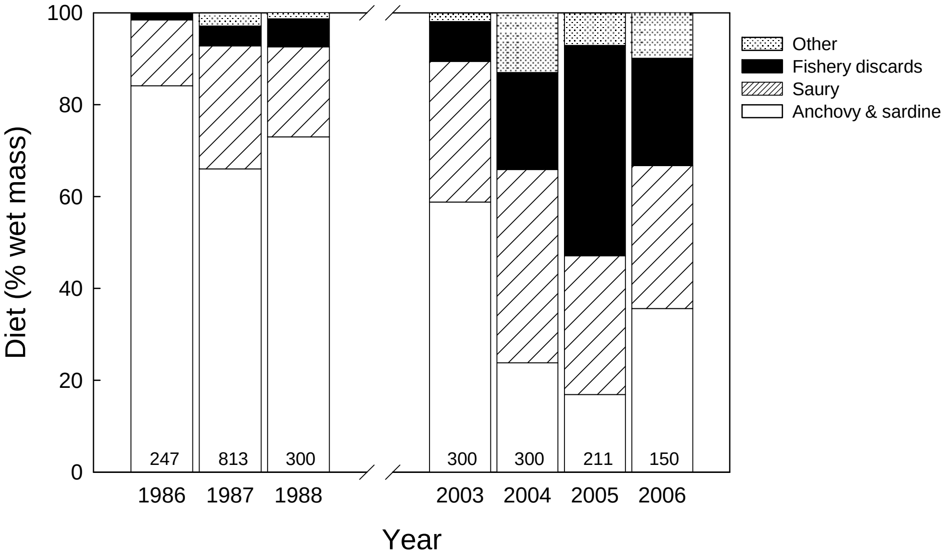

Fig. 2.1. Contribution (in % wet mass) of four categories of prey species to Cape gannet diet per year at Malgas Island. Data are only from months that chick growth was measured and sample sizes are shown at bottom of graph. Main prey species in the category 'other' are snoek, horse mackerel and round herring. Fishery discards consist almost exclusively of hake.

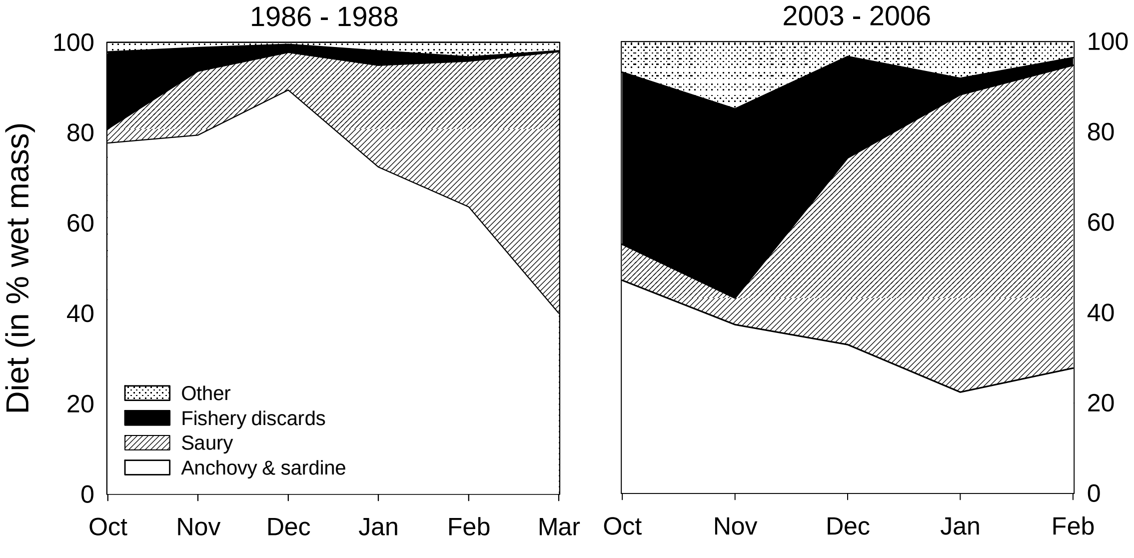

Fig. 2.2. Contribution (in % wet mass) of four categories of prey species to the diet of Cape gannets at Malgas Island, per month during the breeding season. Averages are given per month for two contrasting periods.

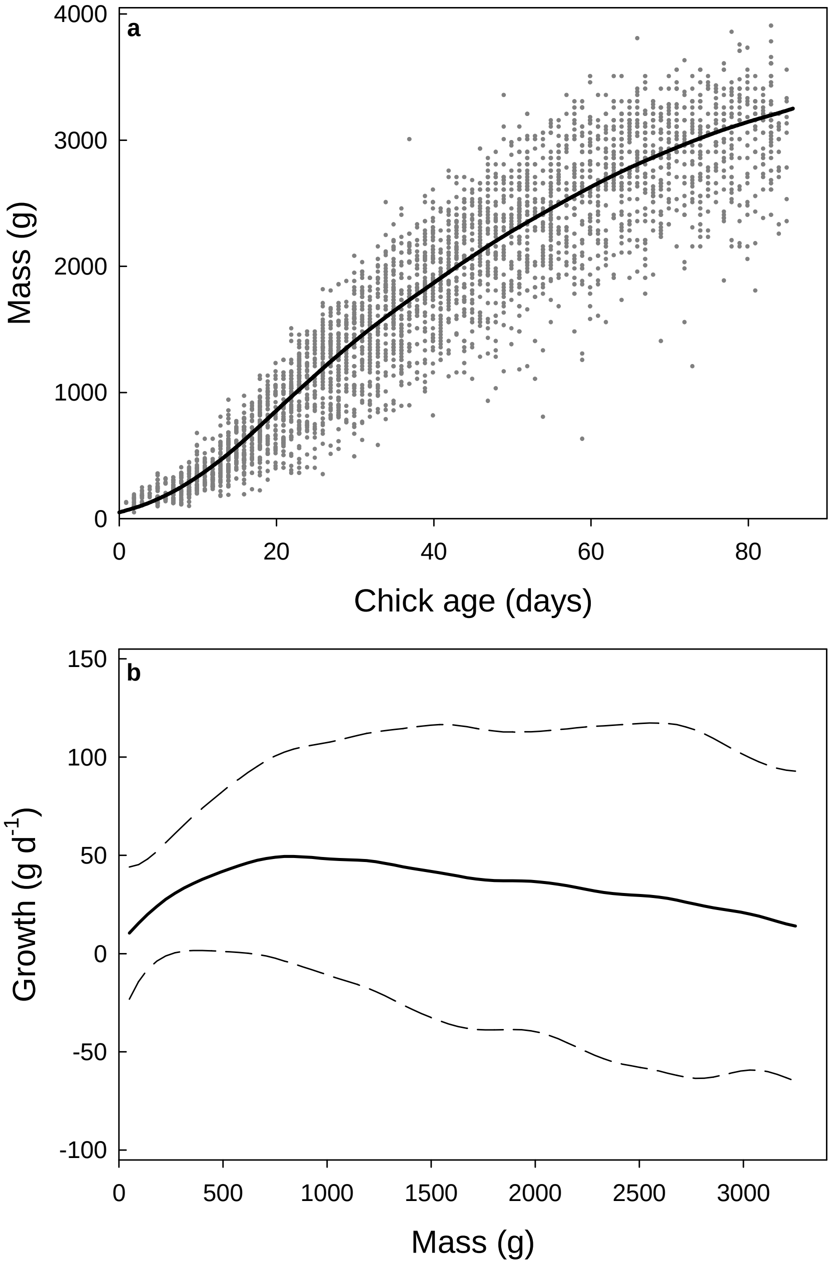

Fig. 2.3. Growth of Cape gannet chicks at Malgas Island, from seven breeding seasons; data of 1 256 individuals and 3 375 measurements. (a) Plot of mass (g) against chick age of Cape gannets in days. The line represents the non-parametric growth curve calculated from plotting growth (g $d^{-1}$) against mass. (b) Plot of growth (g $d^{-1}$) against average mass for chicks. The solid line represent the non-parametric growth curve, and the dashed lines the 95% confidence interval.

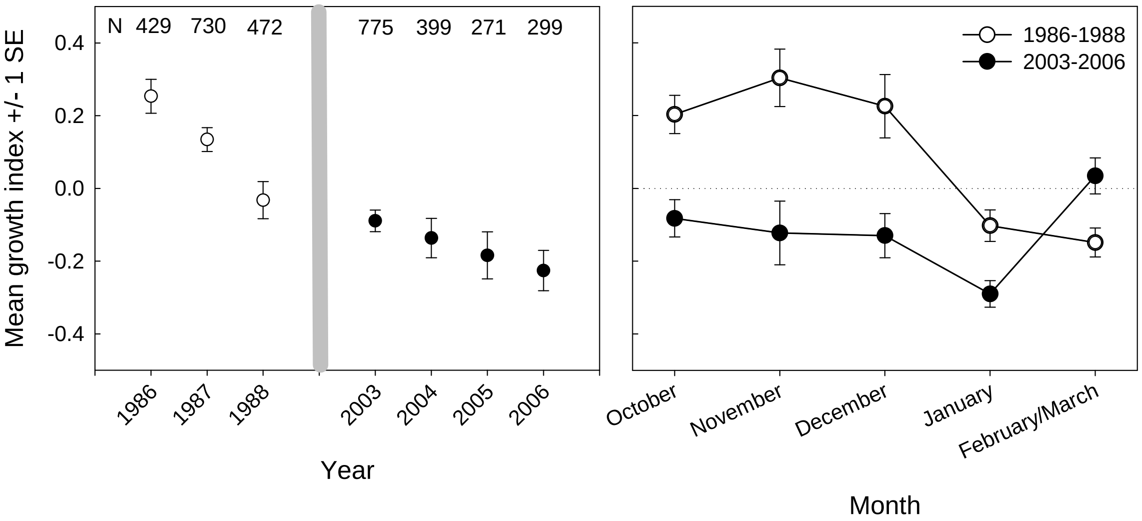

Fig. 2.4. Growth index (mean ± 1 standard error) of Cape gannet chicks at Malgas Island, for each of the seven breeding seasons (a); and monthly means for the years 1986–1988 (open dots) and 2003–2006 (closed dots) combined (b).

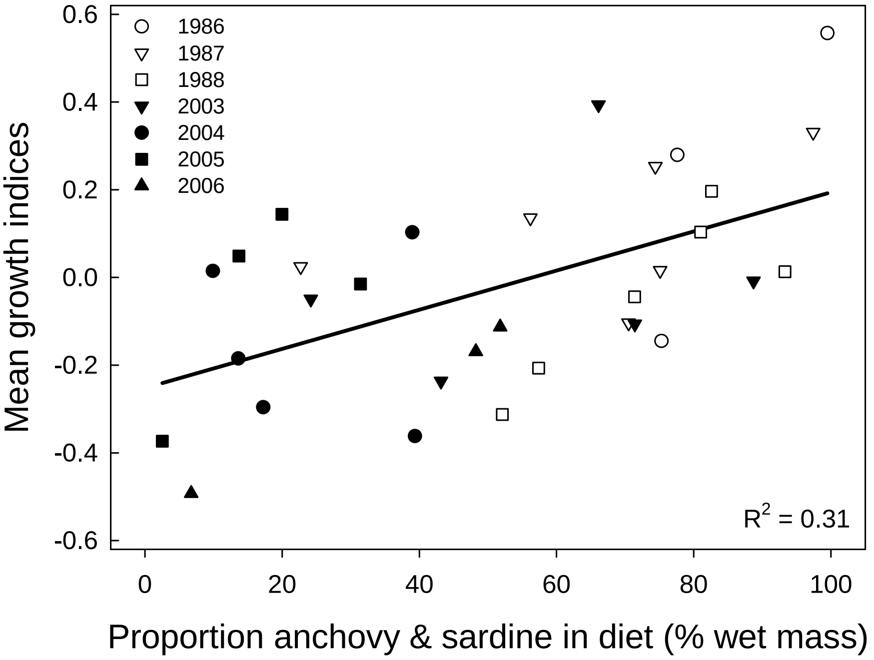

Fig. 2.5. Relationship between the combined proportion of anchovy and sardine in Cape gannet diet and the mean chick growth index per month. Data are for at Malgas Island, during seven breeding seasons (*n* = 32).

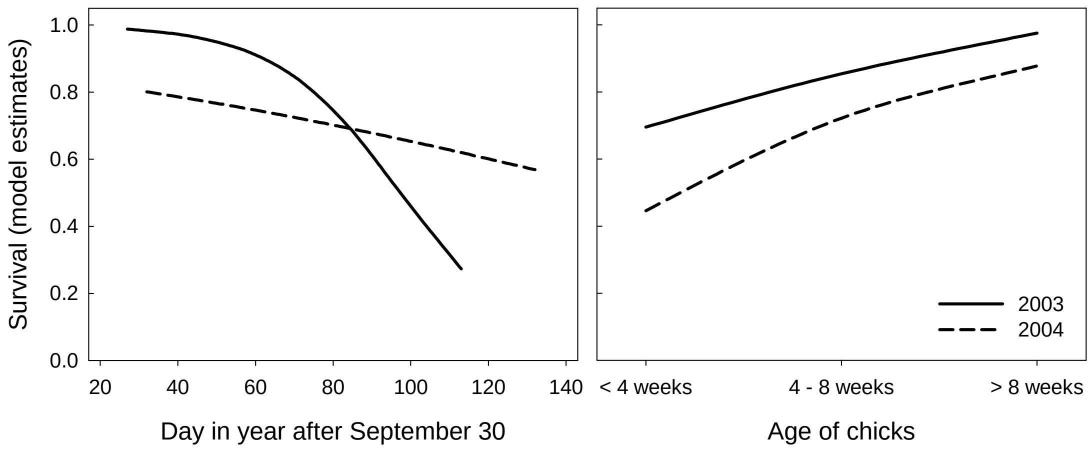

Fig. 2.6. (a) Survival of Cape gannet chicks at Malgas Island, throughout the breeding season for two years (2003 and 2004). Survival rates are estimates from the multi-level model (see results) and predictions are made from the model including year, date and their interaction. (b) Fraction of chicks that survived between consecutive nest check for three age-classes. Survival rates are estimates from the multi-level model and corrected for year, date and location in the colony (periphery or interior) effects.

# Appendix 2.1

## Growth index

Several studies have previously explored growth of Cape gannet chicks and give indications that standard parametric growth models, like Gompertz or logistic growth curves, do not describe chick growth adequately (Cooper 1978, Navarro 1991). The assumption for these parametric models is that the growth rates before and after the point of inflection have the same slope, but in opposite directions. In Cape gannets the rate of decrease after the point of inflection is about three times slower than the rate of increase before the inflection-point. Therefore growth rates were analysed using a non-parametric approach (compare Brown *et al.* 2007).

Growth rates were calculated between each pair of successive mass measurements, so if successive masses at times $t$ and $u$ were $m_t$ and $m_u$, the growth rate over this time period is

$$g = \text{(change in size)}/\text{(time period)} = (m_u - m_t)/(u - t)$$

and the mean of the pair of measurements is $a = (m_t + m_u)/2$.

For a set of observed masses (target mass) the average growth rate was estimated using weighted regression. Weights for all pairs of observations were calculated ($a$, g) in such way that values close to the target mass had large weights and values farther away had increasingly smaller weights. If the target mass was $m^*$, then the weight $w$ attached to observation ($a$, g) was $w = \exp(-((a - m^*)/\sigma)^2)$ where σ was chosen to be 200, which is about 8% of the adult mass. The weight attached to observations 200 g distant from the target mass is substantial (0.37), at 300 g small (0.105), and at 400 g tiny (0.018). A weighted linear regression was fitted using GenStat8 (Genstat Committee 2005) to predict the growth rate $g^*$ at the target mass. By varying σ, the extent of the influential neighbourhood can be modified. The value for σ was selected by visual inspection, but the results do not depend critically on this value. Data exploration showed that if a chosen value was twice as large or half as small, the results would have been nearly identical.

The same weights used for the regression were used to estimate a weighted standard deviation $s_{m^*}$; where $s_{m^*} = (1/\sum w)((w(g–g^*)^2)$. An approximate coefficient of variation for each target mass was calculated as $CV^* = 100 \times (s_{m^*}/m^*)$.

The estimated growth rates and the lower and upper confidence limits at each target mass were plotted, and the points were linked by interpolation. A normal distribution was assumed, so that the lower and upper confidence limits were $g^* \pm 1.96\ s_{m^*}$. Using hatching mass as the starting value on day 0, the growth rate curve was integrated to produce a plot of mass against time. The non-parametric growth curve describes the pattern of growth as determined by the data rather than forcing the data into a pattern as a consequence of the parametric model chosen by the analyst. The growth indices are age-independent.

For the interval between two measurements of a chick, a comparison was made between the observed and expected growth rate. The observed growth rate was computed as the average of the two measurements, and its approximate standard deviation calculated as described above. The standardised growth rate ($z$) was then computed by dividing the difference between the observed and expected growth rate by the standard deviation, so $z = (g–g^*)/s^*$. The $z$-scores are assumed to be approximately normally distributed, so the magnitudes of $z$-values can be expected to stay within the standard normal distribution. For large samples, the overall mean of all $z$-values is asymptotically zero; negative values indicate below average growth rates and positive values indicate above average growth rates.

# CHAPTER 3

CHAPTER 3

# ENERGY EXPENDITURE OF FREE-RANGING CHICKS OF THE CAPE GANNET *MORUS CAPENSIS*

## Abstract

The Cape gannet *Morus capensis*, a large fish-eating seabird, is endemic to southern Africa. To study the energetics of nestling growth the doubly labelled water technique was used to measure field metabolic rates (FMR) of nestlings, from hatchings to large partly-feathered chicks ($n$ = 17) at Malgas Island, Saldanha Bay, South Africa. At the same time the growth rate of a large sample of chicks was measured ($n$ = 338). These data, together with literature values on basal metabolic rate and body composition, were used to construct and partition the nestling energy budget. Nestling FMR (kJ $d^{-1}$) increased with body mass according to: FMR = 1.23 $m^{0.923}$, $r^2 = 0.944$. Mass specific FMR ($FMR_{ratio}$, kJ $d^{-1}$ $g^{-3/4}$) was independent of chick age ($r^2 = 0.20$; $p > 0.05$); mean mass specific FMR was 4.11 ± 1.28, $n$ = 17. Peak daily-metabolised energy (DME), which represents the maximum rate that parents must supply their nestlings at, occurred at age 71 days and was 2 141 kJ $d^{-1}$. Between the ages 51–92 days (43% of the fledging period), the DME of Cape gannet chicks was equal to or surpassed 90% of adult FMR at the nest. Energy demand during this period of peak-DME represented 58% of the total metabolised energy (TME), which was estimated at 1 48.1 MJ for an average chick from hatching to fledging. Sensitivity analysis of the energy budget indicated that the model was robust; the biggest source of error (±15%) was for the mass–FMR equation used in the model.

## Introduction

Energy requirement is such a fundamental process of life that an understanding of energy demands can provide important insights into the biology of organisms (i.e. adaptive strategies), for a range of theoretical questions (e.g. life-history theory) and applied problems (e.g. to determine the impact on fish stocks in the case of a marine species). In this way, energy is seen as a unit of common currency in a community of organisms and their environment (Wiens & Farmer 1996).

Most seabirds are central place foragers, at least during the breeding season, because parents need to return regularly to their nest sites to incubate eggs and to brood and feed chicks. An additional disadvantage for pelagic seabirds is their need to travel long distances to their feeding grounds, and to find sufficient food which is distributed patchily over huge expanses of oceanic waters (Ashmole 1971, Furness & Monaghan 1987). Because of these constraints, seabirds have less energy available for reproduction per unit of energy consumed than terrestrial birds (Visser 2001).

During the breeding season parents have to obtain sufficient food to cover both their own needs and those of their chick(s). Typically, food requirements of the entire family peak during the second half of the nestling period, when chicks are large and growth rate is high. If parents fail to meet the food requirements of their families at this stage, chicks receive insufficient food, which impacts on their growth, rate of maturation, and eventually their fitness, in relation to survival and productivity. Even adult survival is threatened when food availability falls below a threshold. Breeding attempts are then abandoned, leaving the young to starve to death as the adults go in search of food elsewhere (Schreiber & Schreiber 1989). In colonial nesting species, adult mortality and total nest failure due to food shortage can take dramatic proportions; seabirds off Peru die by the million during strong El Niño Southern Oscillation (ENSO) events (Jordan & Fuentes 1966, Duffy 1983). ENSO events in waters off southern Africa have moderate effects on seabirds, mostly resulting in shifts in diet, local breeding failure and increased mortality of young birds (Duffy *et al.* 1984).

Cape gannets *Morus capensis* are central place foragers, having to fly long distances from their breeding colonies to obtain food and bring it back to their brood. Radio-telemetry data indicated that Cape gannets breeding at Malgas Island fly between 180 km and 220 km per foraging trip (Adams & Navarro 2005). But GPS tracking revealed that mean foraging trip length is 460±241 km, n=339 (Mullers & Navarro 2010). At-sea energy expenditure of Cape gannets has been estimated at about 6.5 times basal metabolic rate (Adams *et al.* 1991); a higher value (8.1 × BMR) was found for the northern gannet *Morus bassanus* (Birt-Friesen *et al.* 1989). Both values are considerably higher than 4 × BMR, the level which Drent & Daan (1980) thought was the maximum sustainable metabolic rate for birds.

In the context of the breeding season, parental foraging efficiency is expressed as the total food intake of the family divided by total parental energy spent. In general, parental foraging efficiencies of seabirds are much smaller than in land birds. This is probably the result of relatively low food densities in pelagic ecosystems. Therefore, to collect sufficient food birds have to fly vast distances, which is energetically expensive. Moreover, Cape gannets have a higher absolute at-sea metabolic rate than other seabirds, 143% more than those using gliding and 34% more than those using non-gliding flight (Adams *et al.* 1991). Given these considerations, it is not surprising that many seabird species, including the Cape gannet, manage to rear only one chick per season (Jarvis 1974). However, in good years Cape gannets are able to increase their foraging efforts and have being able to fledge artificial twins quite successfully (Navarro 1991).

In this study the doubly labelled water (DLW) technique was used to measure the field metabolic rate of free-living Cape gannet chicks. The DLW measurements were combined with data on growth (Mullers *et al.* 2009b, Chapter 2), and data on body composition (Navarro 1992) of Cape gannet nestlings to produce energy budgets of growing birds and to examine the energetic cost of breeding birds. Given the constraints imposed on growth by the unpredictability of food supply in seabirds, one could expect seabird chicks to have evolved adaptations to reduce their energy expenditure and or their total metabolizable energy (TME) (Weathers 1992). The first alternative is tested by comparing the mass-specific FMR of Cape gannet chicks with values reported in Weathers' (1992) review of nestling energy requirements. The second alternative, reduced nestling TME, is tested by comparing TME of Cape gannet nestlings with that predicted from models presented by Weathers (1992) and Visser (2001). I also compare the energy budget of free-living Cape gannet chicks with that obtained from chicks reared in captivity by Cooper (1978), and with the energy budget of the congeneric North Atlantic gannet (Montevecchi *et al.* 1984).

## Methods

### Study area

This study was conducted at Malgas Island (33º03'S, 17º55'E), Saldanha Bay, South Africa, over two breeding seasons: 2003/04 and 2004/05. This island lies along the Benguela Upwelling System in the west coast of South Africa (Duffy & La Cock 1985). Various aspects of the Benguela system have been reviewed; see e.g. Berruti *et al.* (1989), Shannon *et al.* (1992), Shannon & O'Toole (2003) and references therein. The breeding population of Cape gannets at Malgas Island increased from 25 040 breeding pairs in 1956/57 to a maximum of the 56 376 breeding pairs in 1996/97, and then decreased to 36 156 breeding pairs in 2005/06 (Crawford *et al.* 2007).

### Chick growth

At the beginning of each field season, a sample of *ca.* 50 chicks in a range of sizes was marked with a numbered plastic-ring. Measurements were taken throughout their development, usually at 5–8 day intervals. To offset mortality and fledging, new chicks were added to the original sample during the course of the field season to maintain the number of chicks being monitored at *ca.* 50. On each bird, the following was measured: (1) culmen length, to the nearest 0.1 mm, using a dial calliper; (2) the length of the flattened wing cord, to the nearest mm, using a metal ruler; and (3) body mass, using the appropriate Salter spring balance: 200 g, 1 kg and 5 kg capacity, with 2 g, 5 g, and 25 g accuracy respectively. An overall mean growth curve was obtained by fitting a Gompertz model to the series obtained from three-day moving-median mass for each day, from age 2 to 96 days inclusive. Similarly, growth curves were obtained for 19 percentiles: 5–95% at 5% intervals and a Gompertz model was fitted to each of these, providing a set of smooth growth paths. Such growth trajectories were subsequently used in the sensitivity analysis of the energy budget (see below).

### Chick age determination

For all chicks of unknown age, age was estimated from measurements of culmen or wind-chord length, which were used in back-transformation growth models from a sample of known age birds. These two structures grow at different rates; culmen grows rapidly during the first three weeks whereas wing-chord initially grows slowly and from the second week grows almost linearly. Wing chord continues to grow after fledging, by which time it has reached 90% of the adult size. Chick's age $d$ (days) was predicted with one of the following models:

$$d = -\log_e ((89.78 - c)/(6.15c))/0.086 \qquad (3.1)$$

$$d = (1.395 - \log_e (\log_e (588.8/w)))/0.0264 \qquad (3.2)$$

where $c$ is the culmen length (mm) and $w$ is the wing-chord length (mm). Equation 3.1 was used for chicks where $w < 40$ mm, otherwise equation 3.2 was used (see Chapter 2).

### Energy expenditure

I determined nestling field metabolic rates (FMR) using the doubly labelled water (DLW) technique (Lifson *et al.* 1955, LeFebvre 1964, Tatner & Bryant 1989, Speakman 1997), in which an estimate of $CO_2$ production is obtained from the loss rate of the stable isotopes $^2H$ and $^{18}O$. The size of the initial body water pool was determined from initial dilution of $^{18}O$ using the plateau method of calculation, and final body water pool was determined by percentage mass from the initial determination (Speakman 1997). The loss rate of $^{2}H$ provides a measure of the water flux (see Chapter 4).

To determine the dosage of DLW a pilot experiment was conducted in September 2002 to measure the rate of water flux using $^{2}H$-enriched water, using a protocol similar to that employed for DLW. Chicks were injected with a dose of $^{2}H$-enriched water (99.9 atom percent $^{2}H$). Chicks less than 1 kg of body mass were given 0.5 ml of enriched water, heavier chicks received 1 ml. The final sample was taken 24 h later. From these measurements the minimal dosage was determined to be 0.6 ml $kg^{-1}$ and that the DLW experiments should be conducted over a 48-hour period.

Nestling FMR was assessed in a random sample of chicks, trying to get an even spread of ages and sizes; 17 experiments were conducted at Malags Island, South Africa, over two breeding seasons (10 in 2002/2003 and 7 in 2003/2004, see Appendix 3.1). Chicks were captured and measured (culmen and wing-chord length to nearest 0.1 and 1 mm respectively), weighed and injected with DLW, under the abdominal skin, with a dose of 0.6 ml $kg^{-1}$ of body mass. Nestlings were returned to the nest for 1–1.5 h to allow the injected DLW to equilibrate with the body water pool, and recaptured to take an initial blood sample. It was assumed that equilibration in chicks was reached within this period because this was the case for adults of this species (Mullers *et al.* 2009a). Blood samples were taken with a new insulin syringe; about 3 ml of blood were drown from a brachial vein; from this *ca.* 5 µl of blood were transferred into each of six 25 µl glass capillary tubes. The tubes were immediately flame-sealed and refrigerated until analysis. After a target interval of two days nestlings were recaptured and a final blood sample taken; birds were again measured and weighed.

The natural background isotope levels were determined in four untreated chicks each season. The values for these background levels were according to expectations for seabirds (i.e. the isotopic composition of their body water is close to that of ocean water). The DLW used was gravimetrically mixed form pure deuterated (>99.9%) water and highly enriched (95%) $^{18}O$ water, such that the mixture contained 60.5 atom% $^{18}O$ and 36.5 atom% $^{2}H$.

Isotopes were analyzed at the Centre for Isotope Research (University of Groningen) using methods described in detail elsewhere (Visser & Schekkerman 1999, Schubert *et al.* 2008). In short, the blood in the capillary tubes was distilled in a vacuum line and brought into a standard vial for automatic injection into the isotope ratio mass spectrometer system.

Local water standards (gravimetrically prepared from pure $^{2}H$- and $^{18}O$-water), that cover the entire enrichment range of the blood samples, were applied for calibration purposes. The actual $^{18}O$ and $^{2}H$ measurements were performed in automatic batches using a High Temperature pyrolysis unit (Hekatech) coupled to a GVI Isoprime Isotope Ratio Mass Spectrometer for the actual isotope analysis (Gehre *et al.* 2004). Analysis of a single sample took *ca.* 25 minutes. In the complete analysis scheme, several quality checks are incorporated, including: duplicate sample analysis; the spread of initial values for similar situations; the spread of $^{2}H/^{18}O$ enrichment ratios for initials and finals; and both absolute and relative differences.

Rates of water efflux and $CO_2$ production of nestlings were calculated from isotope turnover (assuming a single-pool model) using equation 7.17 of Speakman (1997), as rewritten by Visser (2001, equation 13.9):

$$rCO_2 = N/2.078 \times (k_0 - k_d) - (r_G \times 0.025 \times N \times k_d),$$

where $rCO_2$ (moles $d^{-1}$) is the rate carbon dioxide produced; N (moles) is the size of the body water pool; $k_0$ and $k_d$ (units $d^{-1}$) are the fractional turnover rates of $^{2}H$ and $^{18}O$ respectively; and $r_G$ (dimensionless) corresponds to the fraction of the water efflux lost through evaporative pathways. This equation uses a fractional evaporative water loss value of 25%, which has been validated by Visser & Schekkerman (1999). I converted rates of $CO_2$ production ($l\ d^{-1}$) to energy expenditure ($kJ\ d^{-1}$) assuming a respiration quotient equal to 0.72, with the energy equivalent of 27.33 $kJ(l\ CO_2)^{-1}$, as recommended by Visser (2001) for a fish-eating bird.

### Energy density

The energy density, the energy content per unit of fresh mass, (ED, $kJ\ g^{-1}$) of chicks is required to calculate the energy budget of a growing chick (Visser 2001). Navarro (1992) studied the body composition and energy density of Cape gannet chicks and gave a relationship between ED and chick age. However, in the energy budget calculations, the relationship between ED and chick mass is required. To obtain this, the relationship between ED and mass was recalculated using Navarro's original data; for this a simple linear regression model was fitted to ED values in relation to the ratio of chick mass to mean fledging mass.

### Nestling energy budget

Nestling daily metabolizable energy (DME) was estimated as the sum of the energy retained as new tissue (RE) and FMR, using empirically established allometric relationships between ED and mass, and FMR and mass. The energy budget was partitioned in four components: basal metabolic rate, biosynthesis, thermoregulation–plus–activity, and energy retained; FMR measures the first three, the forth is calculated from growth and energy density data. Energy of biosynthesis was estimated using the conventional approach of multiplying the retained energy by 0.33, which represents a synthesis efficiency of 75% (Ricklefs 1974). The relationship DME=FMR was assumed during weight recession, which represents catabolism of body stores, largely fat deposits (Navarro 1992). The Gompertz model (equation 3.3) was used for mass versus age until peak mass was achieved and simple linear interpolation to describe mass during the short weight recession period. Because it was not feasible to undertake respirometry under field conditions, I estimated basal metabolic rate (BMR $kJ\ day^{-1}$) using allometric considerations (Tieleman & Williams 2000, equation 4 for all birds). BMR was thus estimated as

$\text{BMR} = 10^{(0.416 + 0.677 \times \log10(M))}$, where $M$ is fresh mass (g). The BMR curve thus produced was adjusted so that its starting point corresponded to the BMR predicted for hatching birds given by Klaassen & Drent (1991): $\text{BMR}_{h} = F \times 10^{(1.697 + 0.855 \times \log10(M))}$, where F = 0.0201 is the factor to convert ml $O_2$ to kJ.

**Sensitivity analysis**

This was carried out to investigate how total metabolizable energy (TME) is affected by changes to the parameters of the underlying models, giving a quantitative estimation of the model's sensitivity to errors in such parameters. Three aspects of the energy budget model were investigated: (1) chick growth; (2) energy density; and (3) field metabolic rate. For growth we used the Gompertz models fitted to the quantiles 5% to 95% at 5% intervals (see chick growth above). The median (50% growth quantile) was used for the base run. The energy budget was then calculated for each of these trajectories and the TME was used as a summary of the model output. For the energy density and field metabolic rate we used a bootstrapping technique to obtain confidence intervals for TME for each equation separately. Both equations 3.4 and 3.5 have two parameters and they were allowed to co-vary in the bootstrap because in both cases the estimates of the parameters were correlated. For the bootstrapping the actual data used to generate equations 3.4 and 3.5 provided the bootstrap-sample, from which samples of equal original size were taken with replacement (Efron 1979). This means that some pairs of $x$ and $y$ values were repeated several times and others may not have appeared at all. For each such sample the model under study was fitted and applied to the energy budget calculations to produce a TME value. For each equation I generated 1999 bootstrap samples in addition to the base run. Calculation of TME for all trajectories was based on a 96-day fledging period, as chicks growing faster did not necessarily fledge earlier. It seems that in Cape gannets the rate of maturity of tissues and feathers is uncoupled from the rate of mass increase (pers. obs).

### Statistical analysis

Computations and graphics were done using program R (2.10.0, Windows version) (R Development Core Team 2009). Regression models, including ANCOVAs, were fitted with the lm (linear-models) function, whereas fitting of Gompertz growth model was done with the nls (nonlinear least squares) function. Bootstrapping was done with the package boot (Fox 2002); all bootstrap confidence intervals correspond to the 'adjusted bootstrap percentile' for 1 999 sample replicates. To examine the allometric scaling of various physiological variables with body mass we log-transformed (base 10) the data to fit the equations in their linear form using standard least-squared regression techniques. Unless otherwise indicated, means are given ± 1 standard deviation.

## Results

### Growth

Growth of Cape gannet chicks during the period of study is described in Chapter 2. Over the two field seasons 1620 sets of measurements were taken on 338 chicks. Of these, 45 measurements corresponded to chicks whose age estimates were more than 97 days and were excluded from subsequent analysis. Box-and-whisker plots of the chick mass together with the modelled growth curve over the two periods combined are given in Fig. 3.1. The Gompertz (Kaufmann 1981) model for the median was:

$$M_t = 3141 \times \exp(-\exp(-0.0501 \times (t-29.1))) \qquad (3.3),$$

where $M_t$ is the predicted mass (g) at age $t$ (d). The standard errors for the parameters of the model were 20.4, 0.0009 and 0.22 for the asymptote, growth rate and inflection point respectively. This model accounted for 99% of the variance of median mass. From age 92 days onwards chicks started to loose body mass and enter into the weight recession portion of the fledging period. For purposes of the energy budget calculation weight recession was interpolated linearly between peak-mass and fledging mass, which for the 50% quantile was 3050 g at 91 days, and 2938 g at 97 days respectively. Chick growth below the 40% quantile did not exhibit weight recession. Growth rate ranged from 0.0458 for the 5% quantile to a maximum of 0.0589 for the 95% quantile; whereas the inflection time followed an inverse relation with quantile, ranging from 33.5 d to 26.4 d for the 5% and 95% quantile respectively (Table 3.1)

### Energy density

The relationship between energy density ED (kJ/g) and body mass was best described by the following model (Fig. 3.2):

$$\mathrm{ED} = 5.322 + 4.373 \times (m/A)^2 \qquad (3.4),$$

$r^2 = 0.886$, $n = 21$, where $m$ is the body mass (g), and $A$ is the mean fledging mass (g). $A$ was recalculated from Navarro (1991) for 34 control birds to be 3051 ± 257 g (minimum = 2300; lower quartile = 2950; median = 3075; upper quartile = 3200; maximum = 3400). This model provided a better fit than the three-parameter quadratic model (AIC = 41.9 and 43.6 respectively), with the additional advantage of having one fewer parameter. Bootstrap confidence intervals were 5.006 to 5.613 and 3.637 to 4.960 for the intercept and slope respectively.

### Field metabolic rate

Seventeen successful DLW experiments were conducted. Individual measurements from the DLW experiments are given in Appendix 3.1. The median elapsed time between initial and final blood samples was 48.0 h (range: 47.5 to 50.4 h, apart from one experiment that lasted 71.1 hours; this measurement was included in the analysis. The duration of the experiment was almost exactly a multiple of 24 hours, as recommended for DLW experiments (Speakman 1997). There was no significant relationship between the $CO_2$ production and deviation of recapture from 24 h multiples ($r^2 = 0.09$, $p = 0.23$). Similarly, there was no relationship between the $CO_2$ production and the change in body mass ($r^2 = 0.08$, $p = 0.27$). No significant effect in chicks' field metabolic rate between breeding seasons was found ($F_{14;\,2} = 0.09$, $p = 0.77$).

The field metabolic rate (FMR, kJ $d^{-1}$), as determined from DLW experiments, increased exponentially in relation to body mass ($m$, g), according to the model:

$$\mathrm{FMR} = 1.23\, m^{0.923} \qquad (3.5),$$

$r^2 = 0.944$, $n = 17$ (Fig. 3.3a). Bootstrap confidence intervals for the power model were 0.70 to 3.04 and 0.78 to 1.01 for the intercept and exponent respectively. The modified power curve introduced by Tjørve *et al.* (2007) provided a slightly better fit ($r^2 = 0.951$), AIC = 7.9 and 6.8 for the power and modified power models respectively. However, the simpler model was chosen to describe the FMR in relation to body mass because it makes the results directly comparable to those of previous studies.

The mass specific FMR ($\mathrm{FMR_{ratio}}$), calculated by dividing the FMR value by mass to the ¾ power ratio (Weathers & Sullivan 1991), was independent of chick age ($r^2 = 0.05$; $p = 0.19$) (Fig. 3.3b). Mean $\mathrm{FMR_{ratio}}$ was 4.11 ± 1.28 (kJ $d^{-1}$ $g^{-3/4}$), $n = 17$.

**Energy budget**

The energy budget for a hypothetical chick growing along the median Gompertz trajectory is illustrated in Fig. 3.4. Total metabolised energy (TME) was estimated at 150 829 kJ for a 97-day fledging period. TME was partitioned as follows: basal metabolic rate 25.8%, retained energy (tissue deposition) 18.8%, cost of biosynthesis 6.2%, and activity plus thermoregulation 49.2%. Peak daily-metabolised energy occurred at age 71 days and was 2141 kJ $d^{-1}$, metabolised energy was over 2000 kJ $d^{-1}$ between the ages 51 and 92 d, 43% of the fledging period.

**Sensitivity analysis of the energy budget**

The following parameters of the model were investigated:

(1) Energy density (equation 3.4). The estimates of the parameters of this equation were correlated (Fig. 3.5a) and therefore the bootstrap 95% confidence interval for the relative change in TME was derived by varying both parameters at the same time. The change to TME was –1.2% to 1.0% relative to equation 3.4, (Fig. 3.5d), a range of 2.2%.

(2) Field metabolic rate (equation 3.5). The estimates of the parameters of this model were also correlated (Fig. 3.5b), therefore the bootstrap 95% confidence interval was derived by varying parameters simultaneously. The bootstrap confidence interval for TME ranged from ±15% below and

above the values produced by equation 3.5 (Fig. 3.5d), a range of 30% in TME.

(3) Growth model. The effect of different growth trajectories was evaluated by using Gompertz models fitted to the quantile-growth-trajectories (Fig. 3.5c). A fast-growing chick along the 95% quantile trajectory increased TME by 20% above the median growth rate, and a chick with slow growth, along the 5% quantile trajectory decreased TME by 27% below the median growth curve given by equation 3.3. The straight line model fitted to the data in Fig. 3.5d indicated that there was a 4% increase in TME for every 1% increase in the growth quantile.

## Discussion

### Growth rate

Average growth of Cape gannet chicks reported in a previous study at Malgas Island (Navarro 1991) fell almost exactly along the 80% quantile trajectory of this study. Of the three parameters of the Gompertz model, only the asymptote of the previous study lay within the 95% confidence interval for the parameters. The growth rate in this study was below and the inflection time above the respective confidence intervals reported by Navarro (1991). Clearly, the growth performance during the two seasons of the present study was inferior to the growth performance during the 1986–88 seasons. This decrease in growth performance seems most likely to be related to less favourable feeding conditions during the present study brought about by the eastward shift in the stocks of sardine (van der Lingen *et al.* 2005, Crawford *et al.* 2008), the preferred prey, becoming less accessible to gannets breeding at Malgas Island (Chapter 2).

However, faster growth in Cape gannet chicks does not necessarily mean that fledging can be advanced because tissue and feathers need time to mature. For example, mean adult wing length is 478 mm (sd = 12, $n = 27$), whereas fledglings have a mean wing length of 431 mm (sd = 27, $n = 24$) (R. Mullers, unpubl. data), significantly shorter than the adult value ($t = 7.9$, df = 30, $p < 0.001$, Welch two-sample *t*-test). Furthermore, overweight fledglings are not capable of taking off and have to shed excess mass (fat deposits) before they depart from the island, and little parental care is provided to the chicks at this stage (Nelson 1978). Fledglings sometimes returned to the nest site and persistently beg for another meal, but parents usually ignored them or moved away from the nest site (pers. obs). The extra time required by chicks undergoing weight recession allowed additional time for growth of the primary wing feathers, a fitness factor that may be linked to the higher immediate post-fledging survival of heavier fledglings reported by Jarvis (1974), alongside the more obvious benefit of having an energy reserve to see the birds through the initial mastering of their fishing skills (Navarro 1992). Weight recession is typical of seabirds with no parental care after fledging; a phenomenon similar to that shown by aerial foraging birds such as swallows Hirundidae (Lack 1968, Earlé & Underhill 1991).

### Field Metabolic rate

The assumptions of the DLW method were reviewed by Speakman (1997). Of these the one most likely to be violated is the assumption that the injected isotopes ($^{2}$H and $^{18}$O) label the body water only. In growing birds there is a high rate of synthesis of organic molecules and it is likely that some of the $^{2}$H and $^{18}$O is removed from the body water pool and incorporated into tissue, which would cause an overestimate of the total body water (TBW) as well as the water-flux rate (Williams & Nagy 1985). If $^{18}$O is incorporated at a relatively lower rate than $^{2}$H, the $CO_2$ production would be underestimated in proportion to the discrepancy in the incorporation rates of the two isotopes. This underestimation was suggested by Williams & Nagy (1985) to be as high as 25%. However, studies by Visser & Schekkerman (1999), Visser *et al.* (2000) and van Trigt *et al.* (2002) showed that the discrepancy was not caused by growth of the animal, but rather by the assumption, built into the original equation of Lifson & McClintock (1966), that 50% of the body water leaves the animal through breathing, an isotopic fractionating pathway. Using a percentage of 25%, as in the equation given by Speakman (1997, equation 7.17), leads to much better agreement, also in growing birds (average deviation was –2.9%). This equation has also been used in the present study. Therefore, I m confident that the FMR values reported in this study are not underestimated by the high growth rate of Cape gannet chicks. Another check on the importance of tissue incorporation of the labelled isotopes is the comparison of TBW determination based on $^{18}O$ and $^{2}H$ (both from the initial injection). In all animals, and under all circumstances, $^{2}H$ is indeed to some extend incorporated into tissue, which leads to a TBW estimate based on $^{2}H$ that is typically 1–3% larger than that based on $^{18}O$. In our study we found a difference of 1.7%, pointing in no way to an abnormal situation as far as tissue incorporation is concerned.

Comparisons across species must take into account the fact that FMR scales approximately to mass at the ¾ power (0.73 in Willmer *et al.* 2000). Thus, the mean mass specific FMR observed in this study (4.11 ± 1.28) was not significantly different than the mean across 30 species (4.01 ± 0.84, $t = 0.3$, df = 23, $p > 0.7$) quoted by Weathers' (1992) review of nestling energy requirements. The mass specific FMR was calculated from data in Weathers' Table 1 by dividing TME by mass$^{3/4}$ and by days to fledging. This indicates general agreement with the pattern exhibited by species ranging in size from 9.7 g for white-bellied swiftlet *Callocalia esculenta* to 3 700 g for northern gannet, and fledging period from 8 to 97 days. Even when the sample is clearly biased towards the small species, with 25 of them weighing less than 500 g, Cape gannet chicks lie well within the observed pattern.

### Energy budget

At least one third of the nestling period, between the ages 51–92 days (43% of the fledging period), the DME of Cape gannet chicks is equal to or surpasses 90% of adult FMR at the nest (2214 kJ $d^{-1}$, reworked from Adams *et al.* 1991 who used an energy equivalent of 25.8 kJ $l^{-1}$ $CO_2$). Energy demand during this period of peak-DME represents 58% of TME.

According to Weathers (1992) the most important factors that determine TME required to produce a chick are body mass at fledging and the length of the nestling period. Weathers found that these two variables explained over 98% of the variance in TME in a sample of 30 species. This sample included the Cape gannet and northern gannet, both at the high end of the scale. The value predicted from Weathers' equation 8 for a Cape gannet chick ($TME = 6.65 \times m^{0.852} \times t_{fl}^{0.710}$, where the fledging mass $m = 3150$ g and the fledging period $t_{fl} = 97$ d) is 163 678 kJ, 8.5% above the TME estimated in this study. Visser (2001) provides a similar equation for TME of seabirds, which gives a value of TME = 168 363 kJ, 11.6% over the value in this study. Weather's predicted value corresponds to that of chicks at the 80% growth quantile, whereas Visser's value surpasses the TME of chicks in the 95% growth quantile. The lower-than-predicted TME of Cape gannet chicks probably points towards the presence of energy saving mechanisms in this species, which would increase resilience to cope with unpredictable episodes of food shortage by lowering the energy demands of the chick.

Cooper (1978) measured metabolizable energy based on food consumption of two chicks reared in captivity, TME being 185 MJ, 22% above the field value estimated in this study. It is important to note that Cooper's birds were fed to near satiation on a diet of anchovy *Engraulis encrasicolus*, one of the preferred prey of Cape gannets (Crawford & Dyer 1995). Montevecchi *et al.* (1984) estimated TME of North Atlantic gannet chicks at 145 MJ, 4% below the estimate for Cape gannet chicks, both species have similar fledging periods and masses. However, they estimated that about 44% of the chick's TME was allocated to growth (including the cost of biosynthesis), and as much as 33% was accumulated as tissue. This is in great contrast with the finding of the present study that puts these figures at 25% and 18.8% respectively. The difference in methodology: periodic weighing of four captive-reared chicks in the North Atlantic gannet study, and DLW of 17 free-ranging chicks in this study, may account in large part for the great discrepancy in the energy allocation between the two species. Apart from the North Atlantic and Cape gannets, no other species of the family Sulidae has been studied with regard to chick energetics so it is not possible to look for patterns. But it is expected that the closely related Australasian gannet *Morus serrator* share a similar pattern of growth and energy allocation.

**Sensitivity analysis of the energy budget**

The relationship between FMR and mass is the factor that the sensitivity analysis of the model identifies as the most important one with an error of ±15%. The energy density function effect was almost negligible on the TME calculated. The effect of growth pattern on TME was non-linear: a ±25% change in growth quantile produced less than 10% change in TME; but the error rate increased at bigger changes in growth rate (Fig. 3.5d). It may seem counter intuitive that slow growing birds should have a lower TME since they would have a protracted nestling period to reach an optimal fledging mass. However this is not the case of Cape gannets where fledging takes place over a very definite period and chicks sometimes fledge at a mass below optimal (Navarro 1991). Ricklefs *et al.* (1980) suggest in their study of Leach's storm-petrel *Oceanodroma leucorhoa* chick energetics that growth rate would have little effect on energy requirements; however the sensitivity analysis in the present study does not support their hypothesis.

It seems, from the literature reviewed (by no means exhaustive and restricted mostly to bird energetics), that there are no sensitivity analyses available for single species studies on field energetics. If this is the case, then these errors are the first ones reported for the energy budget of a chick.

Furness (1978) produced an energy budget of seabird communities and performed a sensitivity analysis of the model on two species. He found in the great skua *Catharacta skua* that the model was most sensitive to the energy requirement equation; errors of 26.4% and 23.6% for each parameter in the equation. In the case of the Arctic tern *Sterna paradisaea* the model was sensitive to parameters of the energy requirement, and standard metabolic rate equations, with errors ranging from 12.3% to 16.1%. The latter errors are comparable to the error found for the FMR equation in the present study.

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Table 3.1. Growth parameters of models fitted to for each of the quantiles used in the sensitivity analysis of the energy budget of Cape gannet chicks at Malgas Is., South Africa, over two breeding seasons, 2003/2004 and 2004/2005. *k*, $t_i$, and *A* are the parameters of the Gompertz growth model fitted to each of the quantile series; standard errors (se) of the parameters are given. Data for quantile extraction is illustrated in Fig. 3.1.

| **Quantile (%)** | **Growth rate *k* ($d^{-1}$)** | ***k* (se)** | **Inflection time $t_i$ (d)** | **$t_i$ (se)** | **Asymp-tote *A* (g)** | ***A* (se)** | **Peak mass (g)** | **Age at peak mass (d)** | **Fledging mass (g)** |
|---|---|---|---|---|---|---|---|---|---|
| 5 | 0.0458 | 0.0019 | 33.5 | 0.58 | 2501 | 41.2 | - | - | 2482 |
| 10 | 0.0476 | 0.0017 | 31.7 | 0.47 | 2573 | 33.5 | - | - | 2551 |
| 15 | 0.0485 | 0.0015 | 31.0 | 0.40 | 2659 | 29.6 | - | - | 2620 |
| 20 | 0.0495 | 0.0012 | 30.4 | 0.32 | 2727 | 23.7 | - | - | 2689 |
| 25 | 0.0500 | 0.0012 | 29.8 | 0.29 | 2792 | 22.2 | - | - | 2758 |
| 30 | 0.0499 | 0.0012 | 29.7 | 0.30 | 2866 | 23.4 | - | - | 2795 |
| 35 | 0.0507 | 0.0012 | 29.3 | 0.30 | 2925 | 23.8 | - | - | 2832 |
| 40 | 0.0501 | 0.0010 | 29.2 | 0.26 | 3010 | 22.1 | 2920 | 93 | 2869 |
| 45 | 0.0499 | 0.0009 | 29.1 | 0.24 | 3080 | 21.1 | 2964 | 93 | 2903 |
| 50 | 0.0501 | 0.0009 | 29.1 | 0.22 | 3141 | 20.4 | 3050 | 91 | 2938 |
| 55 | 0.0506 | 0.0008 | 28.7 | 0.21 | 3173 | 18.9 | 3069 | 91 | 2972 |
| 60 | 0.0513 | 0.0008 | 28.5 | 0.20 | 3201 | 18.6 | 3088 | 91 | 2998 |
| 65 | 0.0512 | 0.0009 | 28.4 | 0.22 | 3245 | 20.2 | 3106 | 91 | 3007 |
| 70 | 0.0514 | 0.0010 | 28.2 | 0.24 | 3292 | 22.9 | 3135 | 93 | 3016 |
| 75 | 0.0518 | 0.0010 | 28.0 | 0.24 | 3338 | 23.1 | 3169 | 91 | 3025 |
| 80 | 0.0530 | 0.0011 | 27.8 | 0.24 | 3379 | 23.1 | 3213 | 91 | 3047 |
| 85 | 0.0549 | 0.0011 | 27.3 | 0.22 | 3418 | 21.9 | 3298 | 90 | 3068 |
| 90 | 0.0564 | 0.0011 | 27.0 | 0.23 | 3484 | 22.5 | 3375 | 90 | 3090 |
| 95 | 0.0589 | 0.0013 | 26.4 | 0.24 | 3539 | 23.7 | 3452 | 90 | 3112 |

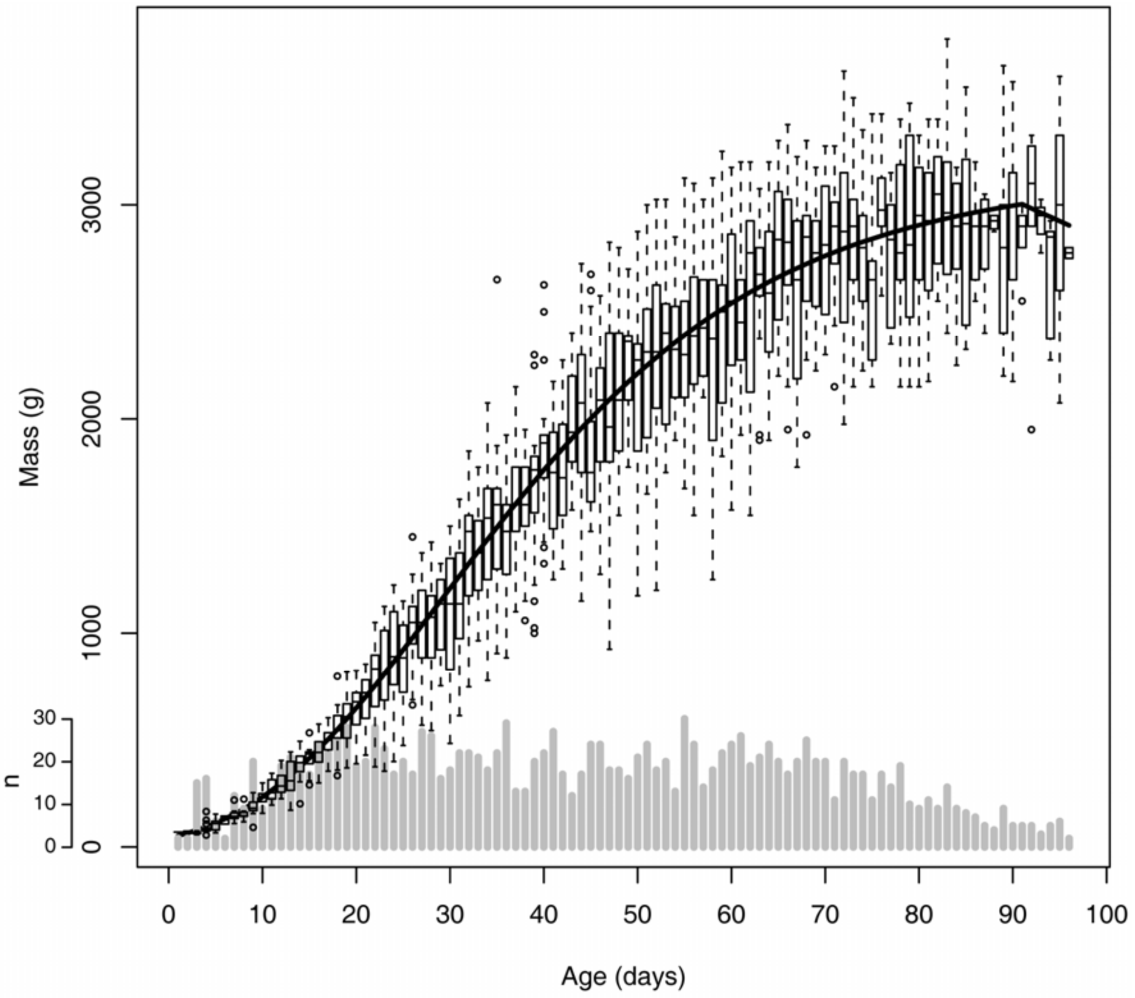

Fig. 3.1. Box-and-whisker plot of body mass in relation to age of Cape gannet chicks at Malgas Island, over two breeding seasons, 2003/2004 and 2004/2005. Based on 1 575 measurements on 338 chicks of known age. Illustrated for each age are lower and upper quartiles (box), the median (line across the box), the range which is 0.75 times the box size over and below the median (whiskers), extreme values are shown separately (circles). A Gompertz model was fitted to the vector of medians (solid line). The bar graph at bottom gives the sample sizes (*n*) for each age.

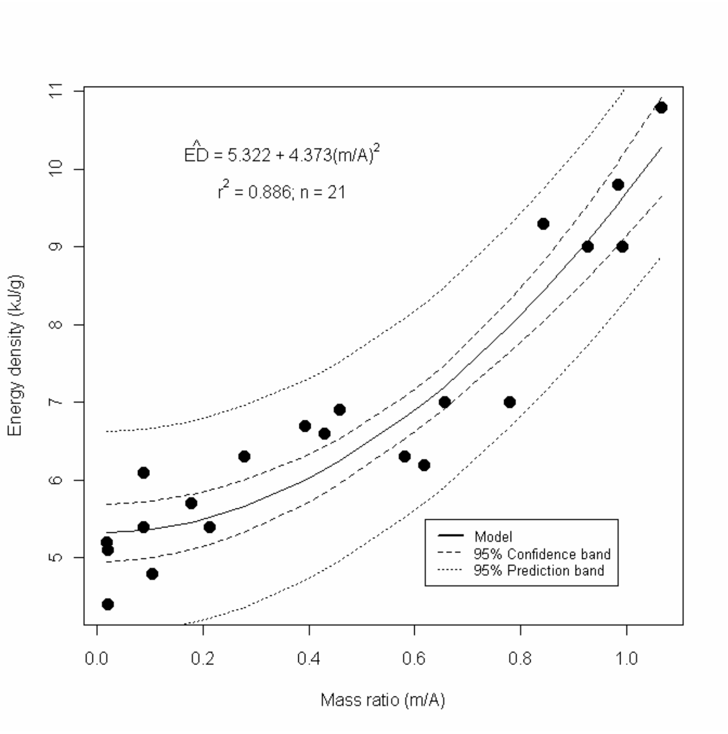

Fig. 3.2. Energy density (kJ g$^{-1}$) of Cape gannet chicks from Malgas Island, in relation to body mass (g, wet), original carcass analysis data from Navarro (1992).

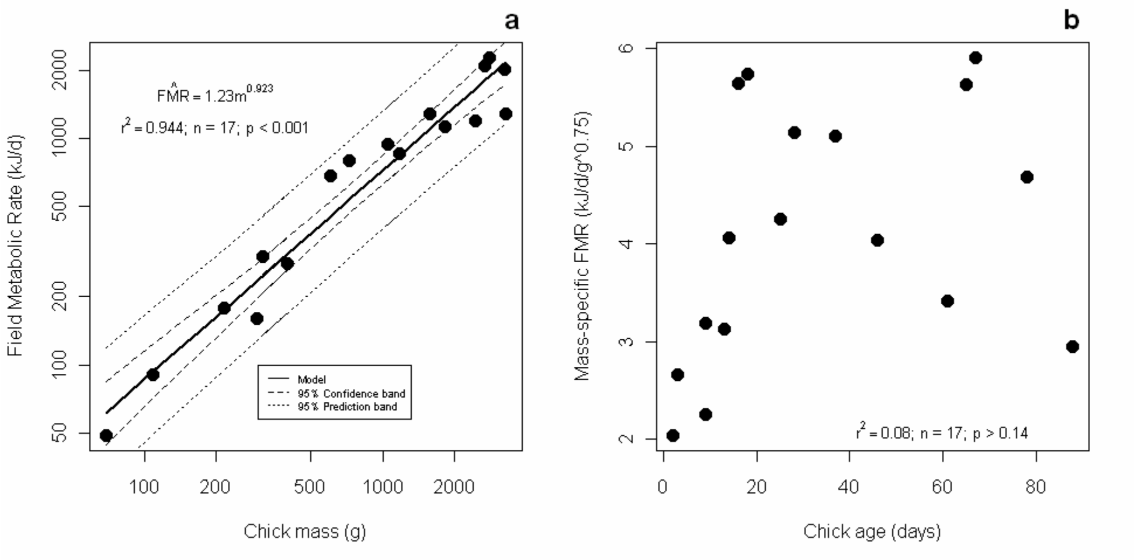

Fig. 3.3. Field metabolic rate (kJ d$^{-1}$), measured using the DLW technique, of Cape gannet chicks at Malgas Island, during the breeding seasons 2002/2003 and 2003/2004. (**a**) Relationship between field metabolic rate and body mass (average mass between initial and final samples). (**b**) Mass specific field metabolic rate (kJ d$^{-1}$ g$^{-3/4}$) in relation to the chick's age (determined from wing and culmen measurements).

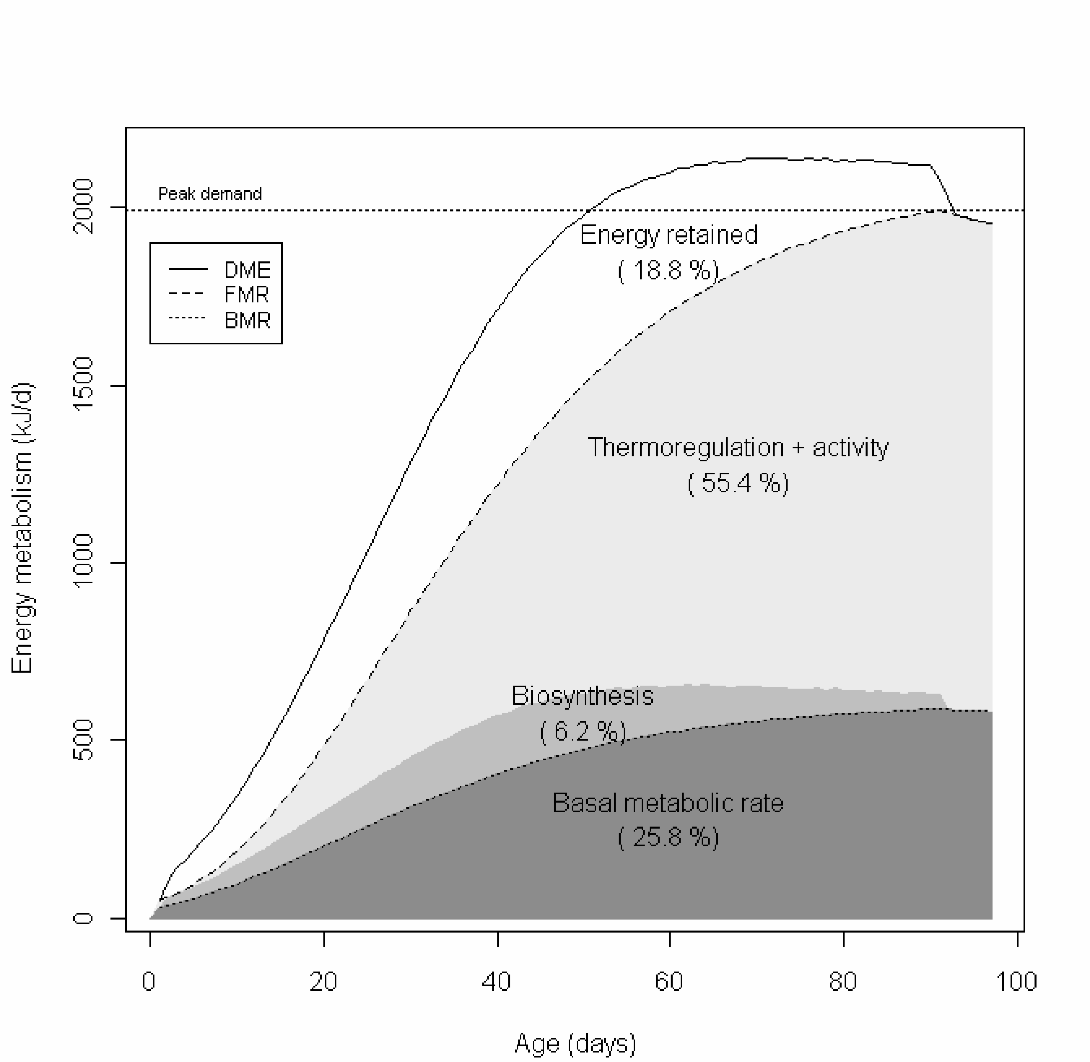

Fig. 3.4. Energy budget of Cape gannet chicks at Malgas Island, over two breeding seasons: 2002/2003 and 2003/2004. The top line corresponds to the daily metabolizable energy (DME); the middle line represents the field metabolic rate (FMR) modelled from DLW measurements of free-ranging birds; and the bottom line represents the modelled basic metabolic rate (BMR), calculated from equation 4 for all birds in Tieleman & Williams (2000). The retained energy was calculated from energy density models based on carcass analysis (Navarro 1992). Peak demand (horizontal dotted line) was defined as 90% of the adult FMR at the nest (2214 kJ $d^{-1}$) (Adams *et al.* 1991, the figured quoted here has been reworked to account for the different value of energy equivalence used in their study).

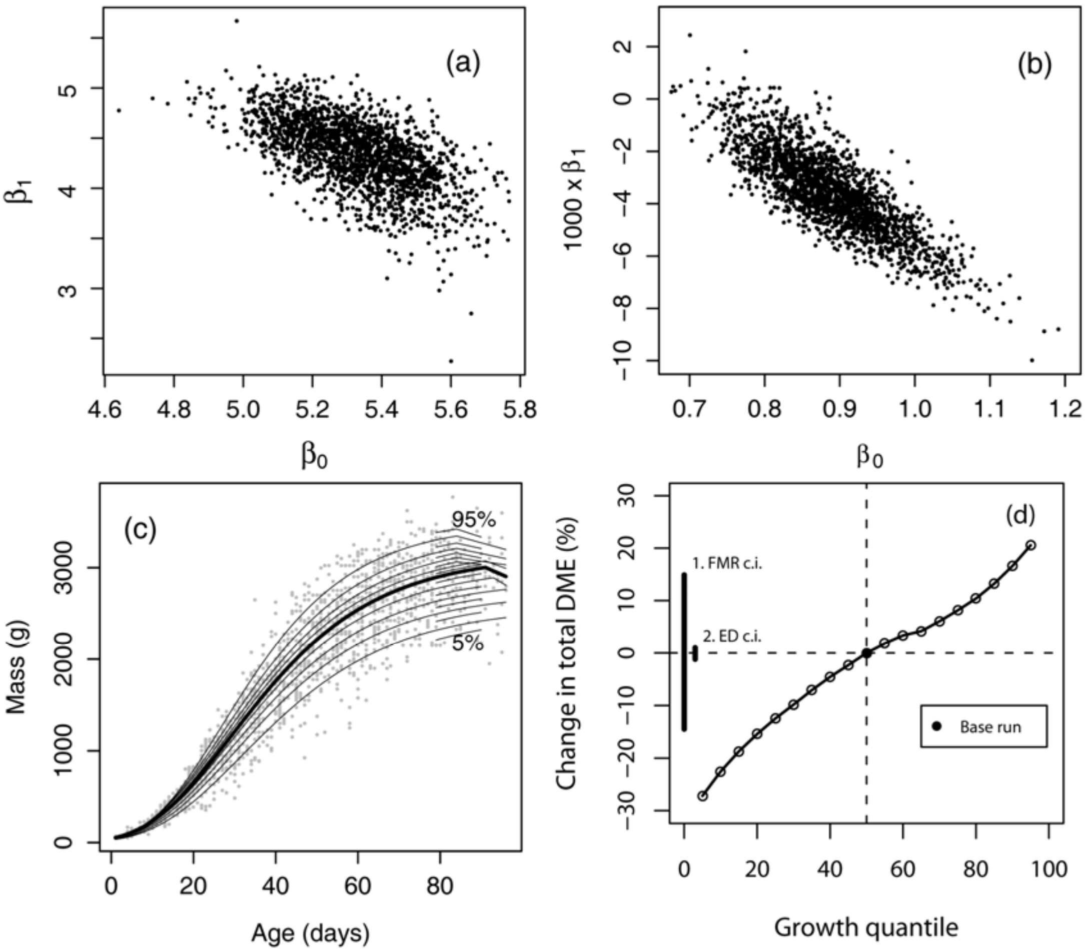

Fig. 3.5. Sensitivity analysis of the energy budget of Cape gannet chicks at Malgas Island over two breeding seasons, 2002/2003 and 2003/2004: (a) energy density model, scatter plot of the parameters from the bootstrap samples; (b) ditto for the FMR model; (c) Gompertz growth-quantiles over the actual data; and (d) summary of the sensitivity analysis. The base run (at the intersection of the dashed lines) corresponds to the energy budget calculated for a chick growing along the median or 50% quantile. The open circles represent changes in total daily metabolizable energy (DME) when the energy budget is calculated for chicks growing along a given quantile, from 5% to 95% at 5% intervals. Such changes were expressed as percentage of the base run. The bootstrap confidence intervals (vertical bars) for the two equations used in the model are also given: (1) field metabolic rate (FMR), Equation 3.5; and (2) energy density (ED), Equation 3.4. Note that the placement of the two vertical bars should be on the 50% quantile but are offset for clarity.

# Appendix 3.1

Individual measurements obtained from the DLW experiments in 17 Cape gannet chicks at Malgas Island, over two breeding seasons, 2002/2003 (chick no. in bold) and 2003/2004.

| Chick # | Start date & time | Time lapse (hh:mm) | Deviation from 24 h multiple (d) | Age in days (d)* | Initial body mass (g) | Final body mass (g) | Mean body mass (g) | Daily mass change (g/d) |
|---|---|---|---|---|---|---|---|---|
| **1** | 01-12-2003 14:47 | 47:58:00 | 0.999 | 2 | 60 | 78 | 69 | 9 |
| **2** | 01-12-2003 14:41 | 48:00:00 | 1.000 | 3 | 94 | 124 | 109 | 15 |
| 3 | 07-01-2003 16:30 | 48:25:00 | 1.017 | 9 | 210 | 220 | 215 | 5 |
| **4** | 02-11-2003 16:07 | 47:50:00 | 0.993 | 9 | 280 | 310 | 295 | 15 |
| **5** | 01-12-2003 14:58 | 47:58:00 | 0.999 | 13 | 370 | 425 | 398 | 28 |
| 6 | 07-01-2003 16:23 | 48:00:00 | 1.000 | 14 | 315 | 310 | 313 | -3 |
| **7** | 02-11-2003 15:50 | 47:50:00 | 0.993 | 16 | 535 | 670 | 603 | 68 |
| **8** | 02-11-2003 16:00 | 48:02:00 | 1.001 | 18 | 715 | 735 | 725 | 10 |
| 9 | 07-01-2003 16:38 | 48:28:00 | 1.019 | 25 | 1150 | 1200 | 1175 | 25 |
| **10** | 28-12-2003 10:33 | 50:40:00 | 1.111 | 28 | 1050 | 1050 | 1050 | 0 |
| 11 | 24-02-2003 17:14 | 48:00:00 | 1.000 | 37 | 1545 | 1620 | 1583 | 38 |
| 12 | 24-02-2003 17:22 | 48:00:00 | 1.000 | 46 | 1770 | 1895 | 1833 | 63 |
| 13 | 24-02-2003 17:32 | 48:00:00 | 1.000 | 61 | 2720 | 2195 | 2458 | -263 |
| 14 | 24-02-2003 17:05 | 48:02:00 | 1.001 | 65 | 2695 | 2695 | 2695 | 0 |
| **15** | 28-12-2003 10:55 | 50:37:00 | 1.109 | 67 | 2900 | 2725 | 2813 | -83 |
| **16** | 01-12-2003 15:10 | 48:01:00 | 1.001 | 78 | 3225 | 3250 | 3238 | 13 |
| **17** | 28-12-2003 13:55 | 71:08:00 | 0.964 | 88 | 3450 | 3150 | 3300 | -101 |

Appendix 3.1 (continued)

| Chick # | Total body water $(g)^{+}$ | Total body water (%) | Water influx ($g\ d^{-1}$) | Water efflux ($g\ d^{-1}$) | Background 2H (ppm) | Background 18O (ppm) | Initial 2H (ppm) | Initial 18O (ppm) | Final 2H (ppm) | Final 18O (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| **1** | 52 | 76 | 22 | 15 | | | | | | |
| **2** | 90 | 82 | 54 | 42 | | | | | | |
| 3 | 166 | 77 | 71 | 68 | 151.8 | 1996.2 | 1363.4 | 4005.3 | 666.3 | 2734.8 |
| **4** | 222 | 75 | 111 | 99 | | | | | | |
| **5** | 326 | 82 | 148 | 125 | | | | | | |
| 6 | 244 | 78 | 87 | 89 | 151.8 | 1996.2 | 946.5 | 3322.6 | 544.0 | 2553.5 |
| **7** | 465 | 77 | 246 | 193 | | | | | | |
| 8 | 552 | 76 | 213 | 205 | | | | | | |
| 9 | 746 | 64 | 221 | 206 | 151.8 | 1996.2 | 419.4 | 2443.0 | 300.1 | 2209.4 |
| **10** | 757 | 72 | 187 | 187 | | | | | | |
| 11 | 1112 | 70 | 148 | 122 | 150.6 | 1994.1 | 382.8 | 2384.6 | 329.1 | 2254.0 |
| 12 | 1297 | 71 | 324 | 279 | 150.6 | 1994.1 | 381.5 | 2380.2 | 291.7 | 2204.9 |
| 13 | 1484 | 60 | 151 | 310 | 150.6 | 1994.1 | 419.7 | 2444.0 | 371.4 | 2327.9 |
| 14 | 1690 | 63 | 449 | 449 | 150.6 | 1994.1 | 408.2 | 2428.8 | 303.1 | 2213.5 |
| **15** | 1808 | 64 | 217 | 271 | | | | | | |
| **16** | 1933 | 60 | 456 | 449 | | | | | | |
| **17** | 2001 | 58 | 283 | 342 | | | | | | |

Appendix 3.1 (continued)

| Chick # | Turnover ratio $k_o$ *(1/d)* | Turnover ratio $k_h$ *(1/d)* | $CO_2$ production (l/d) | Analytical error (%) | FMR (kJ/d)[‡] |
|---|---|---|---|---|---|
| **1** | | | 1.79 | | 49 |
| **2** | | | 3.29 | | 90 |
| 3 | 0.4960 | 0.4246 | 6.55 | 13 | 179 |
| **4** | | | 5.89 | | 161 |
| **5** | | | 10.21 | | 279 |
| 6 | 0.4336 | 0.3531 | 11.05 | 11 | 302 |
| **7** | | | 25.14 | | 687 |
| 8 | | | 29.35 | | 802 |
| 9 | 0.3663 | 0.2924 | 31.28 | 12 | 855 |
| **10** | | | 34.72 | | 949 |
| 11 | 0.2036 | 0.1315 | 46.83 | 13 | 1280 |
| 12 | 0.3026 | 0.2461 | 41.42 | 17 | 1132 |
| 13 | 0.1492 | 0.0988 | 43.65 | 6 | 1193 |
| 14 | 0.3417 | 0.2620 | 77.09 | 11 | 2107 |
| **15** | | | 83.50 | | 2282 |
| **16** | | | 73.58 | | 2011 |
| **17** | | | 47.05 | | 1286 |

* except for chick #2 of known age, chick age was calculated from culmen or wing length, see methods for details

[+] calculated for mean body mass

[‡] $CO_2$ production (l d$^{-1}$) was converted to energy expenditure (kJ d$^{-1}$) assuming an energy equivalent of 27.33 kJ (l $CO_2$)$^{-1}$

# CHAPTER 4

# Chapter 4

# Water everywhere but not a drop to drink: water flux and water economy of Cape gannets *Morus capensis*

## Abstract

I sought to determine the water flux and water economy of Cape gannets *Morus capensis*. I used the doubly labelled water technique to measure water flux and field metabolic rate of free-ranging adults and chicks. Fieldwork was conducted at Malgas Island, Saldanha Bay, South Africa. Nestling total body water BW (g) content was modelled via isotope dilution and carcass analysis to be BW = $0.823m - 6.90\times10^{-5}m^2$ ($r^2 = 0.998$; $n = 38$) where $m$ (g) is chick mass. The water index (WI), i.e. the model for the percentage of nestling mass corresponding to water was WI = $79.83 - 0.262t$ ($r^2 = 0.834$; $n = 38$, where $t$ (days) is chick age. The allometric model for the mean water flux ($W_{\text{flux}}$ , g $d^{-1}$)was $W_{\text{flux}} = 2.499m^{0.628}$, ($r^2 = 0.718$, $n = 17$). The mean water flux of adults was 415 ± 138 g $d^{-1}$ (range: 158.7 – 810, $n = 20$). The ratio between water flux and metabolic rate, or water economy index (WEI, g $kJ^{-1}$), decreased with chick age according to the model WEI = $0.676 - 0.272 \times \log_{10}(t)$, ($r^2 = 0.566$, $n = 17$), indicating that water efficiency increased with age. Similarly, WEI decreased with chick's mass according to the model: WEI = $0.892 - 0.204 \times \log_{10}(m)$, ($r^2 = 0.538$, $n = 17$). At fledging time chick's WEI was at the level of desert birds. Adults' mean WEI was 0.131 ± 0.099 g $kJ^{-1}$ (range: 0.05 – 0.33, $n = 20$). Desert birds maintain a low WEI by also having a low FMR, whereas Cape gannets have a high FMR and are still able to maintain their WEI lower than that of desert birds; clearly Cape gannets outperform desert birds in their water economy.

# Introduction

Mainly due to their lack of water, deserts are considered to be extreme environments. In most cases the water scarcity problem is exacerbated by high temperatures, because animals then need to increase the amount of water used for thermoregulation. For most seabirds there is a direct parallel between the desert environment and the marine environment in that in both situations drinking water may be a limiting factor. The marine environment may be even harsher than a desert as most seabirds have no access to drinking (fresh) water and all requirements for water need to be met by the water in their food plus metabolically produced water. Many seabirds also breed in hot and dry islands; for example, along the coastlines of the major upwelling regions. For example, in spite of the seas surrounding their colonies being cold, Cape gannets *Morus capensis* are exposed to high temperatures and high solar radiation at their breeding islands and both chicks and adults experience heat stress (Hochscheid *et al.* 2002).

Nagy & Peterson (1988) introduced the concept of the water economy index (WEI), which expresses water turnover relative to energy turnover and is determined by calculating water flux in relation to energy expenditure as a ratio. This index is independent of body size and reflects water conservation adaptations; the lower this ratio the less water is used by animals for the same amount of energy output. Tieleman & Williams (2000) and Nagy (2004) found that the WEI of desert eutherians and birds was significantly lower than in non-desert species. Tieleman & Williams (2000) also found that birds from desert habitats have a reduced basal and field metabolic rates compared with species that live in mesic areas; and that the low energy expenditure of desert birds was accompanied by reduced rates of total evaporative water loss (TEWL) and water flux (small WEI).

The objective of this study was to examine how the exclusively fish-based diet of Cape gannets determines the ratio of water to energy turnover. In the absence of drinking, all water requirements of chicks are met solely by pre-formed water in their diet and by metabolic water; the water stress of adults is somewhat lessened because they can ingest sea-water and eliminate the excess salt through salt-glands (Withers 1992). I predicted that Cape gannets should have evolved water saving adaptations comparable to those reported for desert birds, i.e. small values for the water economy index (Tieleman & Williams 2000, Nagy 2004); and that the water saving efficiency of chicks increases with age to reach levels comparable to those of adults by the time they fledge.

## Methods

This study was conducted at Malgas Island (33º03'S, 17º55'E), Saldanha Bay, South Africa. Isotopic measurements on Cape gannet chicks were carried out over two breeding seasons: 2002/2003 ($n$ = 10) and 2003/2004 ($n$ = 7); measurements on adults were done during the breeding season 2005/2006 ($n$ = 20).

### FMR, body water content and water flux

I determined nestling field metabolic rates using the doubly labelled water (DLW) technique (described in Chapter 3 for chicks and in Chapter 7 for adults). In the case of chicks I used the standard two-sample protocol (reference), which allowed the calculation of the size of the water pool, rates of water influx and efflux, as well as rate of $CO_2$ production. In adults I used the single sample protocol (Speakman 1997) to minimize handling stress on the study subjects; this only allowed the calculation of rates of water efflux and $CO_2$ production. Isotopic data used for this analysis is the same obtained for chicks in Chapter 3 and the same obtained for adults in Chapter 7.

Estimates of total body water and rates of water flux were obtained from isotope dilution in the DLW experiments. Total body water was calculated from the initial dilution of the $^2H$ isotope, i.e. difference between initial blood sample and background measurements of $^2H$. These measurements were compared with those measured directly from carcass analysis (Navarro 1992). I calculated water influx using equation 3 in

Nagy & Costa (1980). I corrected for the effect of isotope fractionation assuming an evaporative water loss of 25% and a fractionation factor of 0.941, using equation 7.6 in Speakman (1997), also used by Visser *et al.* (2000). Rates of $CO_2$ production were calculated using equation 7.17 in Speakman (1997), and converted into energy expenditure (FMR; kJ $d^{-1}$) assuming an energy equivalent of 27.33 kJ $l^{-1}$ $CO_2$ for a fish-eating bird (Gessaman & Nagy 1988).

### Water economy index

A measure of how animals conserve water is given by the water economy index (WEI; g $H_2O$ $kJ^{-1}$) introduced by Nagy & Peterson (1988), and calculated as the ratio of water flux (g $H_2O$ $d^{-1}$) and FMR (kJ $d^{-1}$). It is assumed that metabolic rates used to calculate WEI were obtained from animals in steady-state regarding water balance. This condition is often not directly measured, but it is assumed to exists when body mass remains constant during the measurement period (Nagy & Peterson 1988). In the present study the steady-state water balance of chicks was established by comparing the rates of water influx and efflux obtained from the DLW measurements. In the case of adults this was assumed because the single sample DLW experiments preclude the simultaneous measurement of rates of water influx and efflux.

### Statistics

Computations and graphics were done using program R (2.10.0), Windows version (R Development Core Team 2009). Regression models, including ANCOVAs, were fitted with the lm (linear-models) function, whereas fitting of Gompertz growth model was done with the nls (nonlinear least squares) function. 95% confidence intervals of regression parameters were calculated using the adjusted bootstrap percentile method; bootstrapping was done with the package boot (Fox 2002). I examined the allometric scaling of physiological variables with body mass by log-transforming (base e) the variables prior to fitting standard linear least-squared regression. Means are given ± 1 standard deviation.

# Results

## Total body water

Nestling total body water content (BW, g), as determined by $^2$H dilution in the DWL experiments, increased with mass ($m$, g) according to $BW_{DLW} = 0.782m - 5.70\times10^{-5}m^2$ ($r^2 = 0.999$, $n = 17$). Body water content derived from carcass analysis had a similar relationship to mass: $BW_{carcass} = 0.851m - 7.68\times10^{-5}m^2$ ($r^2 = 0.998$, $n = 21$). A combined model revealed that both data sets could be described with a common line and that the two methods of estimating water content gave the same results ($F_{2, 34} = 1.8$, $p = 0.18$). The combined model (Fig. 4.1a) was $BW = 0.823m - 6.90\times10^{-5}m^2$ ($r^2 = 0.998$, $n = 38$). Bootstrap 95% confidence intervals of this model were 0.780 to 0.858 and $-0.79\times10^{-6}$ to $-0.53\times10^{-6}$, for the first and second parameters respectively.

The water index (WI), i.e. the percentage of nestling mass corresponding to water, decreased linearly with increasing age according to $WI_{DLW} = 79.735 - 0.258t$ ($r^2 = 0.806$, $n = 17$), where $t$ is the chick's age in days. An almost identical model describes the water index for the carcass analysis: $WI_{carcass} = 79.98 - 0.268t$ ($r^2 = 0.824$, $n = 21$). The model for the combined data sets (Fig. 4.1b) was $WI = 79.83 - 0.262t$ ($r^2 = 0.834$, $n = 38$). Bootstrap 95% confidence intervals for the parameters of the combined model were 78.0 to 81.2 and –0.296 to –0.228, for the intercept and slope respectively.

## Water flux

The rate of water influx ($W_{influx}$, g d$^{-1}$) in relation to chicks' body mass ($m$, g) was described by the allometric model: $W_{influx} = 3.839 \times m^{0.568}$, ($r^2 = 0.591$, $n = 17$). Similarly, the allometric model for the rate of water loss or efflux ($W_{efflux}$, g d$^{-1}$) in relation to chicks' body mass was: $W_{efflux} = 1.651 \times m^{0.687}$, ($r^2 = 0.800$, $n = 17$). Rates of water influx and efflux did not differ significantly from each other as revealed by an ANCOVA: the elevations of the two models were not significantly different ($F_{1, 28} = 0.07$, $p = 0.71$), and neither were the exponents ($F_{1, 28} = 1.35$,

$p = 0.252$). The allometric model for water flux was: $W_{\text{flux}} = 2.499 \times m^{0.628}$, ($r^2 = 0.718$, $n = 17$) (Fig. 4.2). Bootstrap 95% confidence intervals for this model were 0.82 to 7.12 and 0.472 to 0.794 for the elevation and exponent respectively.

Mean water flux of adults was 415 ± 138 g $d^{-1}$ (range: 158.7 – 810, $n = 20$), and it was independent of body mass ($r^2 = 0.025$, $p = 0.763$).

### Water economy index

WEI (g $kJ^{-1}$) decreased with chick age according to the model (Fig.4.3): $\text{WEI} = 0.676 - 0.272 \times \log_{10}(t)$, ($r^2 = 0.566$, $p < 0.01$), where $t$ (days) is the age of the chick. Similarly, WEI decreased with chick's mass according to the model $\text{WEI} = 0.892 - 0.204 \times \log_{10}(m)$, ($r^2 = 0.538$, $p < 0.001$), where $m$ (g) is the chick's mass. The mean WEI of adults was 0.131 ± 0.099 g $kJ^{-1}$ (range: 0.05 – 0.33, $n = 20$).

## Discussion

### Total Body Water

There was close agreement between the total body water of chicks measured by carcass drying (Navarro 1992) and that measured by isotope dilution. Although the carcass and DLW measurements were from two different sets of birds, the results validate the estimate of the size of the body water pool made by isotope dilution.

### Field Water Flux

Rates of water flux in growing chicks of the Cape gannet were close to those predicted from Nagy & Robertson's (1988) model for free living birds. The predicted values lie within the 95% confidence interval of the chick's model (Fig. 4.2), and although Nagy & Robertson's model was formulated for adult birds, it could also be used for growing birds.

Rates of water influx and efflux of chicks were not significantly different, which is an indication that Cape gannet chicks were in a steady-state with regard to water balance. It is also evident that chicks are capable of maintaining water balance soon after hatching. Adams *et al.* (1991) measured rates of water flux in Cape gannet chicks and also did not find differences between influx and efflux rates. The mean water flux measured by Adams *et al.* (1991) was 6% below the value predicted by the combined water flux model.

For gannets, as in most seabirds, the only source of preformed water is through the water contained in their fish prey, as they do not drink fresh water. This makes it possible to directly convert water influx rate into rate of food consumption. The average water content of anchovy *Engraulis encrasicolus*, one of the main prey species consumed by Cape gannets, is 71.5% (Cooper 1978), so that the estimated daily food consumption FC (wet mass, g $d^{-1}$) of a chick of mass $m$ is FC = $1.399W_{\text{influx}}$. This underestimates FC because not all the energy measured by bomb calorimetry is assimilated as some is excreted in faeces and urine (Visser 2001). The assimilation efficiency of Cape gannet chicks on a diet of anchovy is 76.1% (Cooper 1978), and correcting for this factor, then FC = $1.838W_{\text{influx}}$.

**Water Economy Index**

As tissues of growing Cape gannets mature the proportion of body water decreases linearly with age, and at the same time they become more efficient in their utilization of water as the WEI also decreases with age. By the time chicks are ready to fledge their WEI was within 1 SD of the adults' value (Fig. 4.3), and was almost identical to the mean WEI for desert birds (Tieleman & Williams 2000).

WEI calculated for Cape gannets from Adams *et al.* (1991) data was 0.072 g $H_2O$ $kJ^{-1}$, well within 1 SD of the mean value in the present study. Nagy *et al.* (1984) used DLW to measure field metabolic rates, including water flux, of breeding African penguins *Spheniscus demersus;* from data in their Table 1 I calculated WEI to be 0.140 ± 0.01 g $H_2O$ $kJ^{-1}$ ($n = 10$), which is almost identical to the value reported in the present study for Cape gannets. These two species are in the lower spectrum of seabirds WEI, as the mean WEI for all the seabirds listed in Table 1 of Tieleman & Williams (2000) was 0.221 ± 0.094 g $H_2O$ $kJ^{-1}$ ($n = 17$), higher than the value for desert birds, but comparable to that of desert arthropods (Nagy 2004).

According to Tieleman & Williams (2000) desert environments have three characteristics that might favour selection for lower FMR and BMR: (1) individuals with low FMR would fare better in the low primary productivity of deserts; (2) limited supply of drinking water may influence the energy balance of desert birds; and (3) the relatively high environmental temperatures in deserts reduce thermoregulatory requirements and might result in a combined reduction of FMR and BMR. However, higher temperatures increase the need for evaporative cooling, resulting in an increased rate of water flow, which in turn could be reduced by lowering endogenous heat production and/or increasing tolerance to hyperthermia. Most likely, these factors act in concert to select for a combination of reduced FMR and BMR coupled with low rates of water flux in desert birds (Tieleman & Williams 2000). In the case of marine birds and specifically in Cape gannets the low primary production of deserts could be equated to low predictability of food resources; however they do not conform to the prediction of reduced metabolic rates as it is well established that seabirds have higher FMR than terrestrial birds (Birt-Friesen *et al.* 1989, Tieleman & Williams 2000); the benefits of point 3, i.e. reduced metabolic rates by saving energy in thermoregulation do not seem to apply to Cape gannets, who are subjected to heat stress and have the need to invest energy in gular fluttering and increase water flow through evaporative cooling (Hochsheid *et al.* 2002).

Cape gannets seem to out-perform desert birds in their water economy, as desert birds maintain a low WEI by also having a low FMR (Nagy 2004), whereas Cape gannets have a high FMR and are still able to keep a mean WEI below that of desert birds. The smallest WEI yet reported is for the desert-dwelling kangaroo rat *Diplodomys merriami* which has a WEI as small as 0.05 g $H_2O$ $kJ^{-1}$ for at least during part of their yearly cycle (Nagy & Gruchacz 1994). The smallest WEI measured for an adult Cape gannet was 0.051 g $H_2O$ $kJ^{-1}$, which puts this species amongst the best at conserving water given their high field metabolic rates.

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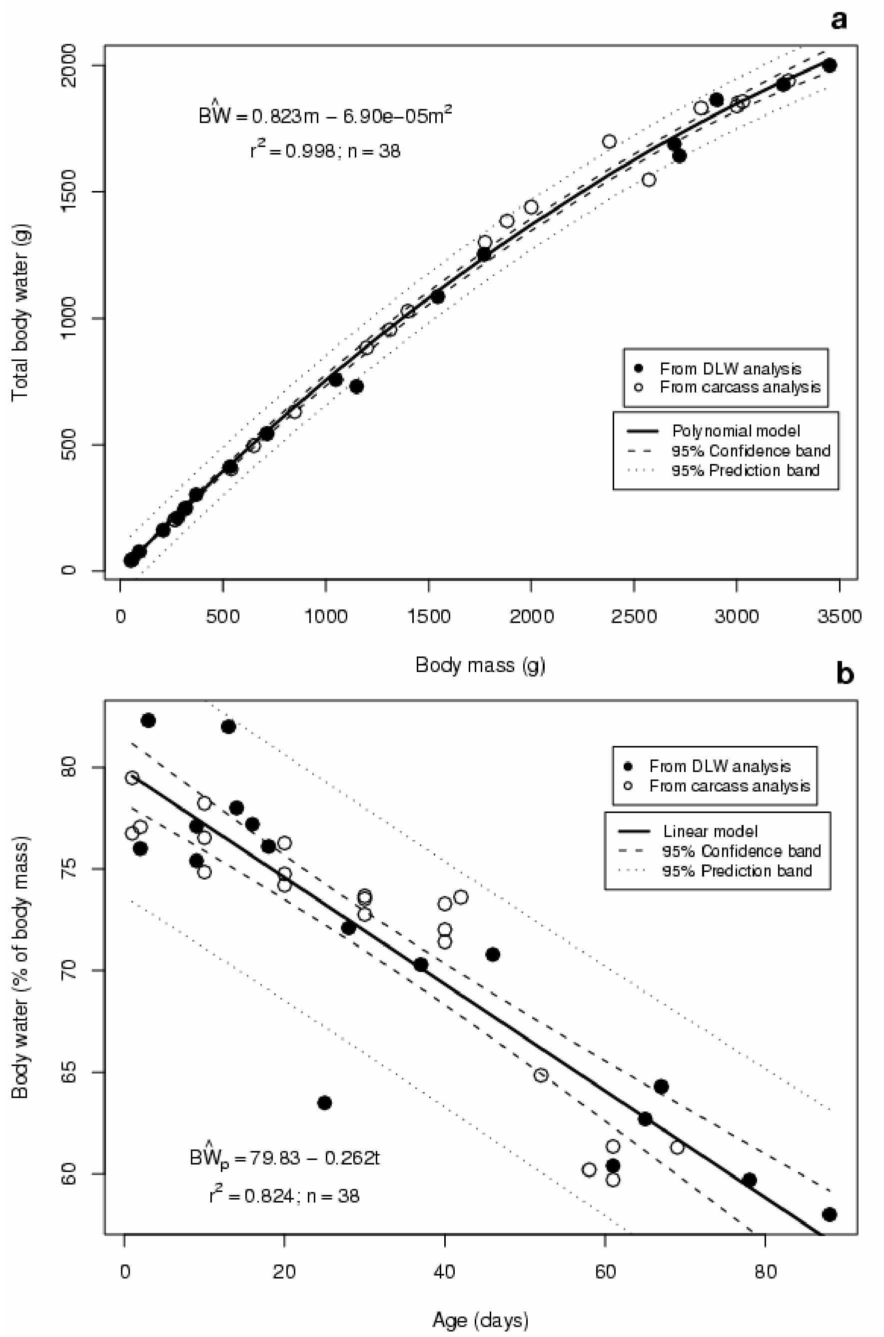

Fig. 4.1. Body water of Cape gannet chicks at Malgas Island, over two breeding seasons 2002/2003 and 2003/2004; (a) total body water in relation to initial body mass, and (b) the fraction of nestling mass corresponding to water in relation to the chick's age. Data corresponds to two different methods of quantifying the amount of body water: (1) from DLW experiments in which the amount of body water was calculated from the initial dilution of the $^2H$ isotope (solid circles); and (2) from carcass analysis (open circles) (Navarro 1992). In both panels the models shown were fitted to the combined data sets.

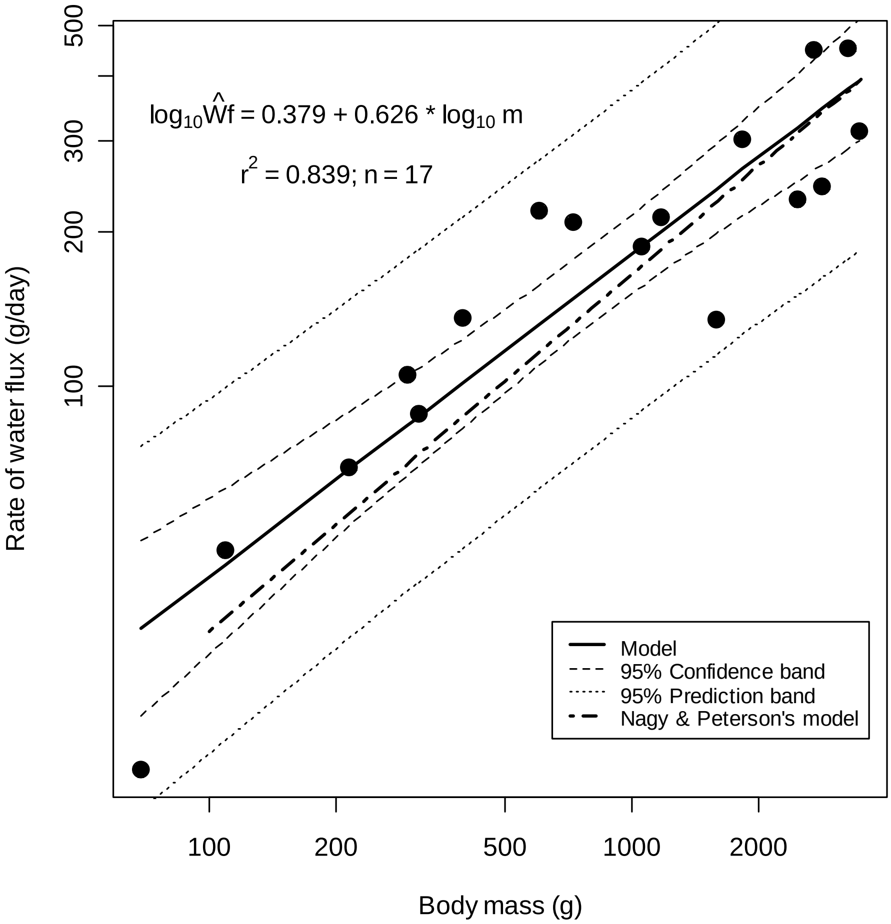

Fig. 4.2. Rate of water flux (g $d^{-1}$) in relation to body mass (g) of Cape gannet chicks at Malgas Island, over two breeding seasons 2002/2003 and 2003/2004. Water flux corresponds to the average rate of water influx and efflux measured in the DLW experiments. Body mass corresponds to the average between initial and final samples. The dot-and-dashed line corresponds to water flux predicted using the model by Nagy &Robertson (1988).

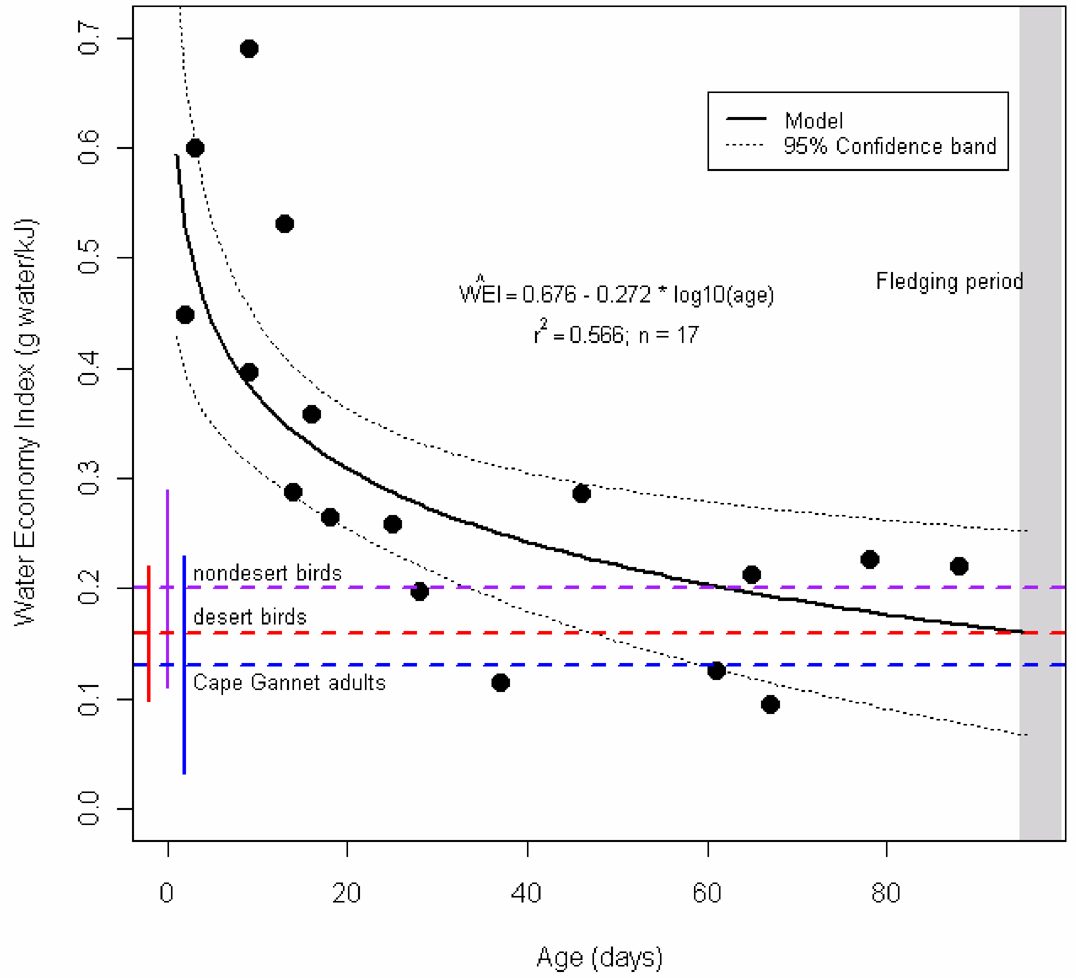

Fig. 4.3. Water economy index (WEI, g $H_2O$ $kJ^{-1}$) of Cape gannet chicks in relation to age, plus WEI for adults (blue line) at Malgas Island. Value for desert (red line) and nondesert (purple line) birds are from Tieleman & Williams (2000). Vertical lines represent ±1 SD.

# CHAPTER 5

## CHAPTER 5

# A NEW LOOK AT TRACK SINUOSITY: USING DISTANCE-RATIO SCALE FOR THE ANALYSIS OF ANIMAL MOVEMENT

## Abstract

Quantifying spatial patterns of animal movement, particularly searching for prey, is of critical importance for understanding an animal's habitat and foraging specialization. The concept of scale is important in understanding the way animals seem to perceive their environment, and can be used to identify behaviour exhibiting movement patterns consisting of area-restricted searching (ARS) at fine scales. Here, I present a new method, the distance-ratio scale (DRS) method, which describes the scale as the sum of the straight line along the path emerging in both directions from a focal point. The straightness (distance along the path divided by the straight-line distance) and length of the line are controlled by a pre-defined tolerance, which is the percentage by which the path is allowed to deviate from the straight line. Tolerance levels examined (1.1–1.8) show good agreement in the overall pattern, but as tolerance is increased, so does the proportion of points with higher DRS values. Tolerance 1.2 was selected as a standard on which to base future use of DRS based methods. Plotting DRS values using log-binning with normalization (LBN) method seemed the most convenient way to assess the scale at which animals seem to operate. Fine scale DRS can be used to identify ARS zones. Coarse scale DRS indicate long distance movement between breeding colony and foraging areas, or between patches.

# Introduction

The way in which animals adjust their movement patterns in relation to the environment is crucial to understand many aspects of their ecology. Foraging behaviour, dispersal, and habitat selection are all dependant on animal movement and on their perception of the environment as they move through it. Reviews by Schick *et al.* (2008) and Calenge *et al.* (2009) summarized the methods and theoretical models that have been used to analyze animal movement. There are two basic approaches to the analysis of animal trajectories. The first involves fitting a theoretical model that, it is hoped, provides a realistic account of the animal's movement. Some examples of these are random walk models (Broadbent & Kendall 1953), correlated random-walks (Kareiva & Shigesada 1983, Morales & Ellner 2002), Lévy flights (Viswanathan *et al.* 2001, Bartumeus *et al.* 2003, but see Edwards *et al.* 2007 for a critique on the validity of Lévy flight models in a biological context), hidden Markov models (Patterson *et al.* 2009), and hierarchical Bayes models (reviewed by Schick *et al.* 2008). The second approach does not involve model fitting but looks for patterns emerging from the data themselves. Three types of methods have been developed: calculation of a fractal index (Wiens *et al.* 1995, Nams & Bourgeois 2004, Tremblay 2007), calculation of the first passage time (FPT) (Fauchald & Tveraa 2003, Weimerskirch *et al.* 2007, Bailleul *et al.* 2008), and calculation of an area-interest-index (Wilson *et al.* 2007). These approaches are based on different ways of measuring the tortuosity, or sinuosity, of the movement path. In this paper we develop a fourth sinuosity-based method that provides a direct estimate of the scale at which animals operate in their environment. We compare this approach with the first-passage time method.

First passage time (FPT) is defined as the time required for an animal to move through a circle of a given radius. It represents a scale dependent search effort because this measure integrates path sinuosity (how convoluted is the path they follow before exiting the circle) and changes in speed (a decrease in speed is usually associated with higher turning rate). FPT is calculated by positioning a circle of radius *r* on a point along the path and recording the time the animal takes to leave the circle; this is repeated for every measurement point along the path. The whole calculation is repeated with increasing values of *r*. FTP calculation requires that the points or fixes along the track are taken at the same regular time intervals, this usually means that the track needs filtering and interpolation to regularize it. To assess how FPT scales with *r* a plot of variance(log(FPT)) vs. the radii is visually examined, peaks in variance(log(FPT)) are taken as the scale at which FPT represents search intensive behaviour (Johnson *et al.* 1992). Thus, large values of FPT for a particular scale are used to identify area-restricted search zones along the path (Fauchald & Tveraa 2003).

Based on the concept of FPT I turned the idea around and asked the question: "What is the distance that an animal can move within a given sinuosity threshold before its course deviates enough to go over such threshold" In other words, I considered the distance which is covered almost linearly. When animals are moving quickly to and from a patch this distance should be much larger that when actively searching. I call this measure the 'distance-ratio scale' (DRS). In this chapter I introduce DRS through a detailed analysis of a sample track. I explore alternatives for its analysis and visual presentation, I introduce an algorithm to partition the tracks into its main behavioural components, and I compare the DRS with the FPT method. Finally, with a simple modification of the DRS calculation it is possible to split the track into straight-line segments of varying length according to the chosen tolerance; these segments were used to test if Cape gannets use Lévy flights (Viswanathan *et al.* 2001, Bartumeus *et al.* 2003) in their search strategy.

## Methods

### Fieldwork and foraging tracks

Details of the field work and methods for collecting foraging tracks of Cape gannets *Morus capensis* were given in Chapter 6. Briefly, gannets brooding chicks were caught and fitted with GPS-data loggers (Technosmart, Rome) attached to tail feathers (Fig. 5.1) and released; upon return from a foraging trip, birds were recaptured to retrieve the device and download the data. Loggers were set to record a fix of the birds' geographic position every 10 seconds.

### Data processing

GPS locations were downloaded from the loggers and pre-processed before analysis:

(a) Fixes before departure from the colony and fixes after arrival back at the colony were deleted.

(b) Some birds undertook a second foraging trip before recapture to remove the data logger; in these cases the data file was split and the trips analysed separately.

(c) Geographic coordinates were converted into metres using Albers' Equal Area Projection (Snyder 1987). This converted the three-dimensional geographic coordinate system of the terrestrial globe into a two-dimensional flat surface. Projected coordinates were relative to the colony's centre point, the coordinates in metres obtained from the projection were further standardized and made relative to the starting point, i.e. all tracks started at point (0, 0).

(d) Using coordinates in meters the distance and speed between pairs of consecutive fixes was calculated. These distances were used to calculate a sinuosity index using a 7-point window. Sinuosity is defined as the ratio between the distance flown and the straight line for a set of consecutive points centred on the focal point. Grémillet *et al.* (2004) used a 4-point window for their sinuosity calculation, but I have adopted a 7-point window because the additional smoothing produced a less noisy sinuosity signal.

### Behavioural algorithm

Five basic behaviours were identified based in changes of speed, sinuosity and time spent on the water surface:

1. Out-flight: from the start of the track (departure from the colony) until the sinuosity of the track was >3.3 or a drifting event (see below) which lasted for more than 240 seconds. This section was characterized by rapid flight speeds, usually over 40 km $h^{-1}$.
2. Commuting or search flight: the remaining sections of the track, characterized by medium flight speeds (between 10–40 km $h^{-1}$) and larger values of sinuosity than out- or return-flight.
3. Fishing or dives: section of the track, usually a single fix, characterized by a sudden drop in speed, from >10 km $h^{-1}$ to values close to zero (plunge dives); or by being airborne in a drifting sequence, representing shallow-dives.
4. Drifting or swimming: characterized by speeds below 10 km $h^{-1}$. gannets cannot remain airborne at such slow speeds (Weimerskirch *et al*. 2002). This event includes the overnight section, when gannets sleep on the water surface and drift with ocean currents and prevailing winds.
5. Return-flight: section of the track from last fishing activity back to the colony, with characteristics similar to out-flight and identified in a similar way by the algorithm (traversing the track in reverse order).

The following algorithm was implemented in the computer language Perl. On a first pass, each fix was classified either as airborne or drifting according to point 3 above. Then, out-flight and return-flight were identified. The remainder points were assigned to commuting/search flight. Finally, the whole track was traversed forward to identify fishing/dives, which were ‘instantaneous’ events involving a single fix.

The ability of the behavioural algorithm to correctly identify the out-flight, return-flight and overnight-drifting was done by visual inspection of plots like the one illustrated in Fig. 5.2, the tracks were scored for success/failure of the feature identified.

### Distance-ratio scale (DRS) calculation

The new direct approach to measuring the scale at which an animal is operating is described by the following algorithm. As in the case of FPT, for each point along the track we positioned a circle that expands (or contracts) to include subsequent points along the track until the distance ratio, i.e. the actual distance covered divided by the radius, was greater than a pre-defined tolerance level. The radius for the point immediately before surpassing the given tolerance was considered the forward scale value ($DRS_f$). Similarly, the calculations were repeated using preceding points along the track; this is the backward scale value ($DRS_b$). The DRS of the focal point was defined to be $DRS_f + DRS_b$. I explored the consequences of setting the tolerance level at values ranging from 1.01 to 4.0; results for the range 1.1 to 1.8 are reported here.

Weimerskirch *et al.* (2007) used FPT to identify area-restricted search (ARS) in wandering albatross *Diomedea exulans*. In their study a preliminary analysis revealed that drifting or swimming completely removed the ability of the method to detect ARS at a scale >100 m by inflating the FPT variance. A similar phenomenon was observed for the calculation of DRS. To remove this problem I eliminated fixes obtained during periods in which the bird was drifting; this is appropriate because these fixes do not represent active movement by the birds but rather passive displacement with oceanic current, wave action and wind. For the purpose of DRS calculation deleting the drifting sections is equivalent to a direct flight at constant speed, a similar approach to that adopted by Weimerskirch *et al.* (2007).

The scale values thus generated can be examined with various techniques: (a) as bouts of movements (Fig. 5.3c); (b) histograms with regular bin sizes (Fig. 5.4); (c) log-binning trend-line with normalization (Fig. 5.5a); (d) rank-frequency plots that not requiring binning can display the data without loss of information (Fig. 5.5b). The last two are particularly useful to represent several tracks in a plot, or as used in Fig. 5.5 compare the scale landscape derived from different tolerance values; or to compare scale values of the flight types in a track (Fig. 5.6)

The log-binning with normalization (LBN) method involves setting the bin breaks such that each bin is twice the width of the preceding bin

(Edwards 2008). The starting value of the series was set at 20 m, assumed as the minimum distance that a gannet could cover, allowing for some turnings, in the 10-second interval between consecutive fixes; 13 bins were required to include the full range of scale values. The count in each bin was normalized by dividing the count by the width of that bin to get a count per unit interval (Newman 2005).

### Lévy flight

The DRS algorithm was modified as follows to split a track into straight-line segments according to a given tolerance. On the forward calculation (see above) the DRS of the focal point is calculated; the break-point for a chosen tolerance becomes the next focal point and so on. The DRS values thus obtained represent the straight-line segments of the track; the rank-frequency plot of these values should be a straight line if the segments come from a distribution with exponential decay in the right tail, as expected for a Lévy flight distribution (Edwards 2008).

### First-Passage-Time (FPT) calculation

For the first-passage time calculation the tracks need to be regular, i.e. all fixes must be at the same time interval, and although the loggers were set to record every 10 seconds, the resulting track was never regular because the logger would miss some fixes and/or skip a few seconds. I used linear interpolation to regularize the track and to generate fixes for gaps of 60 seconds or less; longer gaps were treated as missing values. FPT was calculated for radii of 1–50 km in steps of 1 km; then the variance of log(FPT) was plotted against the radii to identify ARS behaviour by looking for peaks in the multimodal distribution of variance log(FPT).

### Statistical analysis

Initial data processing was done with scripts written in QuickBasic, Perl and FORTRAN. Statistical analyses and graphics were done using program R (2.10.0, Windows version) (R Development Core Team 2009). The R-package *adehabitat* version 1.8.3 (Calenge 2006) was used for FPT analysis; and the package *FactoMineR* was used for correspondence analysis.

## Results

### Behavioural algorithm

A representative movement track is given in Fig. 5.2, in which the five components identified by the behavioural algorithm are highlighted. This is a typical overnight track because it includes drifting while the bird remained on the water surface. A set of 367 tracks (310 complete tracks, 84.5%) were visually examined to evaluate the performance of the behavioural algorithm. Out-flight was correctly identified in 316 (86.1%) of the tracks; return-flights were correctly identified in 295 (95.2%) of the 310 complete tracks examined. There were 301 (82%) tracks where the overnight-drifting was present, of these 298 (99%) were correctly identified.

### Distance-ratio scale (DRS) calculation

Fig. 5.3 illustrates the distance-ratio scale calculation for the same sample track. Both, the backward (Fig. 5.3a) and forward (Fig. 5.3b) calculation showed the effect of decreasing scale value as the focal point approaches the point where the path changes from straight-line flight to the more convoluted search-flight. By adding the scale values obtained from the forward and backward calculations this artifact was removed (Fig. 5.3c).

The effects of different tolerance values on the scale calculation are illustrated in Figs 5.4–5.6, in which the same data have been represented in three ways. The scale values increased with increasing tolerance levels; however the pattern or scale structure of the track was similar throughout much of the tolerances (Figs 5.4 & 5.5). The tolerance of 1.1 missed the scale values around 60 km, a similar effect was observed in other tracks where the mid range of scale values was missing for tolerance 1.1. As the tolerance level is increased there is a concomitant increase in the number of fixes that reach higher scale values. This movement of points to higher scale values erases features found at smaller tolerances (1.2 and 1.3). Of note is the peak at 60–65 km, which at tolerance 1.7 has completely disappeared (Fig. 5.4). The other effect of this movement of points is the appearance of peaks at higher scale values: 70–75 km and 90–95 km. The peak at 80–85 km remains distinctive though all tolerance levels (Fig. 5.4). This effect can be appreciated in both the LBN and rank-frequency plots (Fig. 5.5): as tolerance increases so does the frequency of high scale values in the series.

### Scale

The histogram of DRS for tolerance 1.2 (Fig. 5.4b) revealed the presence of three distinct peaks at scales: 0–5 km, 60–65 km and 80–85 km, which corresponded well to commuting/search, out-flight and return-flight respectively (Fig. 5.6). The dominant spatial scale in the search-flight was at 0–500 m, closely followed by 500–1 000 m (Fig. 5.5), with most of the values below 2 000 m. There was a clear trend to increased speed of flight with increasing DRS values (Fig. 5.7)

The LBN plot (Fig. 5.6a) revealed a dominant scale at 40–640 m, with 63% of the normalized frequencies lying within this scale range; a second peak occurred at the scale range 20481–81920 m, which accounted for the out- and return flights parts of the track. The rank-frequency plot (Fig. 5.6b), in spite of its ability to represent the complete data, was of limited usefulness to clearly identify the scale at which Cape gannets seem to operate.

Based on the fine scale identified by the binning methods, points where DRS < 1 000 m were assumed to represent the ARS zones of the track (Fig. 5.8). There was complete overlap between the ARS zones and the fixes classified as fishing by the behavioural algorithm.

### First-Passage-Time (FPT) calculation

FPT analysis of the sample track (Fig. 5.9) revealed the occurrence of ARS behaviour at the spatial scale of 1 km. A second and larger peak in variance log(FPT) occurred at a scale of 23 km, the range 18–27 km seemed the dominant FPT scale for this particular track.

### Lévy flight

The straight-line segments derived with the DRS algorithm for the sample track do not lie in a straight line (Fig. 5.10) as expected for an exponential decay in the right tail.

## Discussion

### Behavioural algorithm

The behavioural algorithm had a high performance rate at identifying the behaviours outlined in the method section. The return-flight was correctly identified at a significantly higher rate than out-flight (Fisher's exact test, $p < 0.001$). Misidentification of the flight types was always related to changes of behaviour during out- and return-flights. Cape gannets responded opportunistically to environmental cues all along the flight path, and as expected, they did so more often during out-flights, when they would be actively searching for prey.

### Distance-ratio scale (DRS)

The key parameter in the distance-ratio scale algorithm is a tolerance value that relates the observed length of the flight path with the straight-line distance between the starting point and end point of the path section. As the tolerance value was increased and the flight-path was allowed to become longer before reaching the increasing thresholds, more and more fixes were included at higher scale values; this phenomenon was responsible for increasing the frequency of large DRS values. Fine-scale values showed remarkable agreement for all tolerances examined. As expected, at the coarse scale is where higher tolerance values increase the breadth and relative importance of this scale; however the overall pattern is maintained throughout. The tolerance of 1.2 seemed a good compromise as a standard on which to base the DRS analysis for comparisons between species and studies because it seems to introduce the least amount of bias in the scale values.

The relationship between DRS and the speed of the birds (Fig. 5.7) confirmed the idea that as the scale increases animals were moving faster through the landscape, and conversely. At the lower scales, when the area-restricted search behaviour took over, the speed of the animal was predicted to be substantially slower, allowing more time to search the space they are moving through.

Area restricted search zones identified by DRS analysis for the sample track overlapped completely with the fishing events identified by the behavioural algorithm. Extending this analysis to all tracks, 11 875 (77.4%) out of 15 335 fishing events overlapped ARS zones. The remaining 22.6% of fishing took place opportunistically along the path and was not necessarily associated with active search.

### First-Passage-Time (FPT)

There is general agreement between the two scales identified by FPT and DRS, however the relative importance of the fine and coarse scales was vastly different. In DRS the fine scale is the dominant feature of the track, which is what one would expect from a visual forager such as the Cape gannet. The coarse-scale, greater than 60 km, was used less frequently and was restricted to commuting rapidly between the breeding colony and foraging areas. Cape gannets used coarse-scale in the range 10–20 km for movement between foraging patches. This made better intuitive sense than the patterns conveyed by FPT, which completely downplays the role and importance of the fine scale movements. This shortcoming of the FPT method to identify ARS zones was noted by Tremblay *et al.* (2007). While the FPT analysis identifies a radius (i.e. where the variance in logFPT peaks) and DRS identifies the length of a straight-line segment, the interpretation of results from the two methods cannot be direct and straightforward. However, both methods aim to identify the scale at which animals operate and for this reason the comparison is legitimate. Compared with the fractal landscape method (Tremblay *et al.* 2007), DRS is capable not only of correctly identifying ARS zones, but it can also identify coarser scales.

### Lévy flight

Both, LBN and rank-frequency plots have been employed to assess fitness of the data to models where the tail of the distribution follows an exponential decay; in particular Lévy flight models (Viswanathan *et al.* 2001). Lévy flights are scale invariant and are thought to maximize the areas searched in contrast with correlated-random walks or purely random, Brownian movement (Cole 1995, Viswanathan *et al.* 2001). When plotted on a logarithmic scale the points should lay on a straight line if they indeed do come from a distribution with a negative exponential tail; DRS could be used to asses such fit. From Fig. 5.5 is clear that DRS for the sample track failed to conform to this prediction, nor did any other tracks examined. To pursue this idea further, the DRS algorithm was modified to split the track into straight line segments, which could be assumed to represent movement bouts (Y. Tremblay, pers. com). The rank-frequency plot of the resulting movement bouts clearly indicates that the points clearly do not lie along a straight line (Fig.5.10), therefore not lending support to the presence of Lévy flight for the sample track.

In conclusion, the DRS method provides a direct way of measuring scale, results that were spatially explicit and quantitatively straightforward to interpret.

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Fig. 5.1. Cape gannet fitted with a GPS logger on the lower rump and tail feathers. Inset shows the attachment procedure using waterproof tape.

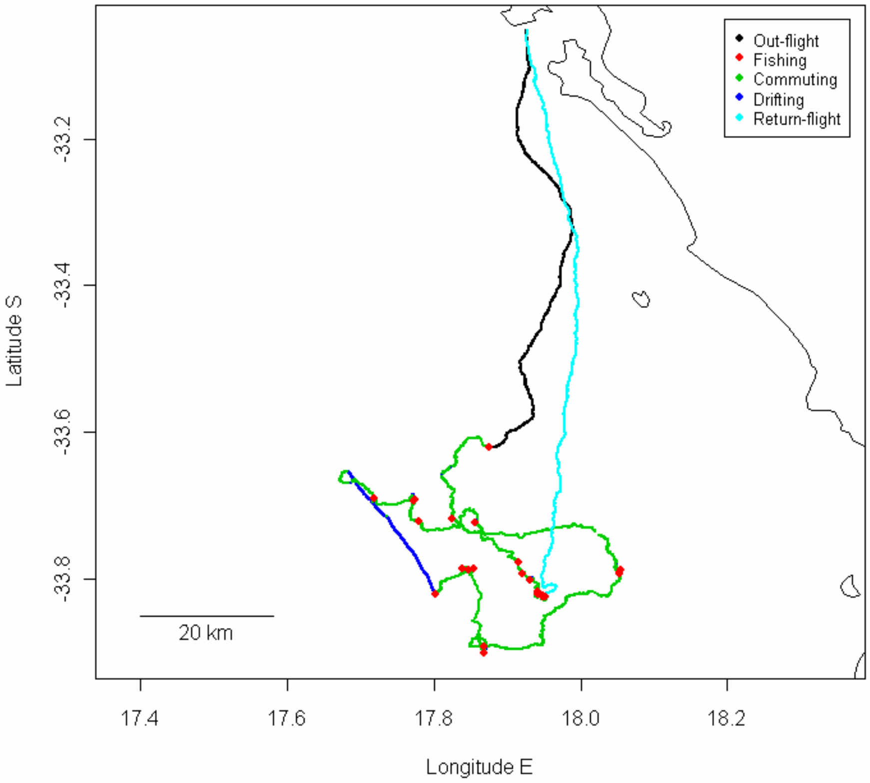


Fig. 5.2. Sample track of a Cape gannet in which different sections of the track are indicated, these were identified by the algorithm described in the methods section (see text). The bird was fitted with a GPS logger at Malgas Island, on the 21st of September 2003.

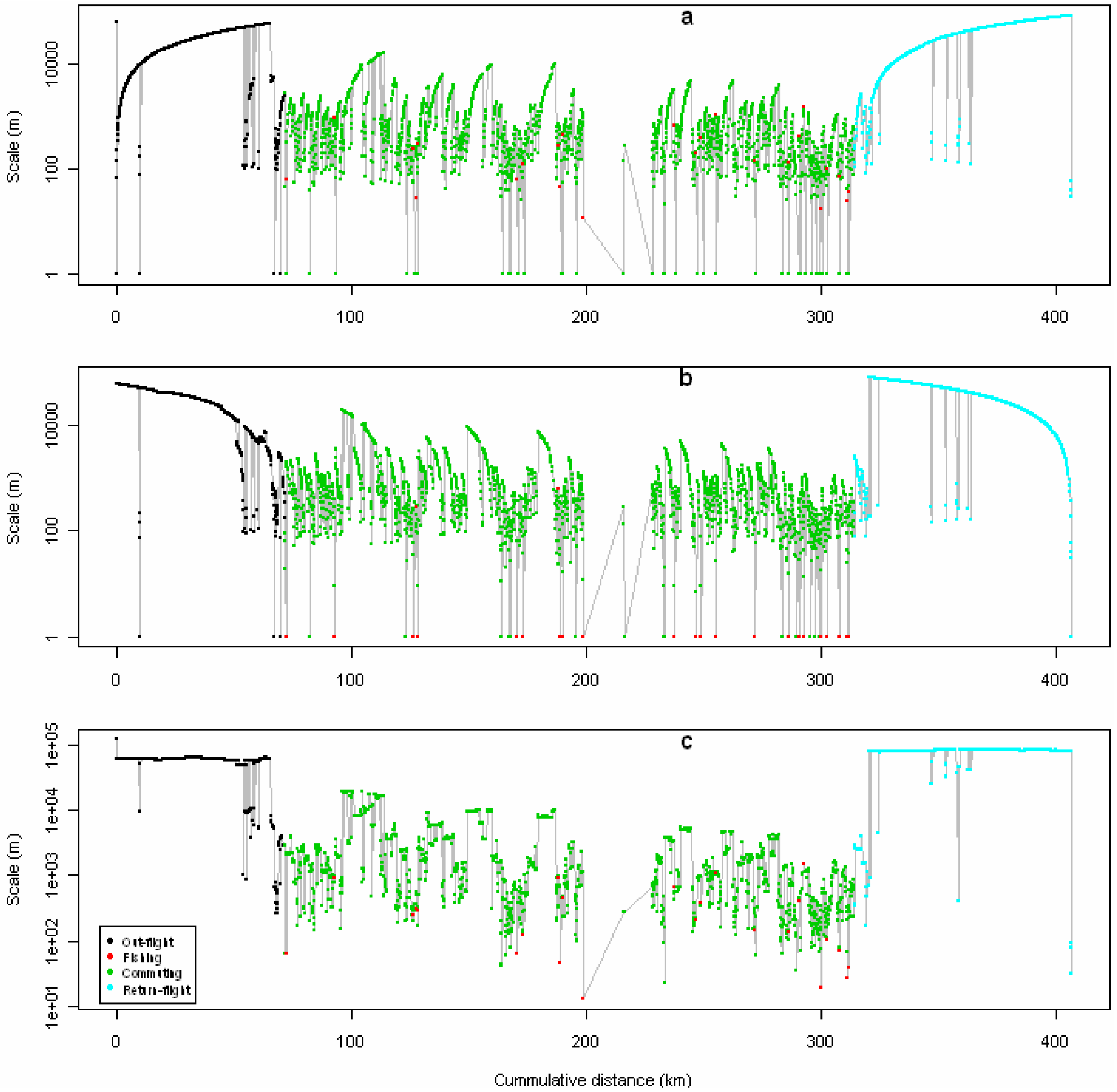


Fig. 5.3.Distance-ratio scale calculation method for the Cape gannet sample track illustrated in Fig. 5.2. The scale is calculated for each point along the track, excluding drifting, the calculation is done backwards (a) and forwards (b) from the focal point, these values are added to give the final scale (c). The behaviours where identified according to the algorithm outlined in the methods section (see text). The tolerance level for the scale is 1.2.

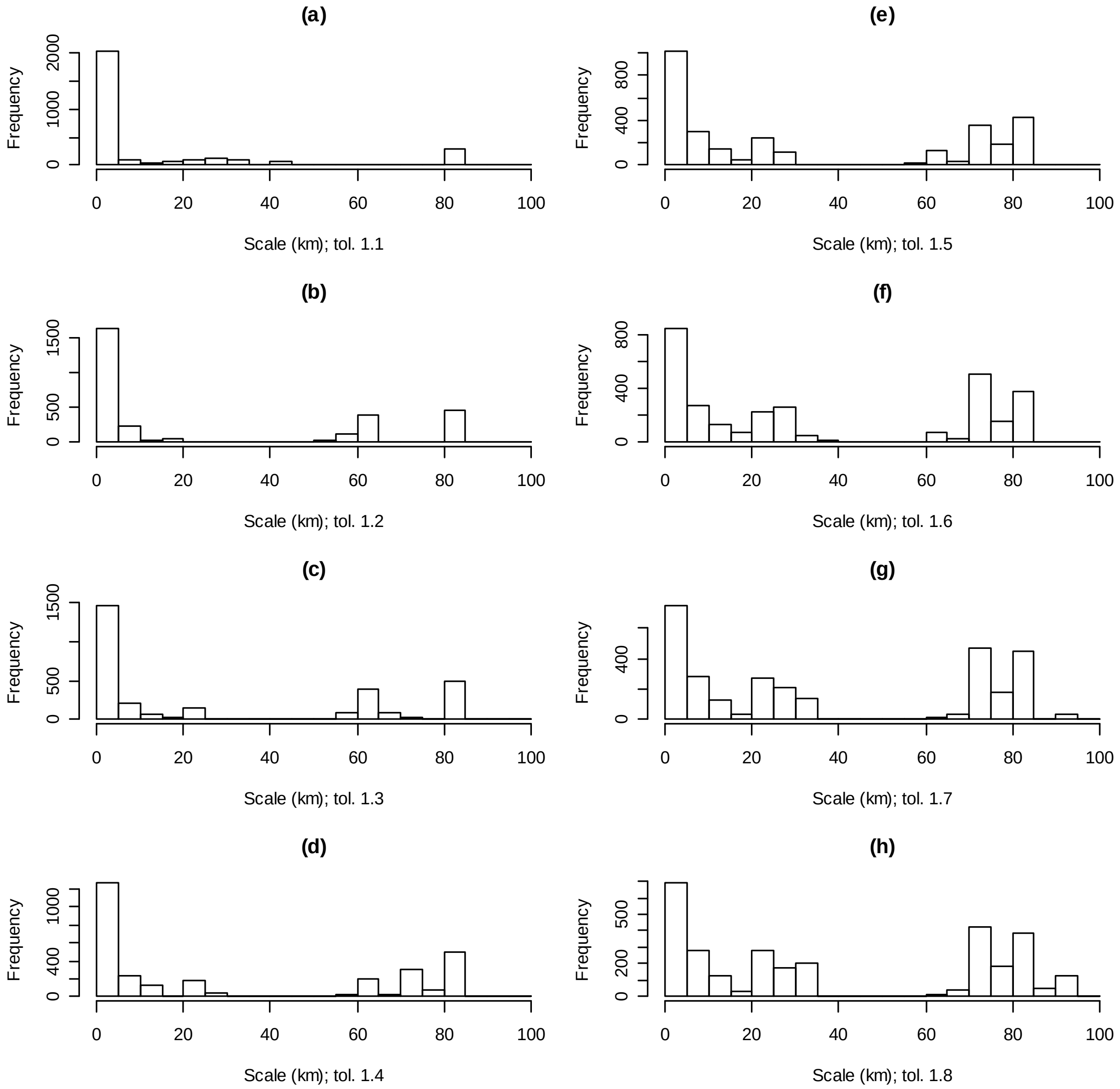


Fig. 5.4.Histograms (with regular bins) showing the effect of different tolerance levels on the scale (DRS) values calculated for the Cape gannet sample track illustrated in Fig. 5.2.

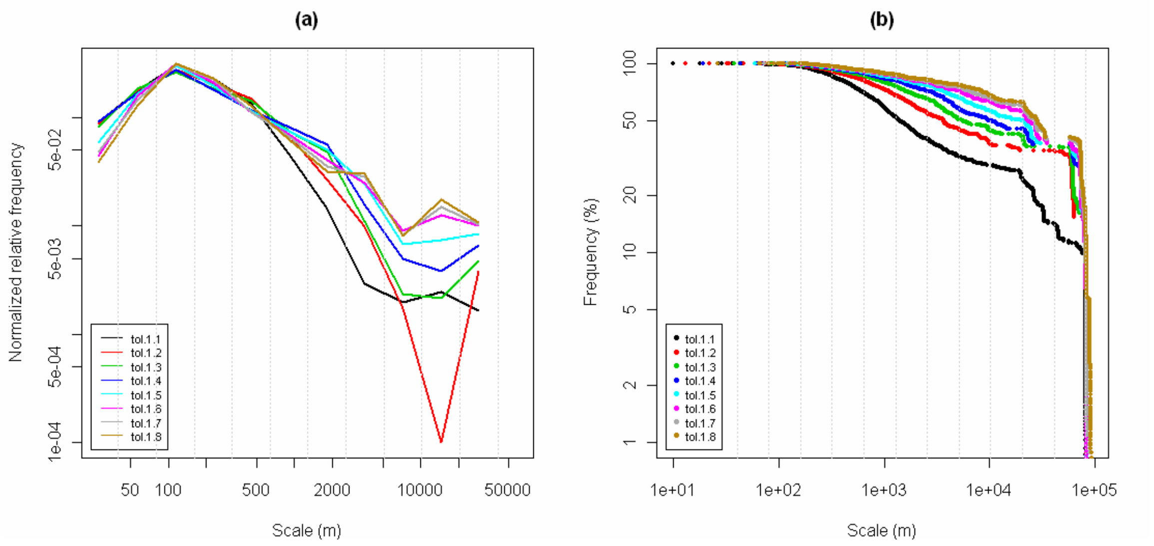


Fig. 5.5. Effect of different tolerance levels on the scale (DRS) values calculated for the Cape gannet sample track illustrated in Fig. 5.2. (a) Log-binning with normalization (LBN), the points along the x-axis have been plotted on the geometric mean of the respective bin (vertical lines). (b) Rank-frequency distribution plot for the same DRS values.

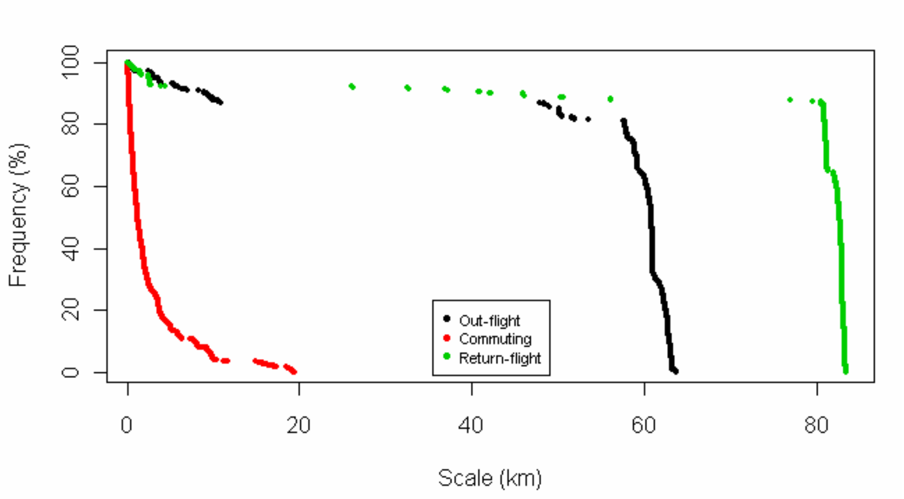


Fig. 5.6. Rank-frequency plot of DRS for tolerance 1.2 for the three main flight categories for the Cape gannet sample track illustrated in Fig. 5.2.

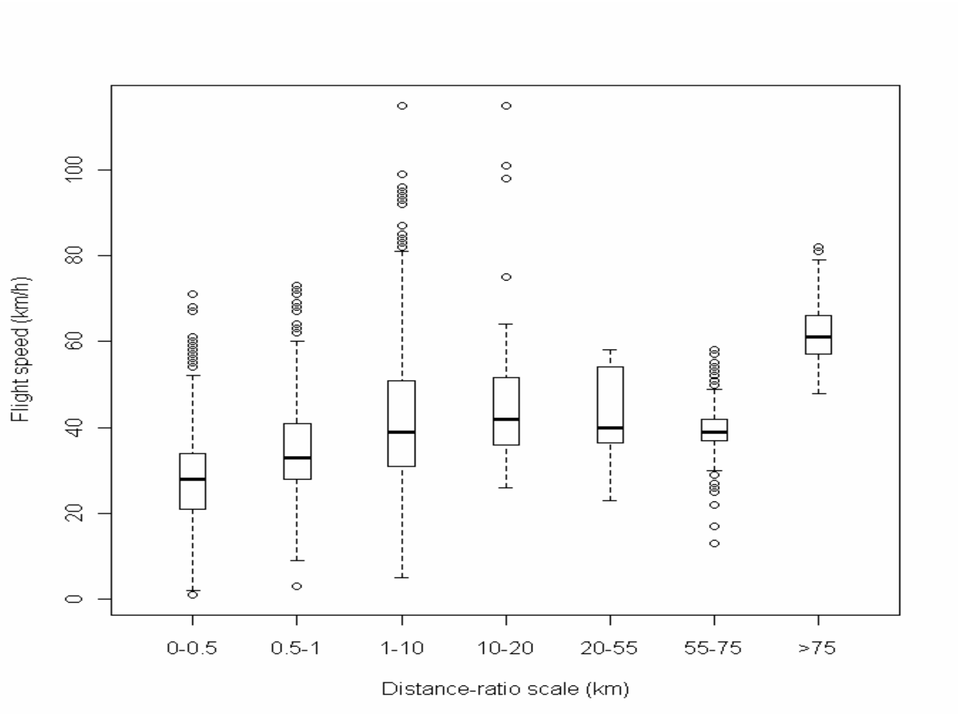


Fig. 5.7. Cape gannet. Box-and-whisker plot of the smoothed speed between successive points in relation to the DRS with tolerance = 1.2 for the sample track (see Fig. 5.2).

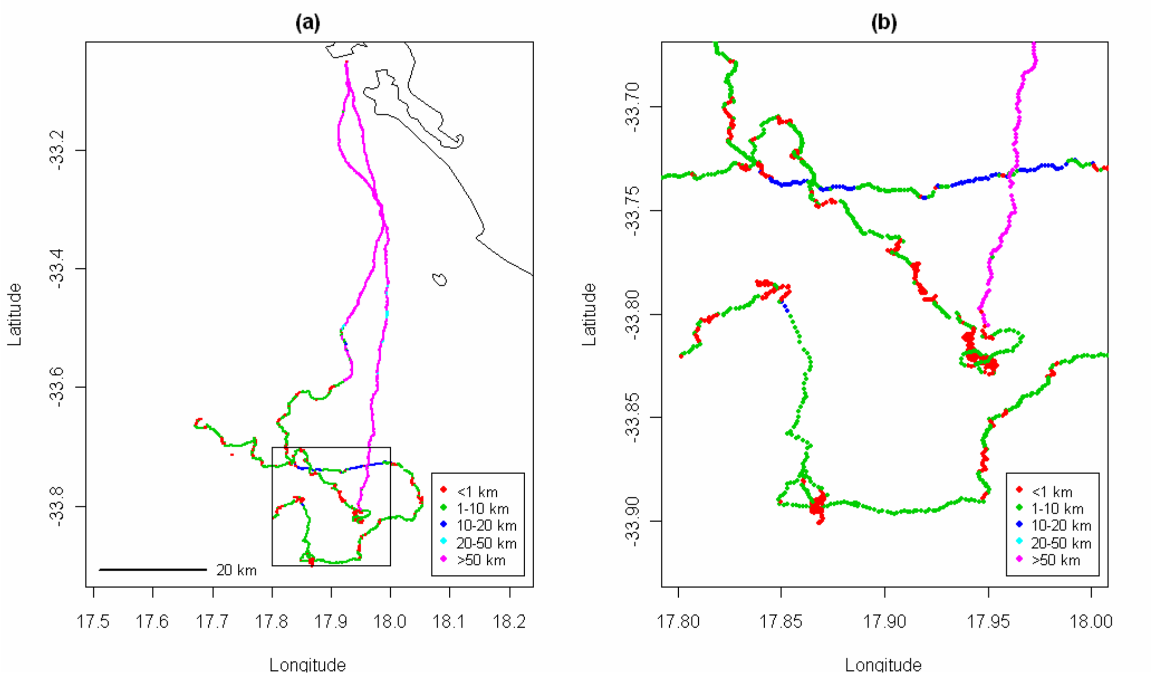


Fig. 5.8. Sample track of Cape gannet in which the drifting/swimming have been omitted, compare with Fig. 5.2. The distance-ratio scale (DRS) calculated for tolerance 1.2 have been colour-coded in five arbitrary intervals: (a) flying parts of the full track, the box indicates the approximate area enlarged in (b). Fine scale values (DRS < 1 km) are considered indicative of zones of ARS behaviour.

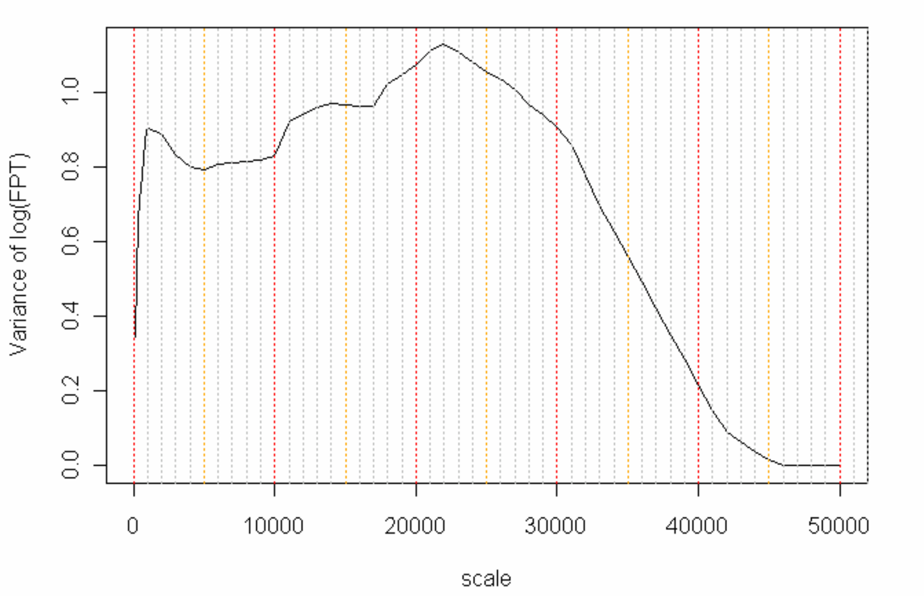


Fig. 5.9. Plot of the variance of log(FPT) in relation to spatial scale for the Cape gannet sample track illustrated in Fig. 5.2.

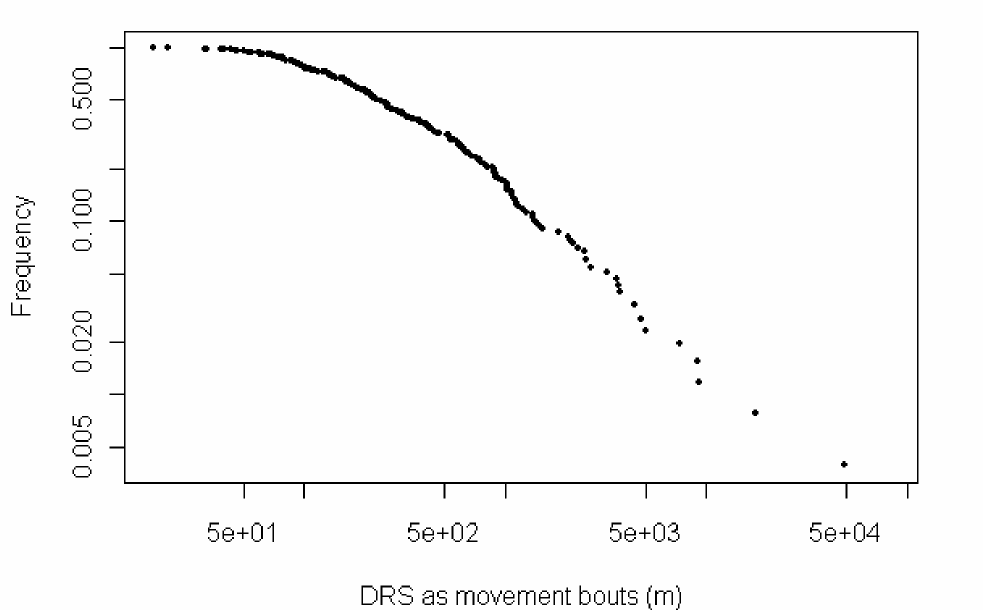
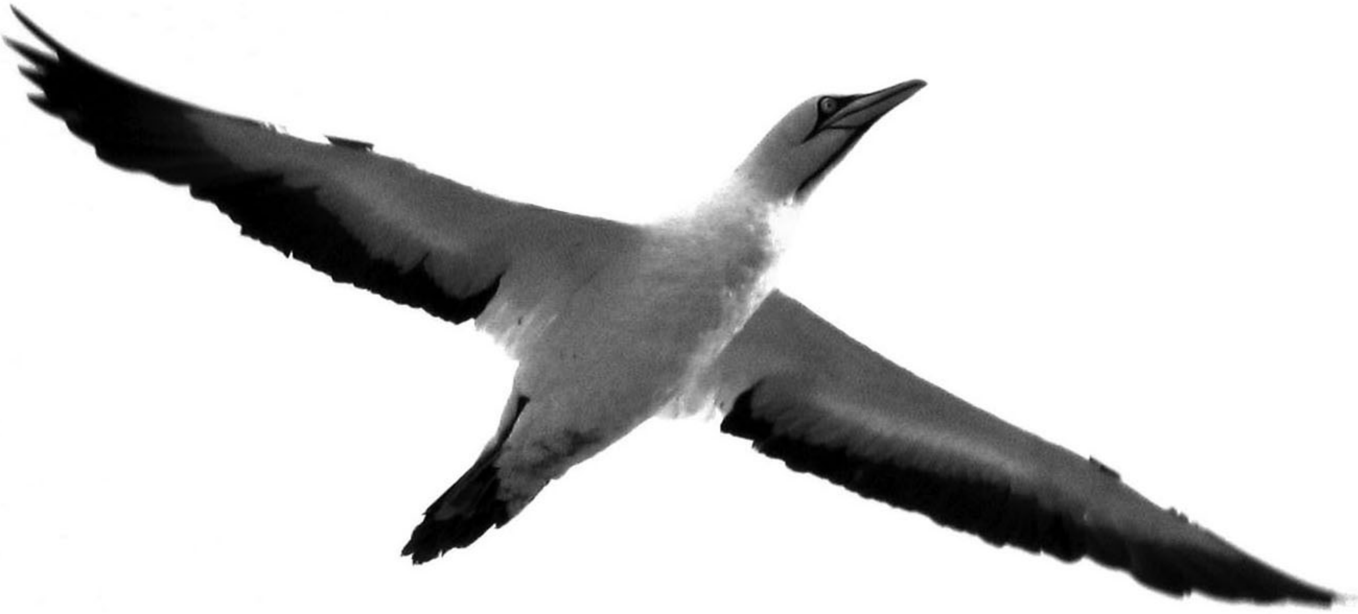


Fig. 5.10. Rank-frequency plot of Cape gannet step-sizes obtained from a modification to the DRS algorithm to give movement bouts, i.e. straight line segments obtained with tolerance = 1.2 for sample track.

# CHAPTER 6



## CHAPTER 6

# UNPREDICTABLE RESOURCES AND FORAGING STRATEGIES IN CAPE GANNETS

## Abstract

Marine pelagic predators preying on shoaling fish can only have a limited knowledge of the actual spatial prey distribution. In a hierarchical system where high-density, small-scale patches are nested within low-density, large-scale patches, a forager should track the spatial distribution of prey toward the small-scale end of the system. Under these circumstances a predator would maximize the rate of patch/prey encounter by using area restricted search (ARS) behaviour. Here I used GPS loggers to obtain fine-scale movement data of foraging Cape gannets *Morus capensis* at two colonies in the Benguela Upwelling System. These data combined with distance-ratio scale (DRS) analysis allowed me to examine the foraging strategy of gannets to test the following hypotheses: (i) that birds adopt a foraging strategy characterized by ARS behaviour; (ii) that most foraging takes place within ARS zones; (iii) that birds experience a higher spatio-temporal patchiness within breeding seasons than between breeding seasons; and (iv) the foraging strategy is a specific character that shows little variability. All 547 complete tracks examined exhibited a large component of fine-scale movement (DRS < 1 000 m represented over 94% of the normalized frequencies), which was equated to ARS behaviour. 77.4% of fishing (plunge-dives) occurred within ARS zones, 21.9% took place at coarse-scale and 0.7% at mesoscale. Spatio-temporal distribution of ARS zones had an overall between seasons similarity of 66.9% ± 9.9 ($n = 7$), significantly higher than the intra-seasonal similarity (39.4% ± 11.2, $n = 72$, $p < 0.001$). The DRS of each track was summarized using log-binning with normalization (LBN); correspondence analysis of the LBN matrix revealed no structure attributable to island, track type or seasonality, confirming the hypothesis that Cape gannets foraging strategy is a fixed trait.

# Introduction

It has been generally assumed that the extreme life history characteristics of pelagic seabird such as low fecundity and slow chick growth have evolved as adaptations to unpredictable and patchy distribution of food resources in the ocean (Lack 1968, Ashmole 1971). During the breeding season, when seabirds become central place foragers, this variability further exacerbates the challenges seabirds face; they have to make frequent trips between their breeding colonies and the foraging areas in order to brood and feed their offspring. The marine environment inhabited by seabirds is dynamic and heterogeneous, and this heterogeneity arises from a variety of scale-physical processes (Stommel 1963).

The largest scale processes, of the order of thousands of kilometers, consist of ocean basin circulation. On scales of order 100–1 000 km are shelf edge currents and most ocean currents. Processes operating on a scale of 1–100 km include events such as eddies, frontal zones and plume upwelling. Fine scale processes (1–1 000 m) include vortices and wind-driven Langmuir cells (Haury *et al.* 1978, Hunt & Schneider 1987). Coupled to this spatial heterogeneity, the environment is also characterized by a temporal dynamic, with events lasting from minutes or hours (for example vortices) to centuries or millennia (ice-age variations), with all the levels in between. Predictability of food resources is time-scale dependent: it appears to be high at mesoscales, but on decreasing spatial and temporal scales resources become increasingly less predictable (Hunt & Schneider 1987). Moreover, fine-scale patches are nested within patches occurring at broader scales in a dynamic hierarchy (Kotliar & Wiens 1990, Fauchald 1999).

The search strategy of a predator when prey has a random distribution in both space and time is crucial for successful foraging (Ford 1983, Stephens & Krebs 1986, Arditi & Dacorogna 1988, Grünbaum 1998). A seabird preying on shoaling fish, which equates to tracking a stochastic prey system, can only have a limited knowledge of the actual spatial prey distribution. In a hierarchical system where high-density, small-scale patches are nested within low-density, large-scale patches, a forager should track the spatial distribution of prey toward the small-scale end of the system (Fauchald 1999). A predator under these circumstances should travel long distances using a directed, low turning path, until a suitable patch is encountered. Once such a patch in found, it should start a fine-scale search, describing a path with high turning rate, covering smaller distances at a reduced speed to maximize prey encounter rate (Fauchald 2009). This behaviour, known as area restricted search (ARS) in the biological literature, corresponds to a biased random walk (Grünbaum 1998). Therefore, the foraging path of a seabird should exhibit a predominance of fine-scale movement, with larger scale movements restricted to searching for medium-scale patches, or to move quickly between patches.

Wiens (1976) considered patches to be defined as areas with discontinuities in environmental character states in relation to their surroundings. An implication of this definition is that such discontinuities have biological significance and that they matter to the organisms. Moreover, perceptions of patch elements and scale should be determined by natural selection and ultimately organisms should respond to those properties that produce fitness differentials. In view of the inherent difficulties in measuring fitness differentials, Wiens (1976) gave the following operational alternative: that the patchiness of the environment could be assessed by the non-random distribution of activity by organisms making use of such patches. In other words, patches can be defined from the consumers' point of view and may be very different from the traditional understanding of the concept (Arditi & Dacorogna 1988).

In this study I used GPS loggers to investigate the foraging behaviour of Cape gannets *Morus capensis* to assess the scale of movement and the predictability of food resources at different spatial and temporal scales in two different colonies: Malgas Island in South Africa and Ichaboe

Island in Namibia. I tested four hypotheses: (i) that birds adopt a foraging strategy characterized by ARS behaviour; (ii) that most foraging takes place within ARS zones; (iii) that birds experience a higher spatio-temporal patchiness within breeding seasons than between breeding seasons; and (iv) that the foraging strategy is a specific character that shows little variability.

## Methods

Data for Malgas Island, South Africa (33º03' S, 17º55' E) were collected during three breeding seasons: 2003/04, 2004/05 and 2005/06. In first two seasons I did field work on a two-week cycle, one week on, one week off, from October to February each field season. Data for the last season was collected by R.H. Mullers. Data for Ichaboe Island, Namibia (26º17' S, 14º56' E) were collected by R.H. Mullers for the seasons 2004/05 and 2005/06. Both fieldworkers followed the same protocol, which is described below.

### Foraging flight-tracks

Cape gannets were fitted with GPS-data loggers (Technosmart, Rome) set to record a geographic fix every 10 seconds. The loggers were sealed in two polyethylene bags, and attached to the birds with waterproof tape (Tesa®-tape manufactured by Beiersdorf AG, Hamburg), which does not damage the feathers (Grémillet *et al.* 2004). The logger was positioned on the upper side of the central tail feathers, partly covering the lower rump (Fig. 6.1). The whole package measured about 80×50×10 mm and weighed about 50 g (*c.* 2% of the adult body mass).

Only birds feeding chicks were fitted with loggers, attempting to cover the whole range of chick ages, from hatchings to fully-grown chicks. I waited for gannets returning from a foraging trip; after the nest relief ceremony was over I caught the partner leaving the nest, thus ensuring that the chick remained attended by the arriving partner. The bird was caught with a hocked pole, measured (length of the flattened wing chord to the nearest mm and bill length to the nearest 0.1 mm) and weighed (to the nearest 25 g). The logger was attached as described above and the bird released on the periphery of the colony, the procedure taking about five minutes. Previous studies using similar devices and handling of the birds had no obvious adverse effects on Cape gannet behaviour (Grémillet *et al.* 2004, Lewis *et al.* 2006). The nests of tagged birds were monitored every hour during daytime. When the tagged bird returned it was recaptured and the logger removed; the birds was then released at the nest site, settling readily. Chicks were captured, weighed (chicks weighing less than 1 kg to the nearest 5 g; those greater than 1 kg to the nearest 25 g) and measured (bill length to the nearest 0.1 mm and flattened wing-chord length to the nearest mm).

### Analysis of GPS tracks

Tracks were analysed according to the methods described in Chapter 5. Briefly, tracks were trimmed and projected to obtain coordinates in meters; using the behavioural algorithm each fix in the track was classified in one of the following: (1) out-flight; (2) fishing; (3) commuting/searching; (4) drifting; (5) return-flight. Then, for each track, and each fix in the track, the distance-ratio scale (DRS) was calculated for tolerance 1.2.

### Data analysis

I used log-binning with normalization (LBN) method to summarize the structure of each track. LBN involves setting the bin breaks such that each bin is twice the width of the preceding bin (Edwards 2008). The starting value of the series was set at 20 m, assumed as the minimum distance that a gannet could cover, allowing for some turnings, in the 10-second interval between consecutive fixes; 13 bins were required to include the full range of scale values. The count in each bin was then divided by the width of that bin to get a count per unit interval (Newman 2005). The LBN matrix thus generated was analysed using correspondence analysis.

I equate ARS zones with fine-scale movement, i.e. fixes with DRS < 1 000 m. The fine-scale fixes were extracted from both complete and incomplete tracks; these were used to estimate Kernel densities in a 0.05 × 0.05° grid (about 5.55 × 4.70 km). Similarity or overlap in density distribution was evaluated with Morisita's index as modified by Horn (Ricklefs & Lau 1980), which varies between 0 (no overlap) and 1 (complete overlap). The similarity matrices thus obtained were converted into distance matrices by taking the 1 complement of the similarity values; this was necessary for the hierarchical cluster analyses used to represent the matrices in graphical form by means of dendrograms. Mean and standard deviation of similarity between seasons, or between periods within season were obtained by calculating Morisita;s index between all possible pairs; the sample size corresponds to $(s^2 - s)/2$, where $s$ is the number of seasons or periods, i.e. four seasons give a sample size of six.

Most computations and graphics were done using program R (2.10.0, Windows version) (R Development Core Team 2009). The R-function *CA* in package *FactoMineR* was used for correspondence analysis; the R-function *kde2d* in package *MASS* of Venables & Ripley (2002) was used to estimate Kernel densities; and the R-function *hclust* was used for hierarchical cluster analysis. Initial data processing was done with scripts written in QuickBasic, Perl and FORTRAN. Means are given ± 1 standard deviation.

## Results

### Foraging trips

A total of 656 tracks were obtained from logger deployments made on 637 birds; 19 deployments recorded two consecutive tracks, which were analysed separately. 17 tracks (2.6%) were excluded from analysis because the bird did not go in a foraging trip. Of the 639 usable tracks, 547 (85.6%) were complete tracks; 205 were from Ichaboe Island of which 188 (91.7%) were complete, and 434 from Malgas Island of which 359 (82.1%) were complete. During a foraging trip birds often spent a night at sea: 80% of tracks involved one or more nights at sea (85% and 77% for Ichaboe and Malgas Islands respectively).

Gannets leaving the colony in a foraging trip flew in a chosen direction and headed directly to the prospective foraging area. When a foraging patch was found during the outgoing phase of the trip, the bird typically searched within a radius of 10 km or less, returning (usually on the same day) to the colony in a path very close to the outgoing one (Fig. 6.1a). This type of foraging trip is termed “commuting” by Weimerskirch (1997). Alternatively, birds searched a wider area, often spent a night at sea, and returned to the colony in a path with a bearing very different to the outgoing one (Fig. 6.1b). This corresponds to the “looping” type of foraging trip of Weimerskirch (1997). Most complete trips were loop shaped (72% and 77% for Ichaboe and Malgas Islands respectively), and the remaining were commuting type. The proportions of looping and commuting trips were not significantly different between the two islands ($p = 0.21$, Fisher’s exact test). Cape gannets used significantly more of the looping type of tracks during overnight trips (79%) than during day trips (60%; $p < 0.001$, Fisher’s exact test).

Table 6.1 gives a summary of the basic parameters calculated from the foraging tracks by the behavioural algorithm. Mullers & Navarro (2010) gave a full account of these parameters in relation to sex, diet, chick-growth and colony and this will not be repeated here. On average birds from Ichaboe Island flew for a significantly longer time, covered a larger distance and did so at slower speeds than birds from Malgas Island. However this was an effect of the search component of the flight because there were no significant differences in the outgoing flight (excepting for speed) and return flight between the two islands. Time spent drifting was similar for both islands (Table 6.1).

### Distance-ratio scale (DRS)

DRS values across all tracks were summarized in Fig. 6.2 using a log-binning method (LBN) and the frequencies were normalized according to the bin width. The largest normalized frequency was for the 161–320 m bin. DRS values <1 280 m are the dominant feature with at least 95% of the normalized frequencies within this bin. As the DRS values increased the frequency of movements in these bins decreased steadily to less than 1% for DRS values in the mesoscale bin (100–1 000 km).

The structure of the matrix of LBN normalized frequencies for complete tracks was investigated using correspondence analysis. The first four dimensions accounted for 76.8% of the variance (Fig. 6.3). The tracks form a single group, with some points dispersing away from the core grouping, corresponding to tracks with higher than average frequencies for particular LBNs. The scores were examined with regard to island, duration, type, and season, but no structure was evident in any of these (only island classification is illustrated in Fig. 6.3).

### Spatial scale of movement

As the distance-ratio method calculated a DRS value for each fix in a track, it is possible to partition the track into the following scales (after Haury *et al.* 1978): fine-scale (1–1000 m); coarse-scale (1–100 km); and mesoscale (100–1 000 km).

**Fine-scale:** This was the dominant scale of movement, representing over 94% of the normalized frequencies. The birds from Ichaboe Island spent significantly more time, covered more distance, performed more dives and flew at slower speeds than birds from Malgas Island; Ichaboe Island birds also had a larger frequency of fixes at this scale than Malgas Island birds (Table 6.2).

**Coarse-scale:** This was the second most used scale of movement; its parameters followed the same pattern as for fine-scale, except that Ichaboe Island birds had a smaller frequency of fixes in this ambit than Malgas Island birds (Table 6.2).

**Mesoscale:** the least used scale of movement; the birds from Ichaboe Island spent significantly more time, covered more distance, performed more dives and flew at slower speeds than birds from Malgas Island; there was no significant difference in the normalized frequency of fixes in this ambit between the two islands (Table 6.2).

Flying speed was significantly different among the three scales of movement ($F_{2,1638} = 1332$, $p < 0.001$); it was slowest at fine-scale

(33.4 ± 7.2 km $h^{-1}$), intermediate at coarse-scale (45.0 ± 5.5 km $h^{-1}$), and fastest at mesoscale (52.2 ± 5.5 km $h^{-1}$). The same patterns were observed for distances covered at the different scales ($F_{2,1638} = 652$, $p < 0.001$): it was least at fine-scale (62 ± 46 km), intermediate at coarse-scale (88 ± 56 km), and largest at mesoscale (249 ± 143 km). The times spent at the different scales were significantly different ($F_{2,1638} = 368$, $p < 0.001$): longer at mesoscale (4.8 ± 2.7 h), that at fine-scale (2.0 ± 1.5 h) and coarse-scale (2.0 ± 1.3 h).

Fishing activity (plunge-dives) identified by the behavioural algorithm, occurred with the highest frequency at the fine-scale (77.4%), followed by coarse-scale (21.9%), and was infrequent at mesoscale (0.6%). The median DRS of fishing was 251 m (quantile range: 84–834 m). The frequency of plunge-dives per track was significantly larger for Ichaboe Island birds than for Malgas Island birds at the three scales of movement (Table 6.2).

### Time-space analysis of fine-scale movement

Variability between breeding seasons in the distribution of fine-scale movement, i.e. fixes with DRS < 1 000 m, is shown in Fig. 6.4. The kernel density distribution showed overlap breeding seasons at both colonies (Table 6.3). For Malgas Island the mean similarity between seasons was 69.1% ± 7.7 ($n = 6$). For Ichaboe Island the similarity between the two seasons was 50.8%.

Variability within breeding seasons in the distribution of fine-scale movement is shown in Figs 6.5–6.7 for Malgas Island, and in Figs 6.8 and 6.9 for Ichaboe Island. There was variability in the spatial and temporal distribution of fine-scale movement for all seasons and both islands. At Malgas Island the mean intra-season similarity was 39.4% ± 13.8 ($n = 21$, season 2003/2004); 38.2% ± 10.5 ($n = 15$, season 2004/2005); 34.2% for the two periods in season 2005/06; and 34.4% ± 13.4 ($n = 10$, season 2006/2007). In contrast, at Ichaboe Island mean intra-season similarity was 44.6% ± 5.9 ($n = 6$, season 2004/2005); and 38.8% ± 13.6 ($n = 10$, season 2004/2005). Overall between seasons ARS similarity was

66.9% ± 9.9 ($n = 7$), whereas overall intra-seasonal similarity was 39.4% ± 11.2 ($n = 72$). A mixed effects model revealed significant differences between inter- versus intra-seasonal similarity ($p < 0.001$), but not between periods within seasons ($p = 0.34$), or between the two islands ($p = 0.50$); the model accounted for 39% of the variance in ARS similarity.

## Discussion

This study finds significant differences in the basic parameters of the foraging tracks (distance, duration and flight speed) and in their components (out-, return- and search-flight), for Cape gannets between Ichaboe and Malgas Islands (Table 6.1). This difference is related to poorer feeding conditions experienced by Ichaboe Island birds (Mullers & Navarro 2010). Tracks from Malgas Island showed significant differences between seasons in some of the foraging parameters examined by Mullers & Navarro (2010) working with the same set of tracks used in the present analysis. However, despite such differences, the search strategies revealed by DRS analysis were indistinguishable between the birds from the two colonies (Fig. 6.3).  Similarly, no differences in search strategy were found in relation to seasonality, track type, duration or foraging range. This is consistent with the conservative search strategy reported for northern gannets *Morus bassanus* (Hamer *et al.* 2009) and for petrels and albatrosses (Pinaud & Weimerskich 2007). Fauchald (1999) suggested that marine pelagic predators employ a hierarchical nested search strategy. The fact that ARS areas are nested within areas of higher DRS values provided empirical evidence in support of this hypothesis.

The results of this study confirmed the hypothesis that Cape gannets use an area-restricted search (ARS) strategy to track a highly dynamic patch system. At the largest scale used by Cape gannets, i.e. mesoscale, the birds made almost linear displacements of more than 100 km, particularly when moving to and from the colony and between foraging grounds. The upper end of the coarse scale was also used for commuting between colony and foraging areas. During mesoscale displacements occasionally birds responded opportunistically and engaged in short ARS events nested within a scale of tens of kilometers. Once engaging into a search path the birds increased their turning rate and DRS dropped to the lower end of the coarse-scale. The search area was further reduced by moving in the fine-scale ambit, displaying typical ARS behaviour: high turning rate and low flying speed punctuated with active fishing behaviour (plunge dives). This strategy is a clear indication that Cape gannets adjust their searching pattern in a hierarchical manner to match the patchiness of the environment. Similar findings have been reported for murres *Uria* spp. (Fauchald *et al.* 2000), wandering albatrosses *Diomedea exulans* (Fritz *et al.* 2003), Antarctic petrel *Thalassoica antarctica* (Fauchald & Tveraa 2006), and for the northern gannet (Hamer *et al.* 2009), and no doubt it must be a widespread strategy among seabirds.

The non-random distribution of the ARS of Cape gannets provided a representation of the spatio-temporal patchiness of the shoaling fish prey in the area, *sensu* Wiens (1976). This study, based on a large sample of tracks gathered in the course of several breeding seasons at two colonies, confirmed the idea that seabirds experience a high turnover of foraging areas. This has been reported for the Antarctic petrel by Fauchald & Tveraa (2006). The predictability of a system is related to its spatio-temporal scale, the larger the scale the more predictable a given system becomes (Haury *et al.* 1977). As expected, the overall spatial and temporal variability of the patchiness experienced by Cape gannets was greater within breeding seasons than between breeding-seasons, as revealed by the overlap in the ARS; in fact, the distribution of ARS activity changed markedly in a matter of days.

It could be argued that the search pattern of individual birds probably leads to an underestimation of the spatial scale of their potential foraging area (Fauchald & Tveraa 2006), because it is unlikely that a predator can search through the entire potential feeding area before entering a patch at a smaller scale. This shortcoming is addressed in part by looking at the simultaneous foraging pattern of many birds. Also, Cape gannets are not solitary predators, but move in small groups that can increase the effective area searched through social facilitation. Foraging activity can attract neighboring birds that otherwise could have missed a patch in a solitary search, and this social facilitation is not limited to members of the same species. Duffy (1989) found that Cape gannets occurred in 45% of multi-species foraging flocks in the Benguela region, and that the number of Cape gannets in such flocks varied widely (98 ± 484, $n = 315$). Haney *et al.* (1992) using geometric relationships calculated theoretical upper (20–30 km) and lower (0.7–6.2 km) limits to horizontal distances over which volant seabirds can be visually recruited to join a feeding flocks in the open ocean. Empirical estimates for recruitment distances indicated that potential recruitment distances were closer to the lower theoretical limits, with a mean distance of 4.5 km. This social facilitation, in combination with the ARS behaviour reveals the patchiness, as experienced by the birds, of the environment at the fine- and coarse-scale levels.

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Table 6.1. Foraging trip parameters (mean ± 1 SD) derived from the behavioural algorithm (see methods) applied to all complete tracks of Cape gannets foraging from Ichaboe (Namibia) and Malgas (South Africa) Islands. Data for Malgas Island are for four breeding seasons (2003/2004 to 2006/2007) and for Ichaboe Island for two breeding seasons (2004/2005 and 2005/2006). Differences between means were tested with simple linear models; excepting number of dives, which was tested with a GLM (Poisson distribution). Significant *p*-values are shown in bold type.

| | Ichaboe Island | Malgas Island | *p* |
|---|---|---|---|
| No. complete tracks | 188 | 359 | |
| Total duration (h) | 26.8 ± 12.9 | 23.6 ± 12.9 | **< 0.001** |
| Total distance (km) | 483 ± 214 | 446 ± 273 | 0.069 |
| Overall speed (km $h^{-1}$) | 19.2 ± 5.2 | 20.9 ± 7.0 | **0.004** |
| Flight duration (h) | 10.3 ± 4.4 | 7.9 ± 4.4 | **< 0.001** |
| Flight distance (km) | 447 ± 199 | 376 ± 209 | **< 0.001** |
| Flight speed (km $h^{-1}$) | 43.1 ± 4.9 | 47.8 ± 5.5 | **< 0.001** |
| Out-flight duration (h) | 0.89 ± 0.80 | 0.81 ± 0.68 | 0.168 |
| Out-flight distance (km) | 42 ± 43 | 39 ± 32 | 0.232 |
| Out-flight speed (km $h^{-1}$) | 43.7 ± 11.1 | 48.2 ± 7.2 | **< 0.001** |
| Return-flight duration (h) | 1.5 ± 1.1 | 1.3 ± 1.2 | 0.072 |
| Return-flight distance (km) | 75 ± 52 | 76 ± 69 | 0.878 |
| Return-flight speed (km $h^{-1}$) | 49.1 ± 11.2 | 50.8 ± 15.6 | 0.174 |
| Search flight duration (h) | 7.7 ± 4.3 | 5.7 ± 4.0 | **< 0.001** |
| Search flight distance (km) | 328 ± 195 | 260 ± 178 | **< 0.001** |
| Search flight speed (km $h^{-1}$) | 41.9 ± 5.0 | 46.0 ± 6.7 | **< 0.001** |
| Drift duration (h) | 16.5 ± 9.4 | 15.6 ± 9.7 | 0.342 |
| Drift distance (km) | 37 ± 21 | 69 ± 74 | **< 0.001** |
| Drift speed (km $h^{-1}$) | 2.3 ± 0.6 | 4.3 ± 3.0 | **< 0.001** |
| Number of dives | 34 ± 21 | 17 ± 12 | **< 0.001** |

Table 6.2. Parameters (mean ± 1 SD) derived from DRS values according to scale per island for all complete foraging tracks of Cape gannets. Data for Malgas Island are for four breeding seasons (2003/2003 to 2006/2007) and for Ichaboe Island are for two breeding seasons (2004/2005 and 2005/2006). Differences between means were tested with simple linear models.

| | | Ichaboe Island | Malgas Island | *p* |
|---|---|---|---|---|
| Fine scale | time (h) | 2.6 ± 1.4 | 1.7 ± 1.5 | < 0.001 |
| | distance (km) | 74.8 ± 42.2 | 56.3 ± 47.4 | < 0.001 |
| | speed (km/h) | 29.1 ± 3.7 | 35.6 ± 7.5 | < 0.001 |
| | frequency * | 96.8 ± 2.2 | 94.4 ± 5.2 | < 0.001 |
| | Number of dives | 28.9 ± 19.2 | 13.6 ± 11.5 | < 0.001 |
| | % total dives | 81.4 | 73.9 | |
| Coarse scale | time (h) | 2.3 ± 1.3 | 1.8 ± 1.3 | < 0.001 |
| | distance (km) | 98 ± 56 | 83 ± 56 | < 0.01 |
| | speed (km/h) | 42.4 ± 4.1 | 46.4 ± 5.6 | < 0.001 |
| | frequency * | 2.8 ± 2.1 | 5.3 ± 5.2 | < 0.001 |
| | Number of dives | 6.2 ± 4.7 | 4.7 ± 4.1 | < 0.001 |
| | % total dives | 17.6 | 25.8 | |
| Meso scale | time (h) | 5.4 ± 2.8 | 4.4 ± 2.6 | < 0.001 |
| | distance (km) | 273 ± 144 | 235 ± 140 | < 0.01 |
| | speed (km/h) | 50.3 ± 5.7 | 53.2 ± 5.1 | < 0.001 |
| | frequency * | 0.43 ± 0.51 | 0.44 ± 0.61 | n.s. |
| | Number of dives | 0.4 ± 0.8 | 0.1 ± 0.3 | < 0.001 |
| | % total dives | 1.0 | 0.4 | |

* Frequencies have been normalized by dividing the count by the bin width and then standardized so that the frequencies add-up to 1 for a given track.

Table 6.3. Percentage of overlap in ARS-zones of Cape gannets between seasons for Ichaboe Island (above diagonal) and Malgas Island (below diagonal). Overlap was calculated from the Kernel densities using Morisita's index as modified by Horn (Ricklefs & Lau 1980).

| Season | 2003/2004 | 2004/2005 | 2005/2006 | 2006/2007 |
|---|---|---|---|---|
| 2003/2004 | — | | | |
| 2004/2005 | 63.5 | — | 50.8 | |
| 2005/2006 | 58.4 | 73.4 | — | |
| 2006/2007 | 66.9 | 80.2 | 72.4 | — |

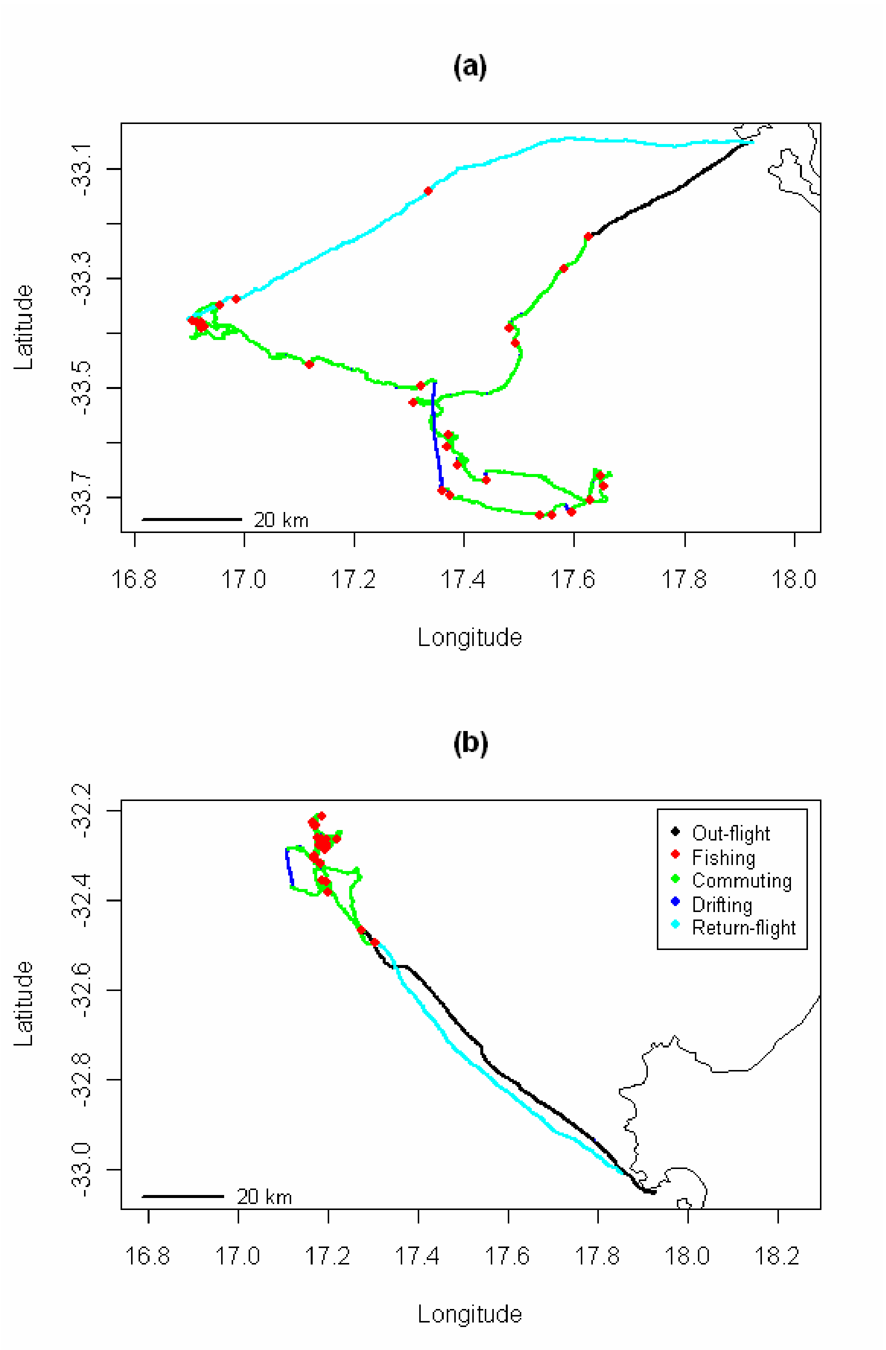

Fig. 6.1. Foraging trips of two Cape gannets from Malgas Island illustrating the two basic strategies of movement: (a) looping trip, where the bird returns to the colony in a direction different from the outward path; (b) commuting trip, where the bird follows a very similar path for both the outward and return phases (Weimerskirch 1997).

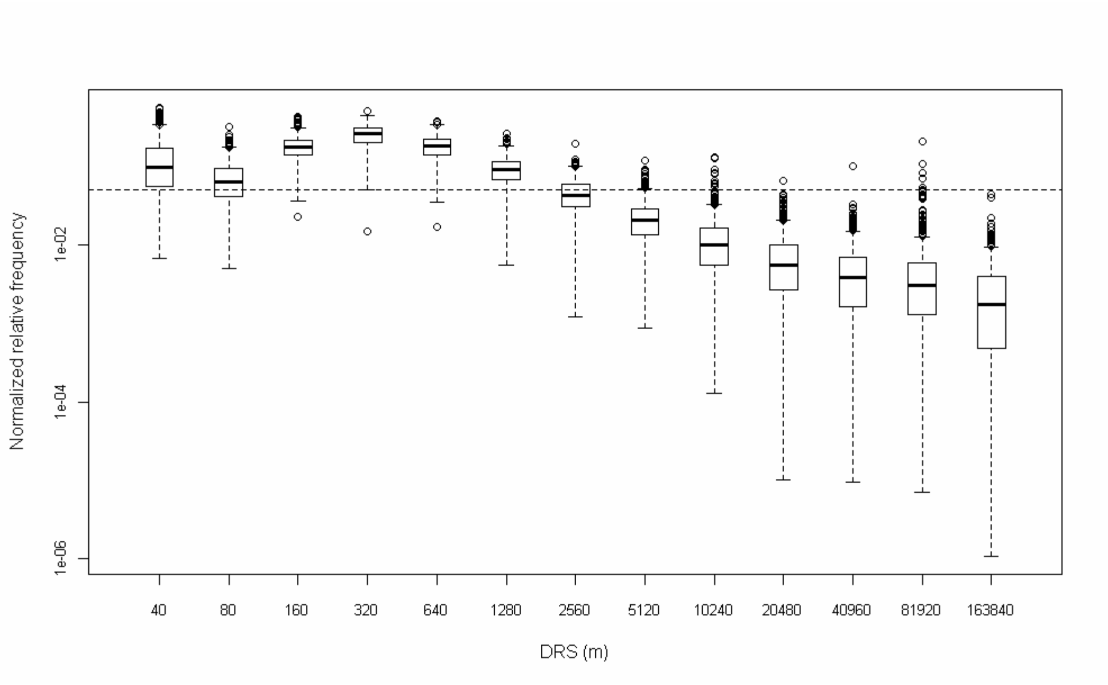

Fig. 6.2. Box-and-whisker plot of distance-ratio scale (DRS) values for Cape gannets across all complete foraging tracks (Malgas Island *n* = 359; Ichaboe Island *n* = 188), with a total number of 1 614 176 GPS fixes. The data has been plotted on the upper limit of the respective log-bin; the horizontal dotted-line represents 5%.

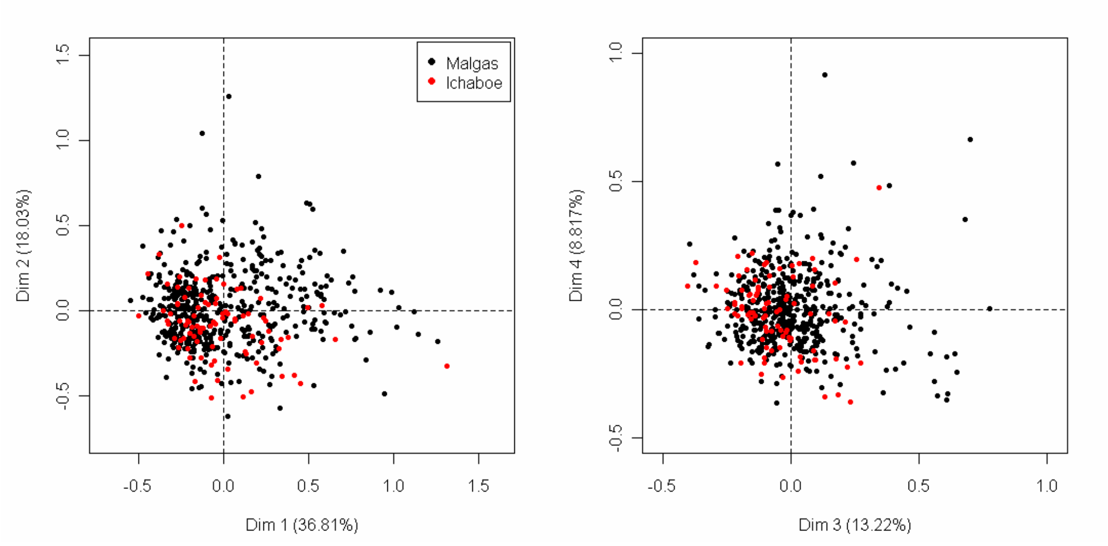

Fig 6.3. Correspondence analysis of the log-binning normalized frequency matrix of DRS for all complete tracks of Cape gannets from Malgas and Ichaboe Islands.

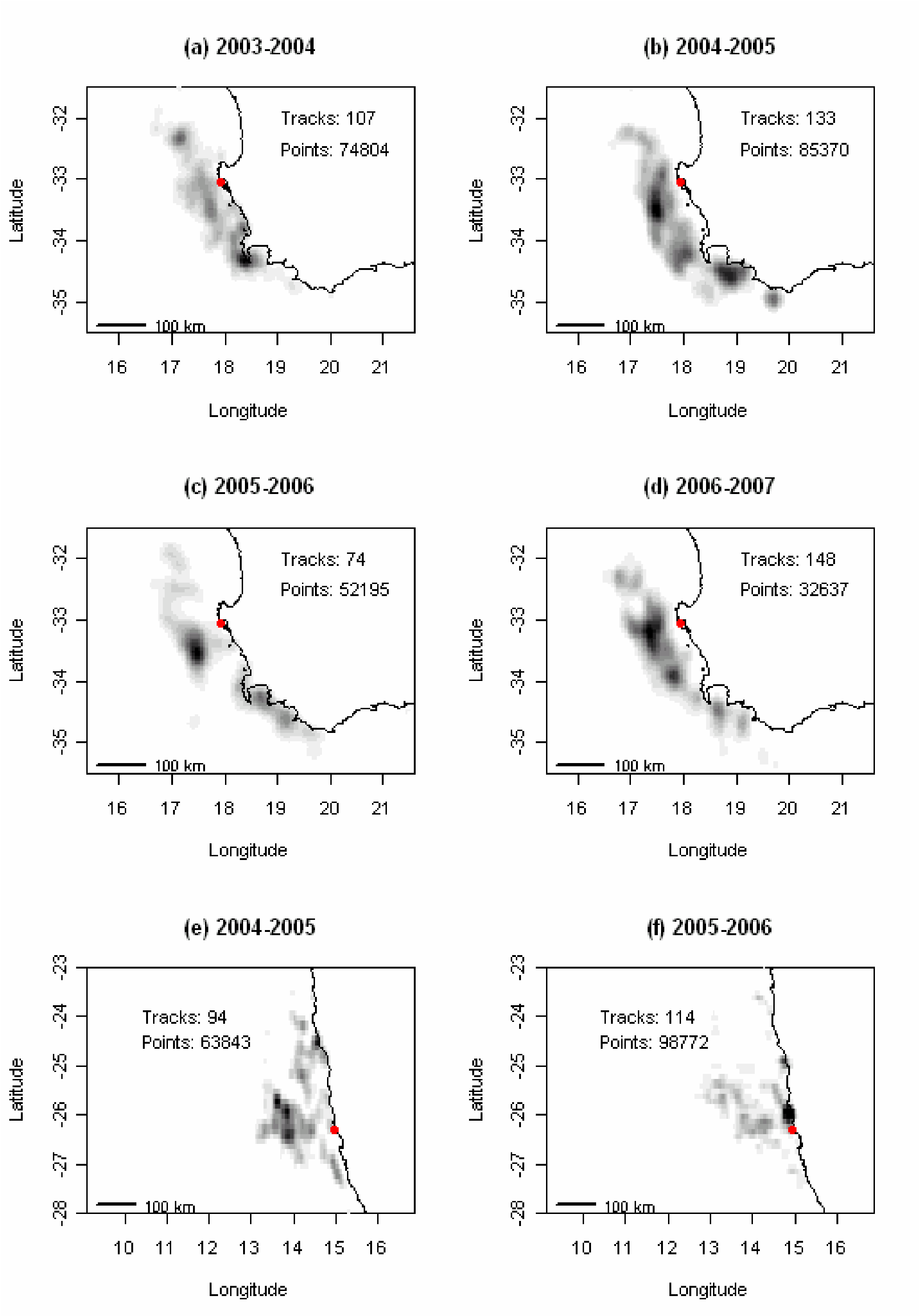

Fig. 6.4. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Malgas Island (a-d) and Ichaboe Island (e & f) during different breeding seasons. Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of the respective island.

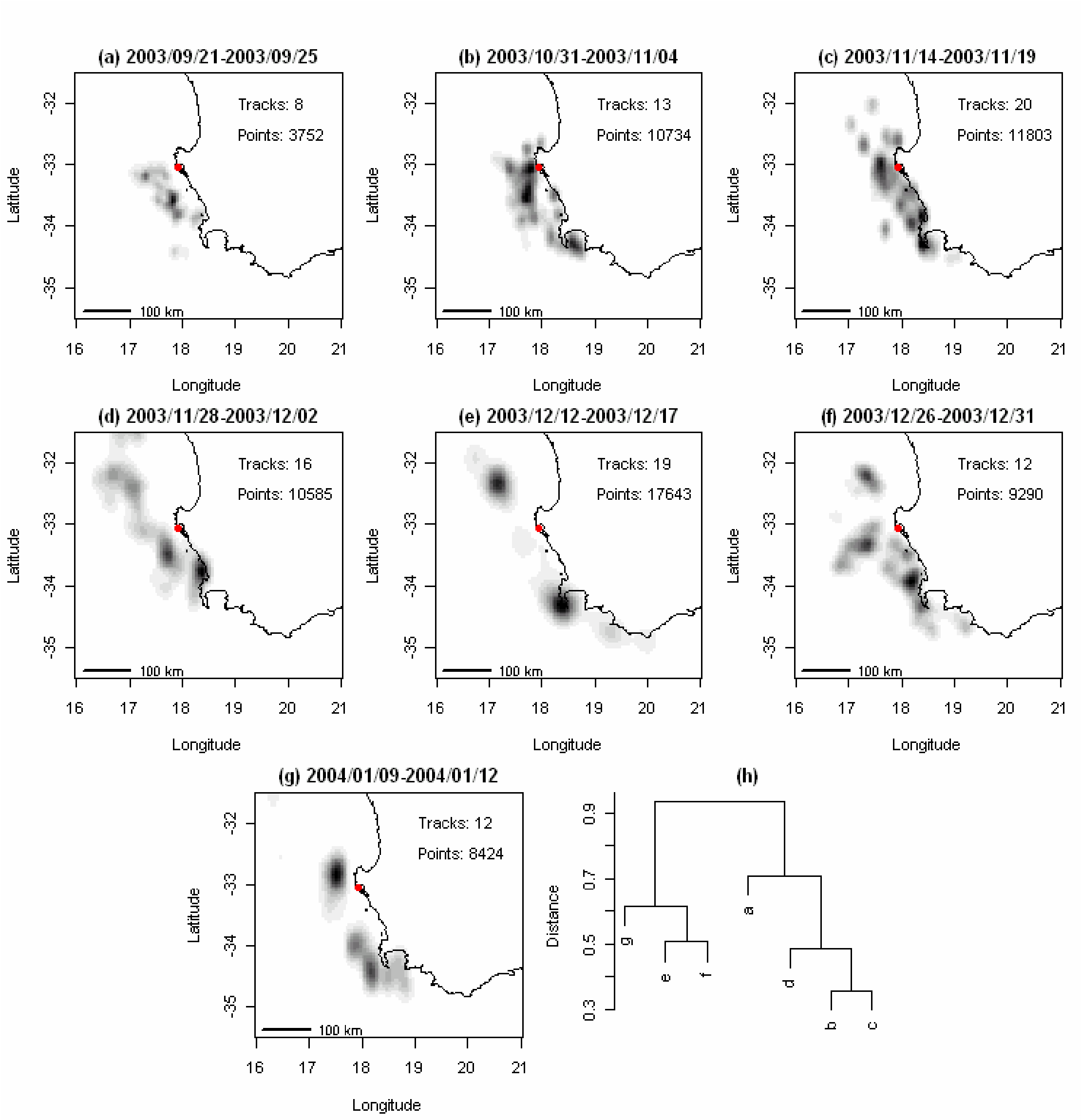

Fig. 6.5. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Malgas Island during different periods within the 2003/2004 breeding season (a–g). Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of Malgas Island. The dendrogram (h) summarizes the distances and clustering of the periods.

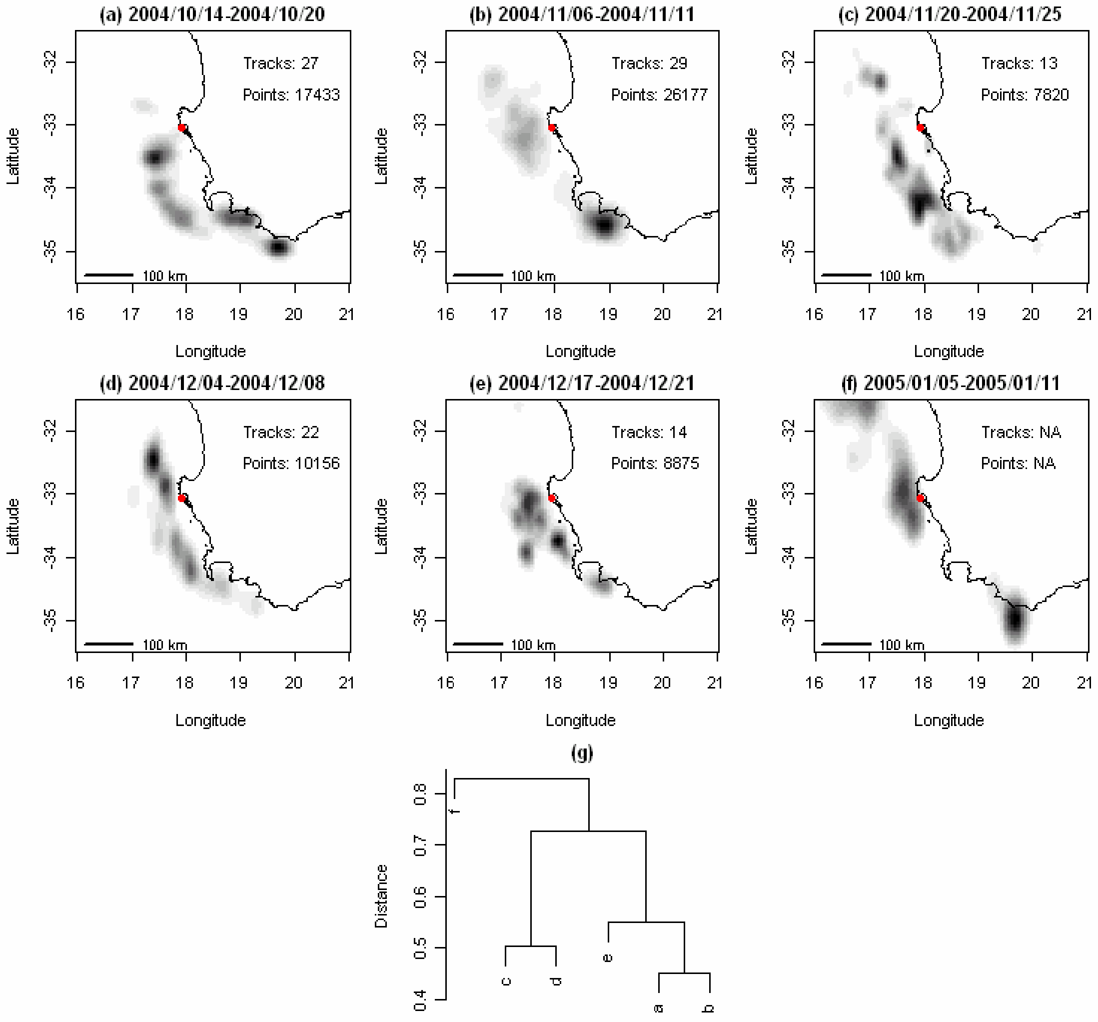

Fig. 6.6. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Malgas Island during different periods within the 2004/2005 breeding season (a–f). Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of Malgas Island. The dendrogram (g) summarizes the distances and clustering of the periods.

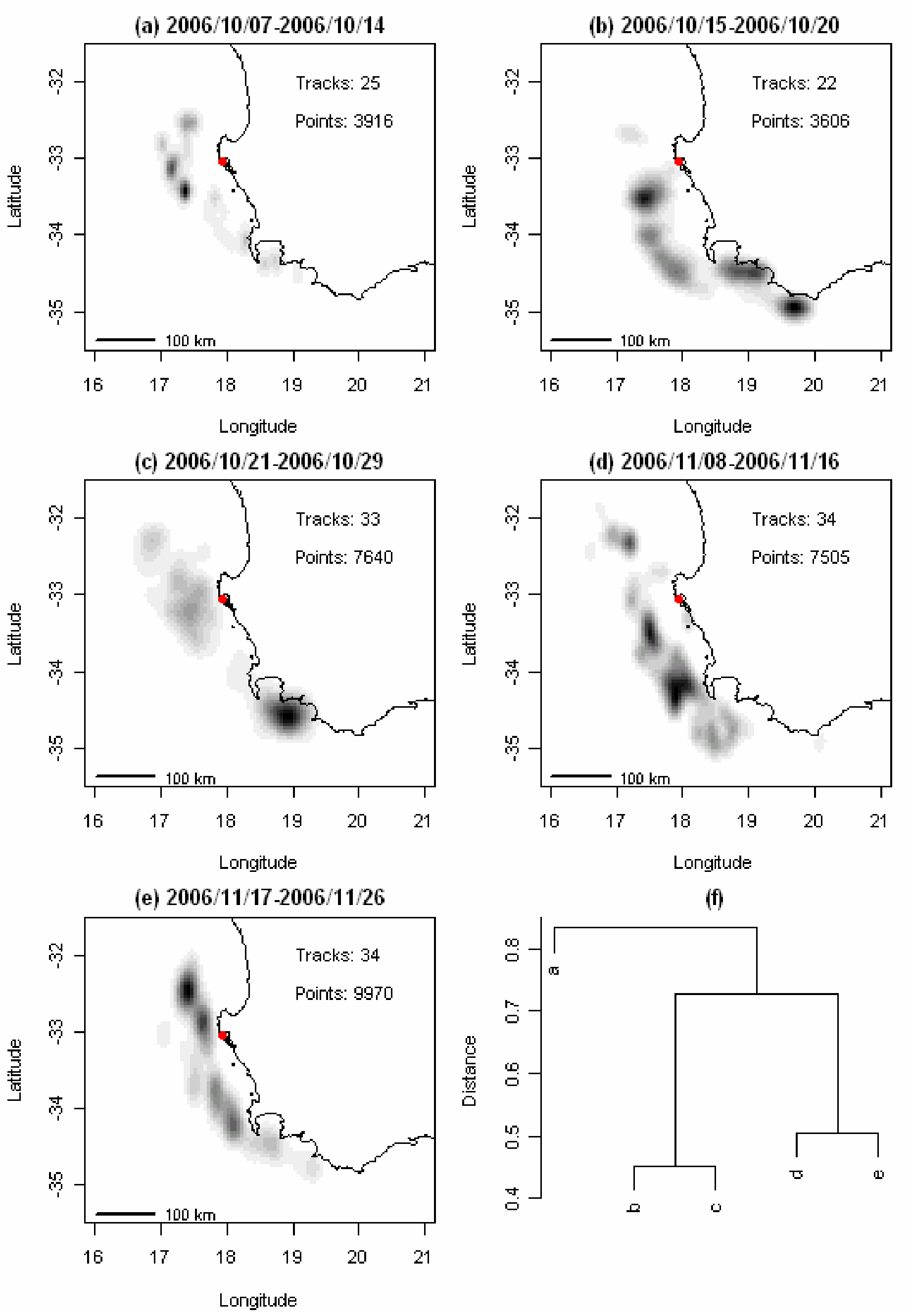

Fig. 6.7. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Malgas Island during different periods within the 2006/2007 breeding season (a–e). Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of Malgas Island. The dendrogram (f) summarizes the distances and clustering of the periods.

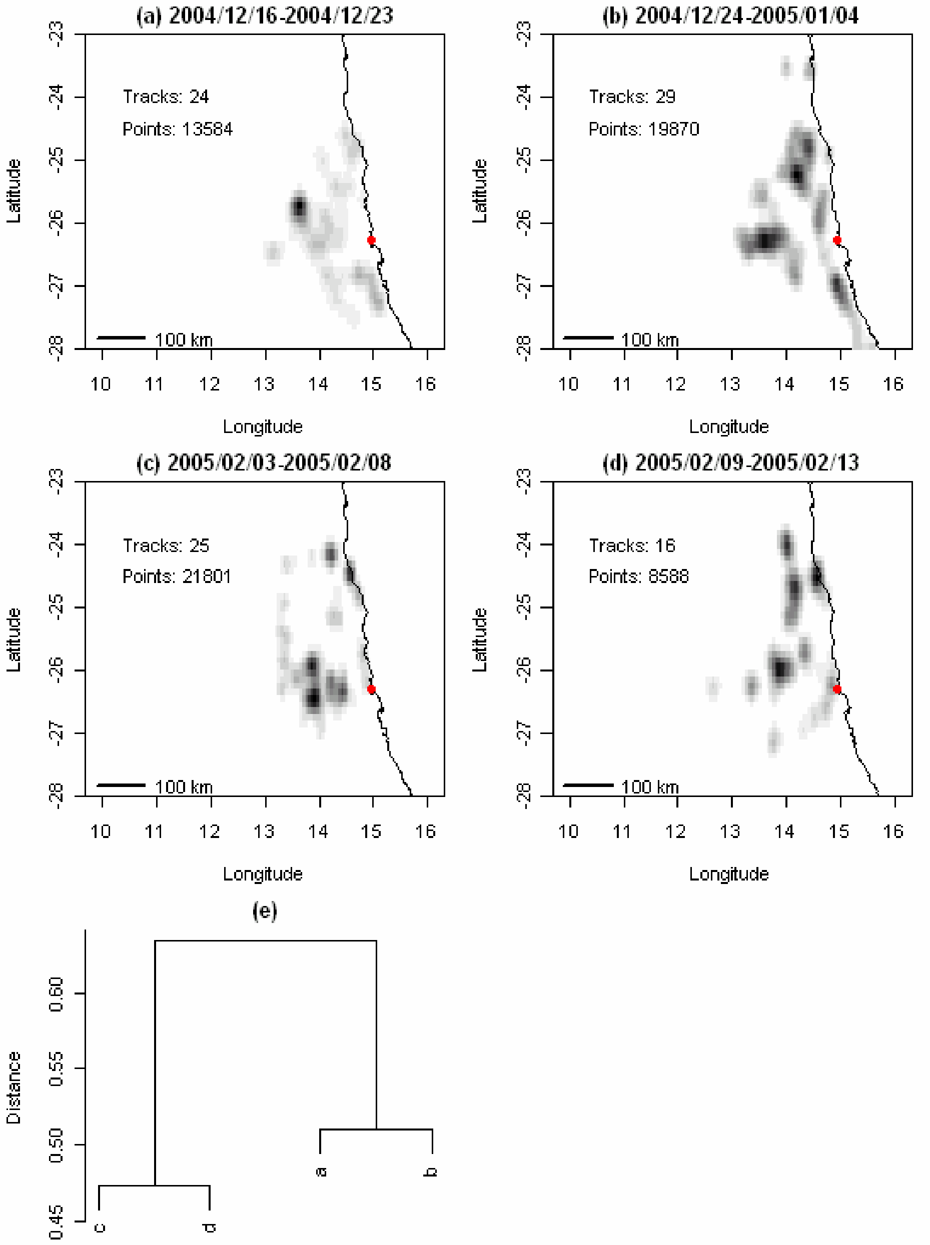

Fig. 6.8. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Ichaboe Island during different periods within the 2004/2005 breeding season (a–d). Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of Ichaboe Island. The dendrogram (e) summarizes the distances and clustering of the periods.

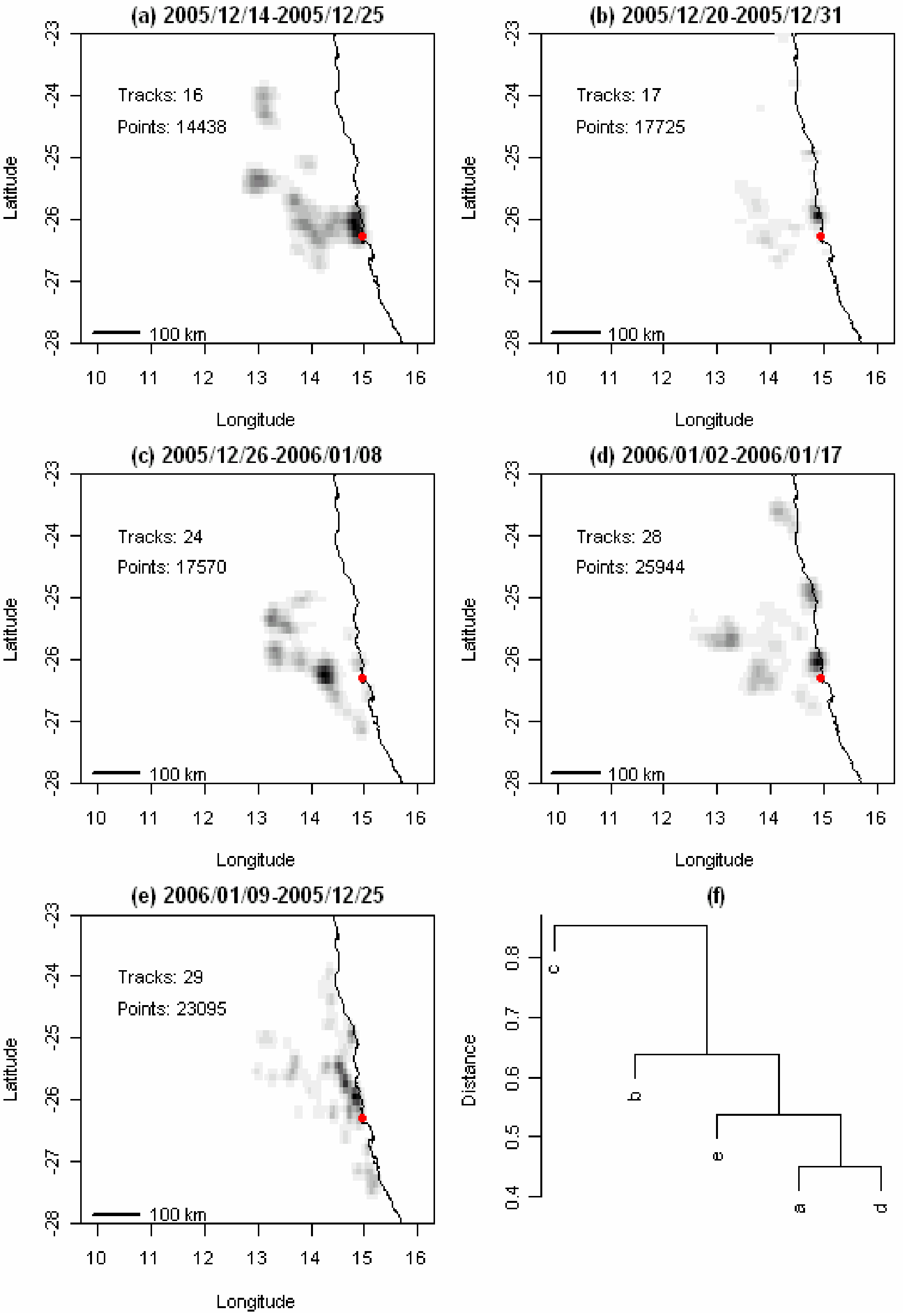

Fig. 6.9. Kernel density estimation of fine-scale positions (DRS < 1 000 m) recorded for Cape gannets foraging off Ichaboe Island during different periods within the 2005/2006 breeding season (a–e). Densities were estimated on a 0.05° × 0.05° grid (*ca.* 5.55 × 4.70 km); data included both complete and incomplete tracks. Grey intensity indicates increasing densities per unit area. The red dot indicates the position of Ichaboe Island. The dendrogram (f) summarizes the distances and clustering of the periods.

# CHAPTER 7

CHAPTER 7

# ENERGY EXPENDITURE OF CAPE GANNETS *MORUS CAPENSIS* IN RELATION TO FORAGING BEHAVIOUR

## Abstract

I sought to determine the energy expenditure and activity specific metabolic cost of Cape gannets *Morus capensis* during foraging trips of chick rearing birds. I used the doubly labelled water technique to measure field metabolic rate of free-ranging adults. Experimental birds were, at the same time, fitted with GPS data loggers set to record geographic fixes every 10 seconds during duration of the a complete foraging trip. Field work was conducted at Malgas Island, South Africa. Foraging track data was used to partition the time budget at sea in the following component: outgoing flight; search/foraging flight; return flight; drifting/swimming; and time at the nest. Flying time was also partitioned into components related to the scale of movements: fine, coarse, and mesoscale flights. The daily energy expenditure during a foraging trip was 4 311 ± 1 616 kJ $d^{-1}$ (5.1 × BMR) for a 2.6 kg bird. The overall cost of flying was estimated at 227.3 ± 31.5 kJ $(kg\ h)^{-1}$ (19.6 × BMR; 63.1 W). Activity specific costs were as follows: (1) according to the behavioural algorithm: outgoing flight 22.6 × BMR; return flight 25 × BMR; search/foraging flight 14.7 × BMR; drifting/swimming 2.0 × BMR; and at nest 2.3 × BMR. (2) According to the distance-ratio scale: fine-scale flight 6.0 × BMR; coarse-scale flight 24.5 × BMR; and mesoscale flight 18. × BMR. The various flight costs estimated in this study are the biggest yet reported for a seabird.

## Introduction

Pelagic seabirds are conspicuous top predators of the open ocean and their biology and adaptations are constrained by the energetics demands imposed by large geographic separations between foraging and breeding areas (Lack 1968; Ricklefs 1983). For this reason seabirds have featured prominently in studies of field ecological energetics. Field metabolic rates have been related to extrinsic factors such as wind regime (Ballance 1995), weather conditions (Jouventin & Weimerskirch 1990; Furness & Bryant 1996), brood size (Fyhn *et al.* 2001), and food availability (Jodice *et al.* 2002). However, large variability in energy expenditure at sea is the result of intrinsic factors and individual differences in foraging strategy. Although energy expenditure at sea is correlated with the time spent away from the nest, there is still a large component of that variance that remains unexplained; for example the models reported by Birt-Friesen *et al.* (1989) and Adams *et al.* (1991) time off the nest accounted 47% and 53% of the variance respectively. A more detailed time-activity budget can not only lead to a partitioning of metabolic rates at sea (Ellis & Gabrielsen 2002), but can also increase the explanatory power of the fitted models used to estimate activity specific costs.

The main stumbling block in the understanding of the relationship between metabolic rates measured in free-ranging birds and the various activities they engage on during the period of measurement has been the difficulties of simultaneously recording detailed time activity budgets and their metabolic rates. A particularly difficult task in seabirds than can cover large expanses of open ocean in a single foraging trip lasting for a few hours to several days. This has been achieved by Bevan *et al.* (1995) who studied the energy expenditure of black-browed albatrosses *Diomedea melanophrys*. The birds carried satellite transmitters to record their geographic location, salt-switches to record time spent on/off the sea, and implanted data loggers to continuously record the heart rate and abdominal temperature. Heart rate was used to determine energy expenditure. This array of devices allowed them to calculate activity specific metabolic rates. However, the technique has some drawbacks: to convert heart rate into energy expenditure requires species-specific calibration, which may be more difficult to achieve than the special surgical skills needed to implant and remove the devices. A different approach was followed by Jodice *et al.* (2002); in their study of field energetics of black-legged kittiwakes *Rissa tridactyla.* They used doubly labeled water (DLW) to measure metabolic rate and direct observation of radio-tagged birds to quantify time-activity budgets. Partitioning of measured metabolic rates was done with multiple regression linear models, which allowed them to estimate the cost of different types of flight. Shaffer *et al.* (2001) measured metabolic rates on wandering albatrosses *Diomedea exulans* fitted with satellite transmitters and reported the smallest flight costs (3.4–5.1 W $kg^{-1}$, 1.4–2.0 × BMR) for any seabird to date.

The energetics of Cape gannets has been studied by several authors. Cooper (1978) measured the energy requirements for growth of two chicks reared in captivity. He found that mean total metabolised energy (TME) was 185 MJ. In Chapter 3 I studied the energy requirements of chicks in the field using the doubly-labelled water (DLW) technique and mean TME was estimated at 151 MJ; Cooper’s TME value is 123% of the field estimate. With regard to the energy requirements of breeding Cape gannets, Adams *et al.* (1991), and more recently Mullers *et al.* (2009) have both measured field metabolic rate using the DLW technique, findings from both studies are in good agreement: mean at sea metabolic rate was reported to be 4670 and 4203 kJ $d^{-1}$ respectively (a 11% difference).

In this study I used DLW to measure at-sea metabolic rates on Cape gannets *Morus capensis* equipped with GPS data loggers, which allowed the collection of data at a high spatio-temporal resolution. The objective was to relate the metabolic rates at sea with time activity budgets in order to estimate the cost of different types of flights.

## Methods

This study was conducted at Malgas Island (33°03'S, 17°55'E), Saldanha Bay, South Africa, over two breeding seasons: 2004/05 and 2005/06. This island lies along the Benguela Upwelling System in the west coast of South Africa. The Benguela ecosystem was reviewed by Berruti *et al.* (1989), Shannon *et al.* (1992), Shannon & O'Toole (2003) and references therein. The status of the Cape gannet population was reviewed by Crawford *et al.* (2007).

### Foraging flight-tracks

Cape gannets were fitted with GPS-data loggers (Technosmart, Rome) set to record a geographic fix every 10 seconds. The loggers were sealed in two polyethylene bags, and attached to the birds with waterproof tape (Tesa®-tape manufactured by Beiersdorf AG, Hamburg), which does not damage the feathers (Grémillet *et al.* 2004). The logger was positioned on the upper side of the central tail feathers, partly covering the lower rump (Fig. 6.1). The whole package measured about 80×50×10 mm and weighed about 50 g (*c.* 2% of the adult body mass).

Only birds feeding chicks were fitted with loggers, attempting to cover the whole range of chick ages, from hatchings to fully-grown chicks. I waited for gannets returning from a foraging trip; after the nest relief ceremony was over I caught the partner leaving the nest, thus ensuring that the chick remained attended by the arriving partners. The bird was caught with a hooked pole, measured (length of the flattened wing chord to the nearest mm and bill length to the nearest 0.1 mm) and weighed (to the nearest 25 g). The logger was attached as described above and the bird released on the periphery of the colony, the procedure taking about five minutes. Previous studies using similar devices and handling of the birds had no obvious adverse effects on Cape gannet behaviour (Grémillet *et al.* 2004, Lewis *et al.* 2006). The nests of tagged birds were monitored hourly during daytime. When the tagged bird returned it was recaptured and the logger removed; the birds was then released back into the nest site, settling readily. Chicks were captured, weighed (<1 kg to 5 g; >1 kg to 25 g) and measured (bill length to the nearest 0.1 mm and flattened wing-chord length to the nearest mm). Additional foraging tracks from untreated birds were compared to the tracks obtained from DLW birds.

### Wind data

Data on wind direction and speed was obtained from the South African Weather Bureau for the period 2003/09 to 2004/02. The closest station to Malgas Island was Langebaanweg (-32.97S 18.17E, height: 31 m), 23 km inland from the study colony.

### Energy expenditure

I determined field metabolic rates (FMR) of breeding adult Cape gannets using the doubly labelled water (DLW) technique (Lifson *et al.* 1955, LeFebvre 1964, Tatner & Bryant 1989, Speakman 1997). The DLW technique estimates the $CO_2$ production from the loss rate of the stable isotopes $^2H$ and $^{18}O$. The size of the initial body water pool was determined from initial dilution of $^{18}O$ using the plateau method of calculation, and final body water pool was determined by percentage mass from the initial determination (Speakman 1997). The loss rate of $^2H$ provides a measure of the water flux (see Chapter 4).

Adult FMR was assessed in a random sample of birds fitted with a GPS data logger (see above). After the bird had been measured, weighed and fitted with the data logger, it was injected with DLW, under the abdominal skin, with a dose of 0.5 ml $kg^{-1}$ of body mass. Birds were released in the periphery of the colony. In the course of the pilot experiments (se Chapter 3) it was noted that confinement of the birds to take the initial blood sample greatly increased the stress levels of the birds. Therefore, in order to reduce handling stress of the experimental birds I opted for the single sample method, so no initial blood samples were taken. Upon return from a foraging trip, the birds were captured, weighed, the GPS tag removed and a final blood samples was taken. About 3 ml of blood was drawn from a brachial vein using a fresh insulin syringe; from this *ca.* 5 µl of blood were transferred into each of six 25 µl glass capillary tubes. The tubes were immediately flame-sealed and refrigerated (but not frozen) until analysis. The natural background level of $^{2}H$ and $^{18}O$ isotopes were determined in nine untreated birds. The DLW used contained 60.5 atoms percent $^{18}O$ and 36.5 atoms percent $^{2}H$.

Details of the isotope analysis are given in Chapter 3. In the single sample method it is not possible to have a direct measure of initial enrichment to estimate isotope turnover or body pool size. In a separate experiment Mullers *et al.* (2009) measured initial enrichment and body water pool size in seven Cape gannets for which initial and final blood samples were taken. From this body water was estimated at 57.9% and initial enrichment was scaled according to the subject's body mass and amount of label injected. Rates of water efflux and $CO_2$ production were calculated from isotope turnover (assuming a single-pool model) using equation 7.17 of Speakman (1997). This equation uses a fractional evaporative water loss value of 25%, which has been validated by Visser & Schekkerman (1999). We converted rates of $CO_2$ production ($l\ d^{-1}$) to energy expenditure ($kJ\ d^{-1}$) assuming a respiration coefficient (RQ) of 0.72, with the energy equivalent of 27.33 $kJ\ l^{-1}\ CO_2$, as recommended by Visser (2001) for a fish-eating bird.

I injected 20 adult Cape gannets with doubly labelled water, but only 15 measurements could be used: four were excluded because the track recorded by the GPS logger was incomplete, and one because of a large analytical error (123%). The sample size was increased by including another 13 DLW measurements (plus the corresponding complete GPS track) conducted at Malgas Island by Mullers *et al.* (2009), who followed identical field protocols to those described above. DLW measurements reported here were conducted in the following breeding seasons: 2004/2005 ($n$ = 15); 2005/2006 ($n$ = 7); and 2006/2007 ($n$ = 6), data for the last two seasons was collected by R.H. Mullers.

### Data analysis

The analysis of foraging tracks was done according to the methods described in Chapter 5. Computations and graphics were done using program R (2.10.0, Windows version) (R Development Core Team 2009). Regression models, including ANOVAs, were fitted with the *lm* (linear-models) function. Bootstrapping was done with the package *boot* (Fox 2002); all bootstrap confidence intervals correspond to the 'adjusted bootstrap percentile' for 1 999 sample replicates. Unless otherwise stated, means are given ± 1 standard deviation.

Adams *et al.* (1991) converted $CO_2$ production into metabolic rate assuming an energy equivalent of 25.8 kJ $ml^{-1}$. In this study, I used an energy equivalent of 27.33 kJ $ml^{-1}$ (Visser 2001); therefore, I have multiplied metabolic rates in Adams *et al.* (1991) by 1.059 to make them comparable to those reported here.

In order to investigate how the different components of a foraging trip, either as time or distance, related to energy expenditure, it was necessary to express the DEE values as total energy expenditure per foraging trip (TEE.f; kJ), therefore

$$\text{TEE.f} = \text{DEE (kJ d}^{-1}\text{)} \times \text{duration of DLW experiment (d)}.$$

Cost specific of activities were calculated by fitting linear models of TEE.f values (response variable) with time-budgets obtained from the tracks (explanatory variables). A foraging track can be divided in various non-overlapping components, I explore two ways: (a) according to the categories identified by the behavioural algorithm (i.e. out-flight, search-flight, return-flight, and drifting); and (b) according to the distance-ratio scale values (i.e. fine, coarse and mesoscale, plus drifting). To these one needs to add the time spent at the nest (i.e. the time not covered by the foraging track but included in the DLW measurement period).

# Results

## Body mass and mass change

The mean initial body mass of the 28 experimental birds was 2 604 ± 174 g. Of the experimental birds, 24 showed body mass increase during the DLW measurements, for these birds mean mass gain was 314 ± 231 g (*n* = 24, quantile range: 100–425 g), representing 12.3 ± 9.4%

(quantile range: 3.7–17.6%) of the initial body mass. This mass increase corresponds to the food load brought back to the nest after the foraging trip. Two birds showed mass decreases (50 and 200 g), and two birds showed no mass change. The overall mean change of mass was 258 ± 261 g ($n = 28$). Mass changes in a control sample was 267 ± 187 ($n = 105$), a non-significant difference ($t = 0.17$, $p = 0.868$).

## Foraging behaviour

Table 7.1 gives a summary of the parameters of the foraging tracks for the 28 experimental birds and 331 control birds for which only tracks were obtained. None of the parameters examined, for both time and distance, showed significant differences between experimental and control birds.

## Wind data

The prevailing wind during most of the 2003/04 breeding season was from a southerly direction (Fig. 7.2); overall median direction was 200° (SSW), first quantile was 170° (S) and 3rd quantile was 270° (W). Daily pattern of wind speed was similar through the period sampled, with a peak in wind speed (4–9 m $s^{-1}$) from 15 to 19h (Fig. 7.3); overall speeds were 2.7, 4.3, and 6.2 for the 1st, median, and 3rd quantiles respectively.

## Energy expenditure at sea

The average DLW measurement period was 29.5 ± 8.9 h (range 18.2–50.8 h, $n = 28$). The daily energy expenditure (DEE) during a foraging trip (DEE.f) was 4 311 ± 1 616 kJ $d^{-1}$ (quantile range: 3 178–5 621 kJ $d^{-1}$); corresponding to 5.1 ± 1.9 × BMR (quantile range: 3.7–6.7 × BMR). DEE.f was not related to the bird's initial mass ($p = 0.833$), nor to mean mass ($p = 0.233$), neither to the chick's mass ($p < 0.834$).

Total trip duration and total trip length were strongly correlated to TEE.f (Fig. 7.1), as well as for most other parameters derived from the foraging tracks (Table 7.2).

Linear models fitted to TEE.f with different combinations of explanatory variables from these two track time-budgets approaches are summarized in Table 7.3. In both cases the model with the lowest IAC was the one including time at nest and excluding drifting time; however, the AIC values of the different models are so close to each other that it makes little difference which model is chosen. The TEE.f variance explained by any of the models is 92%.

### Energy expenditure of foraging components

All regression models were fitted without an intercept term because if no time is spent on any activity, no energy is expended (Eisenhauer 2003). The values of the coefficients represent the cost (kJ $h^{-1}$) for each of the activities for a bird 2.6 kg (average initial mass of DLW birds). In this case model choice can have a large effect on the estimated cost of activities. For the behavioural algorithm categories (Table 7.1a) the largest range in costs was for out-flight (365.7 kJ $h^{-1}$, 72.9% difference), and the smallest for time at the nest (2.3 kJ $h^{-1}$, 3.4% difference). For the DRS categories (Table 7.1b) the largest range on cost estimate was for fine-scale (83.2 kJ $h^{-1}$, 58.5% difference) and the smallest for time at nest (3.3 kJ $h^{-1}$, 5% difference). Therefore, the most parsimonious solution is to use the mean coefficients as the energetic cost of the various activities, these are given in Table 7.1, together with the respective BMR ratios.

For the behavioural algorithm the return flight had the largest cost (290 kJ $kg^{-1}$ $h^{-1}$), closely followed by out-flight (262 kJ $kg^{-1}$ $h^{-1}$); cost of search flight was 171 (kJ $kg^{-1}$ $h^{-1}$). These values correspond to 21.6, 19.4 and 12.7 times BMR respectively. For the DRS categories, the cost was largest for coarse scale (238 kJ $kg^{-1}$ $h^{-1}$), then mesoscale (214 kJ $kg^{-1}$ $h^{-1}$) and fine scale (69.8 kJ $kg^{-1}$ $h^{-1}$), representing 21.1, 15.9 and 5.2 times BMR respectively (Table 7.4).

The cost during drifting and time at nest were derived from the estimates from both sets of models, they were 23 and 27 kJ $kg^{-1}$ $h^{-1}$ respectively. The BMR equivalents of these activities were 1.7 and 2 respectively (Table 7.4).

The overall cost of flying, regardless of the finer classification, was 227.3 kJ $kg^{-1}$ $h^{-1}$ (16.9 × BMR; 63.1 W). This value was derived from the coefficient for flying time, divided by mean initial mass (Table 7.4).

## Discussion

### Energy expenditure

Daily energy expenditure of Cape gannets during a foraging trip measured during this study is comparable to that independently estimated by Adams *et al.* (1991). It is also similar to the results reported by Mullers *et al.* (2009); but this is not surprising as nearly half of the data used here comes from their study.

Adams *et al.* (1991) measured metabolic rate of Cape gannets on the nest (2 231 kJ $d^{-1}$, after correcting for mass and $CO_2$ energy equivalent). Assuming that birds spent 50% of the time on the nest and 50% off the nest (nest attendance: 12.5 ± 0.6 h $d^{-1}$, $n = 194$, unpublished data), then FMR = 2 231 / 2 + (227.3 × 12) = 3 843 kJ $d^{-1}$. The equivalent value from Adams *et al.* (1991), corrected for mass and $CO_2$ energy equivalent, was 3 622 kJ $d^{-1}$, a difference of 1%, a remarkable agreement. The observed FMR is 1.4–3.2 times the FMR predicted from six different equations presented by Tieleman & Williams (2000). It is also 1.1–2.6 times the FMR predicted from seven models for seabirds derived by Birt-Friesen *et al.* (1989; Table 4, equations 1–7). The best prediction was from their model for "cold water seabirds using flapping flight", which underestimated the results presented here by 10%.

Birt-Friesen *et al.* (1989) gave three equations to predict FMR at sea: these predictions are compared with the overall cost of flying in Cape gannets (227.3 kJ $h^{-1}$). The predicted values for all-seabirds and for seabirds-using-flapping-flight were 8.3% and 11.3% above the observed value respectively. Whereas the predicted value for seabirds-using-gliding was 16.5% below the observed value.  Cape gannets have an aspect ratio similar to those of albatrosses, but their wing loading is higher that similarly sized albatrosses (Adams *et al.* 1991), this, combined with the use of flapping-gliding flight accounts for the higher metabolic rate of Cape gannets at sea than gliding birds. But it seems more efficient than seabirds using flapping flight, although the sample analysed by Birt-Friesen *et al.* (1989) included eight species with body mass below 0.4 kg, and only one species (the northern gannet) over 3 kg, which may bias the values predicted by the model.

**Metabolic cost of flight**

Metabolic costs of flight predicted from 18 published models are presented in Table 7.4. Of these, the models by Castro & Myers (1988: equation *a*) and Butler & Bishop (2000: DLW equation) both were 3% below the observed value of overall flight cost in Cape gannets. Nudds & Bryant (2000) predicted value in Table 7.4 corresponds to their model for steady-state flight in a wind tunnel, which they suggest it could be used for predictions of sustained flight; this prediction is 20% below the observed value. The model by Teal (1969) was the first such model to be published and produced a predicted value 9% over the observed value. It should be taken into consideration that predictions from all models in Table 7.4 lie well outside the mass range of the data used to formulate such models (see Appendix 7.1) and such extrapolations should be viewed with caution.

The overall mass specific cost of flight of Cape gannets was estimated at 227.3 ± 31.5 kJ kg$^{-1}$ h$^{-1}$, 19.6 ± 2.7 × BMR (error terms correspond to 95% bootstrap confidence interval). There is no comparable figure in Adams *et al.* (1991) study as they could only determine overall metabolic rates at sea since they lacked a time budget of the birds at sea. Birt-Friesen *et al.* (1989) estimated metabolic cost of flight of northern gannets to be 349 ± 107 kJ h$^{-1}$, with a mean mass = 3.21 kg the mass specific being 109 ± 33.3 kJ kg$^{-1}$ h$^{-1}$, 6.1 ± 1.8 × BMR (using BMR from Bryant & Furness 1995; see Ellis & Gabrielsen 2001, p. 362, for reasons to use an alternative BMR value). The reported value is only 0.48 times the figure for Cape gannets; the large discrepancy in mass specific flight cost of these two congeneric species may be accounted for by the methods used to derive such estimates, see below. Using data in Fig. 1 of Birt-Friesen *et al.* (1989), I fitted a model excluding the intercept to obtain a revised cost of flight for northern gannets of 204 ± 21.7 kJ $kg^{-1}$ $h^{-1}$, 11.4 ± 1.2 × BMR (error terms correspond to 95% bootstrap confidence interval); this figure is 1.87 times the original estimate, and 0.9 times the value observed in Cape gannets.

Jodice *et al.* (2003) listed all estimates of metabolic cost of flight measured with DLW in free ranging seabirds, their table is reproduced here (Table 7.5) with the following modifications: the value quoted for the northern gannet was however the metabolic rate at sea and not the metabolic rate of flight, the correct value is now given in Table 7.5. I also include, for the same species, the recalculated cost of flight given above. Albatrosses use dynamic soaring almost exclusively and have the lowest flight cost, whereas gannets, that use a mixture of soaring and flapping flight have higher costs of flight, with Cape gannets having the highest cost of flight yet reported for any seabird.

### Estimation of activity specific metabolic rates

Earlier studies (e.g., Flint & Nagy 1984, Nagy *et al.* 1984, Costa & Prince 1987, Birt-Friesen *et al.* 1989) used simple linear regression of time spent engaged in a particular activity vs total energy expenditure over a specified time period. The slope of the regression line is given as the energy cost of the activity per unit time. Estimates derived in this way have been criticized and deemed biased and underestimated by Wilson & Culik (1993), who considered that some of the cost is hidden in the intercept. More recent studies (e.g., Jodice *et al.* 2002) use multiple regression models to calculate activity-specific metabolic costs. And, following Wilson & Culik's (1993) recommendation, they estimated metabolic cost during each activity by adding the intercept term from the multiple linear regression models to each of the scaled coefficients.

In the present study I have opted for deriving costs from models fitted without the intercept (Eisenhauer 2003), in this way any cost hidden in this term are distributed to the remaining terms in the model. This approach has several advantages: (1) parameter estimates can be directly interpreted as metabolic cost for an average bird, or by dividing by the mean mass are transformed into mass specific costs; (2) the variance explained by the models is greater than models including the intercept (mean $r^2 = 0.917$ and 0.570 for models without and with intercept respectively); (3) costs estimated are more consistent with expected values, e.g. cost of out-flight and return-flight should be of similar magnitude, which is the case for the estimates derived from models without intercept, unlike the estimates from models including the intercept (Table 7.6); another example of this is the estimated cost at the nest: 14.2 and. 26.6 kJ $kg^{-1}$ $h^{-1}$ for models with and without intercept respectively, these values are equivalent to 42% and 78% respectively of the metabolic cost at the nest estimated by Adams *et al.* (1991) of 33.8 kJ $kg^{-1}$ $h^{-1}$. Furthermore, there is no consistency in the direction or magnitude of the bias introduced by the inclusion of the intercept in models used to derive estimates of metabolic rates (Table 7.6).

It may seem counter-intuitive to exclude the intercept because of the assumption that it represents some measure of resting metabolic rate in the absence of the activity modeled. However, this is equivalent to predicting the costs of activities not included in the model. In a time budget, when an individual is engaged in one activity it cannot be performing another, if the bird is flying it cannot be resting or swimming. Therefore, in the context of a time-budget, the cost of spending no time performing an activity is zero, and not some undefined value represented by the intercept, which is equivalent to say that the absence of a particular activity still carries a cost. Clearly, additive models used for this purpose should not include the intercept term.

### Partitioning of metabolic cost of flight

Few studies, using DLW, have measured the cost of flight in free-ranging seabirds (Table 7.5), and only one of these studies have lead to a partitioning of metabolic rates into different types of flight. Jodice *et al.* (2003) were able to assess the cost of commuting and search flight (Table

7.5), but these estimates may be biased in an unknown way due to the inclusion of the intercept on the models (see above).

In this study I have been able to partition flight type in two different ways (Table 7.4):

(1) According to the behavioural algorithm: were the most costly portion corresponded to the return flight (25 ± 1.5 × BMR), closely followed by the outgoing flight (22.6 ± 4.9 × BMR), whereas the search flight was the least expensive of the tree (14.7 ± 2.6 × BMR). These costs are related, at least in part, to the speed of flight: 50.5 ± 16.4; 47.2 ± 7.0; and 43.8 ± 4.9 km $h^{-1}$ for return-, out- and search-flight respectively. The return-flight is expected to be the most expensive as the birds are returning back to the nest laden with a full load of fish, and flying at high speed, most probably using sustained flapping all the way through.

(2) According to the distance-ratio scale the most costly flight occurred at coarse-scale (24.5 ± 4.1 × BMR), then mesoscale (18.5 ± 1.3 × BMR), and fine-scale being the least costly (6.0 ± 1.2 × BMR). The relationship with flight speed is not as clear as in the case above; mean speeds were 44.2 ± 5.2; 51.9 ± 3.0; and 33.7 ± 5.8 km $h^{-1}$ for coarse, meso and fine scale flight respectively.

Although the large-scale foraging movement of some pelagic seabirds are strongly influenced by wind speed and direction (Jouventin & Weimerskirch 1990, Weimerskirch *et al.* 2000), Cape gannets were found to be little affected by these factors (Adams & Navarro 2005). However, Mullers *et al.* (2009) found that there was significant effect of wind speed on total energy expenditure at sea. On account of the persistence of the prevailing wind, gannets returning to Malgas Island from a southerly direction frequently fly with tail winds between 4 and 9 m $s^{-1}$ that may confer an energetic saving of 26% to 48%; whereas headwinds of similar strength increase the energy expenditure by 46% up to 154% (Adams & Navarro 2005). The energy saving conferred by the use of tail winds in the return flight may be even bigger that that calculated by Adams & Navarro (2005), since median wind speed at sea, as measured by remote sensing, was 15 m s$^{-1}$ at the southern Benguela for December 2003 (Gremillet *et al.* 2004).

The high FMR of Cape gannets, coupled with their slow reproduction rate and high site-fidelity makes them more vulnerable to the rapid environmental changes, such as the eastward shift in anchovy (Coetzee *et al.* 2008). As I have shown in Chapter 6, Cape gannets respond rapidly to the highly dynamic and unpredictable prey patchiness at the mesoscale, but once the fish is out of reach of colony-bound breeding birds, they are forced to switch to less profitable prey, with the consequences of reduced breeding output (Chapter 2). The apparent inability of breeding gannets to relocate to a colony with easily accessible natural prey has been termed 'behavioural inertia' by Pichegru *et al.* (2010), and, they argue, could lead to the local extinction of Cape gannets.

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Table 7.1. Summary (mean ± 1 SD) of foraging trip parameters derived from the behavioural algorithm and distance-ratio scale (see text) applied to complete GPS tracks from DLW injected birds (n = 28) and control birds (n = 331). Tracks of Cape gannets foraging from Malgas Island were collected during four breeding seasons (2003/2004 to 2006/2007). Differences between means were tested with simple linear models.

(A) Time (h)

| | control | DLW | *p* |
|---|---|---|---|
| whole trip | 23.42 ± 13.10 | 25.83 ± 11.06 | 0.345 |
| out flight | 0.82 ± 0.69 | 0.68 ± 0.57 | 0.316 |
| search flight | 5.67 ± 3.98 | 6.54 ± 3.82 | 0.539 |
| return flight | 1.33 ± 1.20 | 1.19 ± 1.16 | 0.264 |
| drifting | 15.53 ± 9.95 | 17.32 ± 7.33 | 0.352 |
| fine scale flight | 1.67 ± 1.52 | 1.92 ± 1.45 | 0.406 |
| coarse scale flight | 1.80 ± 1.27 | 2.06 ± 1.20 | 0.283 |
| mesoscale flight | 4.43 ± 2.60 | 4.53 ± 2.48 | 0.846 |

(B) Distance (km)

| | control | DLW | *p* |
|---|---|---|---|
| whole trip | 447.6 ± 240.9 | 438.5 ± 201.8 | 0.847 |
| out flight | 39.7 ± 33.2 | 31.3 ± 24.0 | 0.193 |
| search flight | 259.1 ± 180.3 | 281.0 ± 159.1 | 0.775 |
| return flight | 76.1 ± 69.2 | 71.3 ± 70.7 | 0.535 |
| drifting | 71.2 ± 77.3 | 53.6 ± 32.4 | 0.225 |
| fine scale flight | 55.6 ± 47.7 | 61.2 ± 43.9 | 0.549 |
| coarse scale flight | 82.2 ± 56.8 | 88.3 ± 4710 | 0.582 |
| mesoscale flight | 237.6 ± 142.7 | 235.5 ± 131.1 | 0.940 |

Table 7.2. Simple regression models of total energy expenditure at sea OF Cape gannets at Malgas Island in relation to foraging trip parameters derived from the behavioural algorithm and distance-ratio scale (see text) applied to complete GPS tracks from DLW injected birds (*n* = 28). All models fitted with intercept = 0; 95% confidence intervals (CI) calculated by bootstrapping.

(A) Time (h)

| | slope | 95% CI | $r^2$ |
|---|---|---|---|
| complete trip | 192.2 | 168 – 219 | 0.907 |
| flying time | 591.8 | 508 – 672 | 0.899 |
| out flight | 4 594 | 2 980 – 6 175 | 0.516 |
| search flight | 705.1 | 587 – 831 | 0.884 |
| return flight | 2 747 | 2 085 – 3 496 | 0.640 |
| drifting | 282.0 | 246 – 326 | 0.875 |
| fine scale flight | 2 089 | 1 639 – 2 603 | 0.778 |
| coarse scale flight | 2 216 | 1 933 – 2 593 | 0.867 |
| mesoscale flight | 1 034 | 882 – 1 177 | 0.883 |

(B) Distance (km)

| | slope | 95% CI | $r^2$ |
|---|---|---|---|
| complete trip | 11.25 | 9.9 – 12.6 | 0.917 |
| flying distance | 12.63 | 10.9 – 14.2 | 0.909 |
| out flight | 105.64 | 73.4 – 132.4 | 0.534 |
| search flight | 16.30 | 13.3 – 19.7 | 0.858 |
| return flight | 45.41 | 35.7 – 54.8 | 0.657 |
| drifting | 76.11 | 51.27 – 102.3 | 0.697 |
| fine scale flight | 66.31 | 51.5 – 83.6 | 0.771 |
| coarse scale flight | 52.61 | 44.9 – 61.2 | 0.860 |
| mesoscale flight | 19.68 | 16.5 – 22.8 | 0.872 |

Table 7.3. Estimates for the parameter of different linear models fitted to total energy expenditure during a foraging trip (TEE.f) of Cape gannets at Malgas Island. Energy expenditure was measured with the DWL technique in 28 birds, which at the same time were fitted with a GPS logger. The time budget of the track was divided into non-overlapping sections according to (a) the behavioural algorithm, and (b) to the time spent at different distance-ratio scale (DRS) values. Also indicated for each model are the adjusted $r^2$ and Akaike's information criterion (AIC); in bold the model with the lowest AIC. As models were fitted with intercept = 0, the value of the estimates represent the cost (kJ $h^{-1}$) for each of the activities.

(a) time budget according to behavioural algorithm:

| model | out flight | return flight | search flight | drift time | time at nest | $r^2$ | AIC |
|---|---|---|---|---|---|---|---|
| a.1 | 501.9 | 768.9 | 370.6 | 66.1 | 69.3 | 0.919 | 499.6 |
| a.2 | 639.2 | 701.8 | 381.3 | 69.2 | | 0.916 | 499.7 |
| **a.3** | **715.1** | **809.0** | **503.9** | | **71.7** | **0.918** | **499.1** |
| a.4 | 867.6 | 741.4 | 521.5 | | | 0.915 | 499.2 |
| mean‡ | 261.5 | 290.1 | 170.6 | | | | |
| SD | 58.6 | 17.3 | 30.5 | | | | |

(b) time budget according to DRS scale:

| model | fine scale | coarse scale | meso-scale | drifting | time at nest | $r2$ | AIC |
|---|---|---|---|---|---|---|---|
| c.1 | 142.3 | 617.2 | 533.9 | 49.9 | 66.6 | 0.917 | 500.1 |
| c.2 | 161.5 | 651.9 | 513.6 | 55.9 | | 0.915 | 500.0 |
| **c.3** | **198.1** | **810.7** | **598.3** | | **69.9** | **0.918** | **498.9** |
| c.4 | 225.5 | 871.9 | 585.0 | | | 0.915 | 499.0 |
| mean‡ | 69.8 | 238.4 | 214.2 | 23.1† | 26.6† | | |
| SD | 14.3 | 47.1 | 15.5 | 3.4 | 0.8 | | |

‡ means (kJ $h^{-1}$ $kg^{-1}$) were adjusted dividing by the mean initial mass (2.6 kg)

† means calculated from estimates in both sets of models

Table 7.4. Cape gannet mass specific metabolic costs of flight predicted by allometric models published by various authors, plus empirically determined costs (see Table 7.3). Also given are: the BMR ratio (BMR at night = 11.583 kJ kg$^{-1}$ h$^{-1}$; Adams *et al.* 1991); the power equivalent of the energy expenditure; and ratio relative to overall flight cost. Predictions for all models lie outside the mass range of the data used to derive such models (highest mass is 1.026 kg for most models, see Appendix 7.1).

| | | Mass specific metabolic cost of flight | | | |
|---|---|---|---|---|---|
| | **Model** | Energy expenditure (kJ kg$^{-1}$ h$^{-1}$) | × BMR | Power (W) | × overall cost of flying |
| 1. | Rayner (1990): eq. 1 (mass only) | 62.8 | 5.4 | 17.4 | 0.28 |
| 2. | Masman & Klaassen (1987) | 75.9 | 6.6 | 21.1 | 0.33 |
| 3. | Castro & Myers (1988): equation *b* | 102.2 | 8.8 | 28.4 | 0.45 |
| 4. | Hails (1979) | 104.9 | 9.1 | 29.1 | 0.46 |
| 5. | Norgerg (1996): equation 7.36 | 109.9 | 9.5 | 30.5 | 0.48 |
| 6. | Kendeigh *et al.* (1977): non-passerines | 115.3 | 10.0 | 32.0 | 0.51 |
| 7. | Raveling & LeFebvre (1967) | 117.8 | 10.2 | 32.7 | 0.52 |
| 8. | Castro & Myers (1988): equation $b'$ | 127.8 | 11.0 | 35.5 | 0.56 |
| 9. | Berger & Hart (1974) ; equation 36 | 134.3 | 11.6 | 37.3 | 0.59 |
| 10. | Hart & Berger (1972) | 145.9 | 12.6 | 40.5 | 0.64 |
| 11. | Castro & Myers (1988): equation *c* | 162.3 | 14.0 | 45.1 | 0.71 |
| 12. | Butler & Bishop (2000): wind-tunnel eq. | 168.2 | 14.5 | 46.7 | 0.74 |
| 13. | Kendeigh *et al.* (1977): passerines | 169.4 | 14.6 | 47.1 | 0.75 |
| 14. | Norgerg (1996): equation 7.35 | 172.5 | 14.9 | 47.9 | 0.76 |
| 15. | Nudds & Bryant (2000) | 181.8 | 15.7 | 50.5 | 0.80 |
| 16. | Castro & Myers (1988): equation *a* | 220.0 | 19.0 | 61.1 | 0.97 |
| 17. | Butler & Bishop (2000): p. 399, DLW eq. | 220.9 | 19.1 | 61.4 | 0.97 |
| 18. | Teal (1969) | 247.9 | 21.4 | 68.9 | 1.09 |
| **This study** | | | | | |
| out flight | | 261.5 | 22.6 | 72.6 | 1.15 |
| return flight | | 290.1 | 25.0 | 80.6 | 1.28 |
| search flight | | 170.6 | 14.7 | 47.4 | 0.75 |
| fine scale | | 69.8 | 6.0 | 19.4 | 0.31 |
| coarse scale | | 283.4 | 24.5 | 78.7 | 1.25 |
| mesoscale | | 214.2 | 18.5 | 59.5 | 0.94 |
| drifting | | 23.1 | 2.0 | 6.4 | 0.10 |
| time at nest | | 26.6 | 2.3 | 7.4 | 0.12 |
| overall cost of flying | | 227.3 | 19.6 | 63.0 | — |

Table 7.5. Metabolic rate during flight estimated with the doubly labelled water technique in free-ranging seabirds.

| Species | Metabolic Rate during Flight (×BMR ± 1 SE) | Reference |
|---|---|---|
| Wandering Albatross | 2.3 | Adams *et al.* 1986 |
| Grey-headed Albatross | 3.2 | Costa & Prince 1987 |
| Wilson's Storm-petrel | 4.2 ± 0.4 | Obst *et al.* 1987 |
| Red-footed Booby | 4.5 ± 0.8 | Ballance 1995 |
| Sooty Tern | 4.8 ± 0.6 | Flint & Nagy 1984 |
| Black-legged Kittiwake (commuting flight) | 6.9 ± 1.9 | Jodice *et al.* (2003) |
| Black-legged Kittiwake (search flight) | 7.5 ± 1.5 | Jodice *et al.* (2003) |
| Northern gannet | 6.1 ± 1.8 | Birt-Friesen *et al.* 1989 |
| Northern gannet | 11.4 ± 1.2†* | Birt-Friesen *et al.* 1989: recalculated |
| Cape gannet | 19.6 ± 2.7* | this study |

† calculated from original figure but using BMR from Bryant & Furness (1995) instead of the BMR reported in the original study;

* error terms correspond to 95% bootstrap confidence interval

Table 7.6. Comparison of activity specific metabolic costs ± SD (kJ $kg^{-1}$ $h^{-1}$) of Cape gannet derived from multiple linear regression models fitted with and without the intercept, models fitted are listed in Table 7.3. All estimates represent means across four different models.

| Activity | models including intercept[†] | models excluding intercept[‡] | ratio |
|---|---|---|---|
| out flight | 67.3 ± 17.7 | 261.5 ± 58.6 | 0.26 |
| return flight | 262.8 ± 23 | 290.1 ± 17.3 | 0.91 |
| search flight | 197.4 ± 15.4 | 170.6 ± 30.5 | 1.16 |
| fine scale flight | 176.4 ± 29.8 | 69.8 ± 14.3 | 2.53 |
| coarse scale flight | 274 ± 38 | 283.4 ± 47.1 | 0.97 |
| mesoscale flight | 194.4 ± 16.3 | 214.2 ± 15.5 | 0.91 |
| drifting | 18.6 ± 4.8 | 23.1 ± 3.4 | 0.81 |
| at nest | 14.2 ± 2.7 | 26.6 ± 0.8 | 0.53 |

[†] cost = ((intercept / mean duration) + activity coefficient) / mean mass;

[‡] cost = (activity coefficient / mean mass)

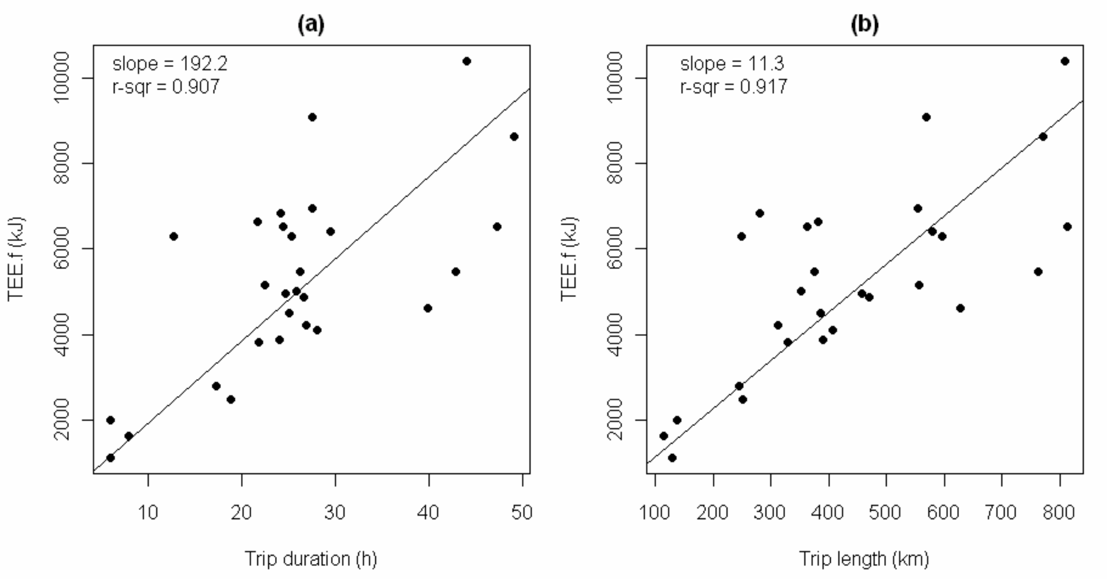

Fig. 7.1. Total energy expenditure per foraging trip (TEE.f, kJ) of 28 Cape gannets from Malgas Island, in relation to the total trip duration (a), and total trip length (b). Energy expenditure was measured using the DLW technique and simultaneous trip parameters were obtained from GPS loggers fitted to the experimental birds (see text for details). Both regression models were fitted through the origin, i.e. the intercept equals zero.

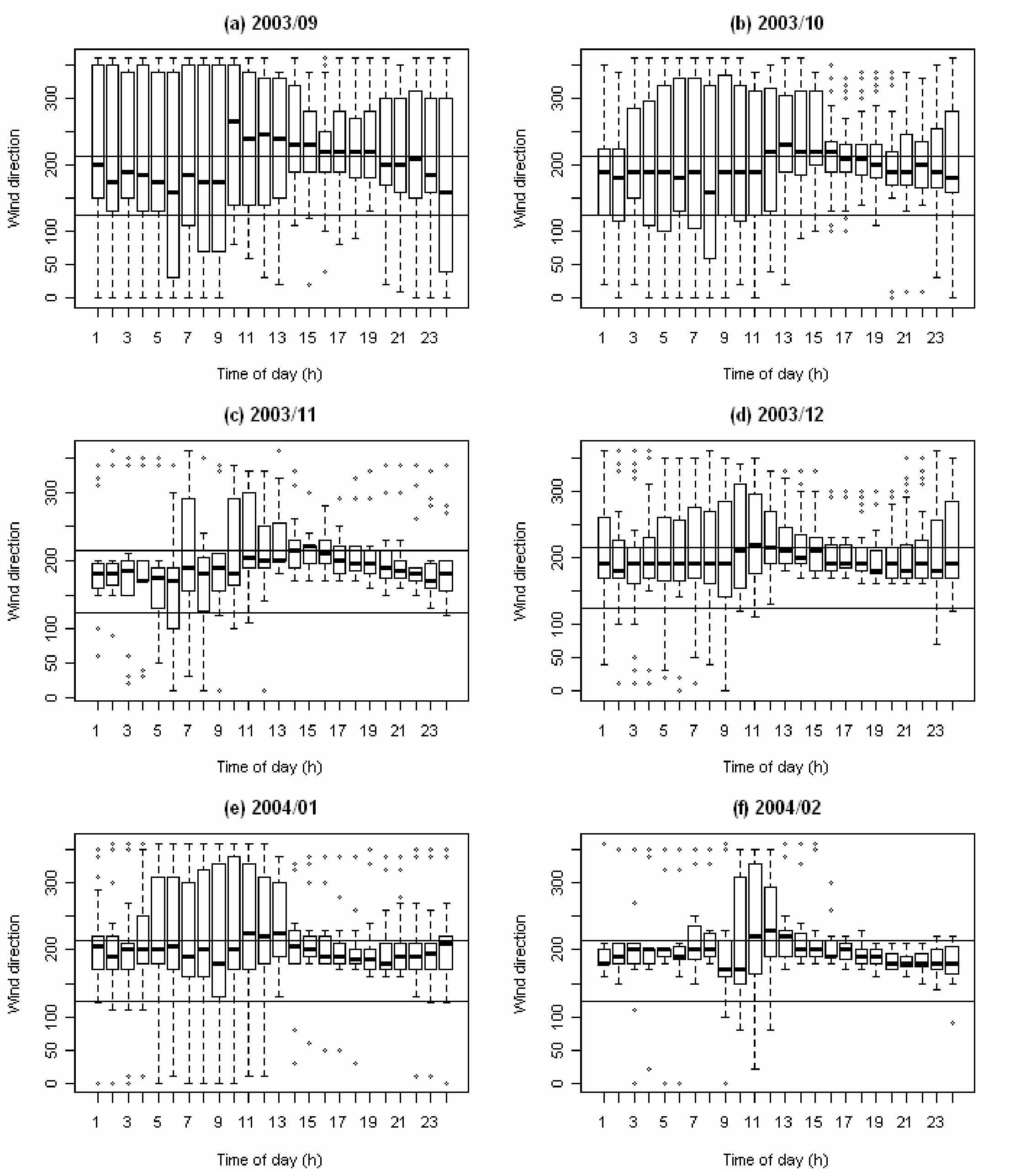

Fig. 7.2. Wind direction (in degrees clockwise from true north) measured at Langebaanweg (-32.97S 18.17E, height: 31 m) for 2003/9 to 2004/02, which corresponds with the period of one field work season; the weather station lies about 23 km inland from Malgas Island. Boxplots summarize, for each hour of the day, the measurements made across the whole month. The horizontal lines mark the SE (123.75º) and SW (213.75º) directions, encompassing the southerly winds. Data sourced from the South African Weather Bureau.

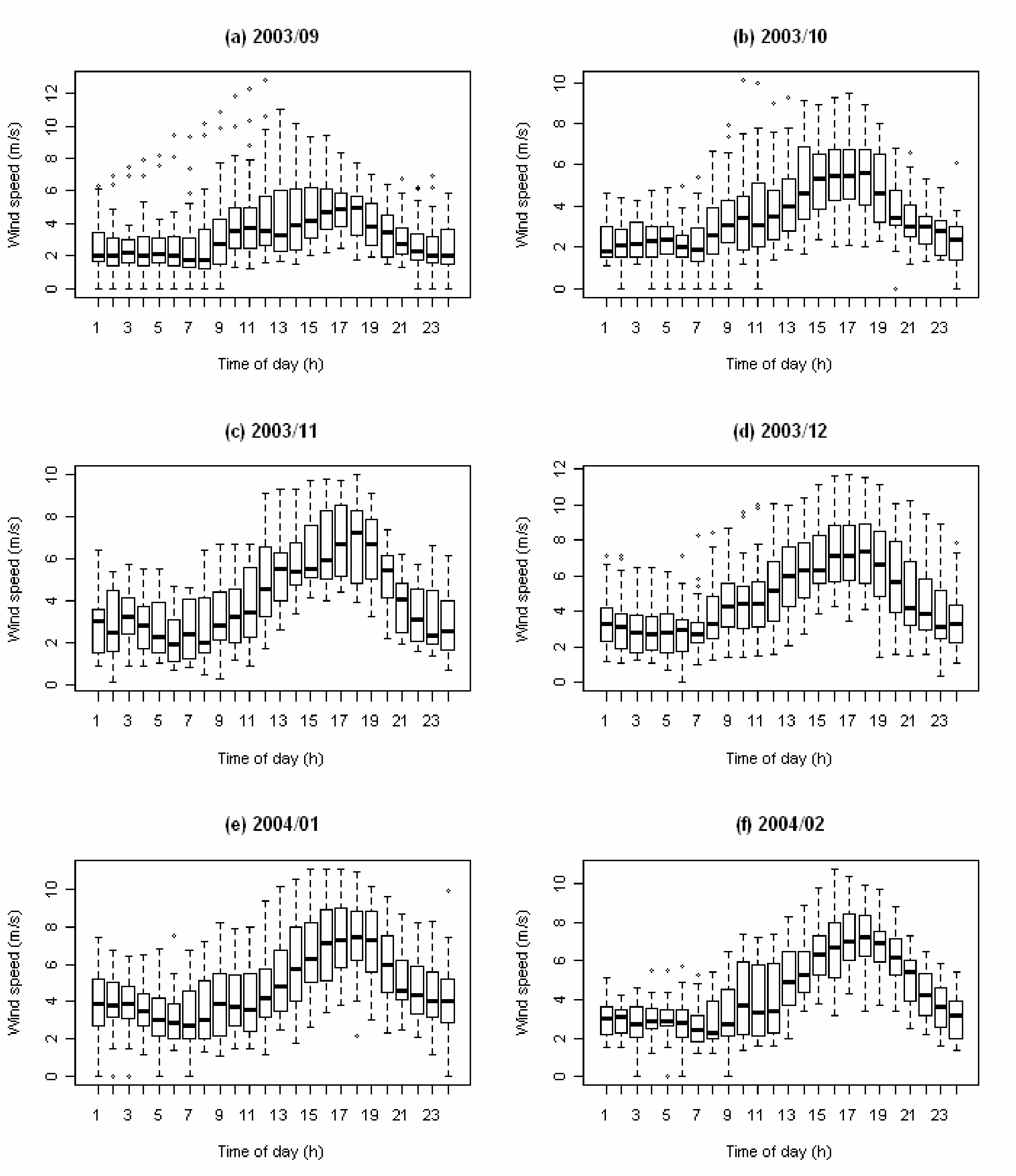

Fig. 7.3. Wind speed (m $s^{-1}$) measured at Langebaanweg (-32.97S 18.17E, height: 31 m) for 2003/9 to 2004/02, which corresponds with the period of one field work season; the weather station lies about 23 km inland from Malgas Island. Boxplots summarize, for each hour of the day, the measurements made across the whole month. Data sourced from the South African Weather Bureau.

# Appendix 7.1

Allometric equations to estimate the cost of flight (kJ $h^{-1}$) based on body mass (m[g] or M[kg]); wing span (b[cm], or B[m]); wing area (s[$cm^2$]); and wing length (l[cm]). Equations including the terms '× 3.6' or '× 4.187' convert the original model's units from Watts or kcal $h^{-1}$ respectively into kJ $h^{-1}$. Models are listed in the order given in Table 7.4.

| Model | mass range (kg) | No. sp. | Equation (kJ $h^{-1}$) |
|---|---|---|---|
| 1. Rayner (1990): eq. 1 (mass only) | (a) | – | $14.95 \times M^{1.161} \times 3.6$ |
| 2. Masman & Klaassen (1987) | 0.0038 – 1.0 | 14 | $17.36 \times m^{1.013} \times b^{-4.236} \times s^{1.926} \times 3.6$ |
| 3. Castro & Myers (1988): equation *b* | 0.0056 – 1.026 | 38 | $3.167 \times m^{1.464} \times L^{-1.614}$ |
| 4. Hails (1979) | (b) | 17 | $1.78 \times m^{0.64}$ |
| 5. Norberg (1996): equation 7.36 | 0.0125 – 1.026 | 33 | $51.5 \times M^{1.37} \times B^{-1.60} \times 3.6$ |
| 6. Kendeigh *et al.* (1977): non-passerines | (b) | 11 | $1.32 \times m^{0.69}$ |
| 7. Raveling & LeFebvre (1967) | (b) | 12 | $0.91 \times m^{0.74}$ |
| 8. Castro & Myers (1988): equation *b′* | 0.0056 – 1.026 | 32 | $2.230 \times m^{1.407} \times l^{-1.381}$ |
| 9. Berger & Hart (1974); equation 36 | 0.003 – 1.026 | 11 | $0.29 \times m^{0.72} \times 4.187$ |
| 10. Hart & Berger (1972) | (b) | 9 | $1.22 \times m^{0.73}$ |
| 11. Castro & Myers (1988): equation *c* | 0.0056 – 1.026 | 39 | $0.679 \times m^{0.818}$ |
| 12. Butler & Bishop (2000): wind-tunnel eq. | 0.037 – 0.48 | 7 | $58.8 \times M^{0.76} \times 3.6$ |
| 13. Kendeigh *et al.* (1977): passerines | (b) | 6 | $1.94 \times m^{0.69}$ |
| 14. Norberg (1996): equation 7.35 | 0.0125 – 1.026 | 33 | $57.3 \times M^{0.813} \times 3.6$ |
| 15. Nudds & Bryant (2000) | 0.003 – 1.026 | 29 | $61.718 \times M^{0.7902} \times 3.6$ |
| 16. Castro & Myers (1988): equation *a* | 0.0056 – 0.8 | 20 | $67.29 \times m^{1.763} \times b^{-2.275}$ |
| 17. Butler & Bishop (2000): DLW eq. | 0.13 – 0.384 | 9 | $69.5 \times M^{0.87} \times 3.6$ |
| 18. Teal (1969) | (c) | – | $271.93 \times M^{0.9034}$ |

(a) equation in Rayner (1990), no mass range or n provided; (b) equation in Castro & Myers (1988), no mass range given; (c) equation calculated by Nudds & Bryant (2000), mass range and no. sp. not given

# CHAPTER 8

# CHAPTER 8

# SYNTHESIS

## ENERGETICS OF FREE-RANGING CAPE GANNETS *MORUS CAPENSIS*: FAMILY AND POPULATION ENERGY BUDGETS

Thermodynamics is the study of the transformation of energy from one form to another, and from one system to another (Kane & Sternheim 1978). Biological systems are governed by the laws of thermodynamics, but contrary to purely physical systems, natural biological systems never reach the steady state predicted by theory. However, in the long term, biological systems must be in energy balance in such a way that the energy consumption equals the energy egested plus metabolized energy (Blem 2000). The egested energy includes the losses through faeces and urine. Metabolized energy can be partitioned into various physiological components: resting metabolism, heat increment of feeding, thermoregulation, activity, biosynthesis, and tissue energy (Visser 2001).

Computation of the energy requirements of entire family units requires the construction of energy budgets of free-living chicks and their parents. This constitutes a key factor in the interpretation of the life histories of seabirds (Drent *et al.* 1992, Visser 2001). It is also important in drawing up the energy requirements of whole populations or assemblages of birds (Blem 2000, Wiens 1984). Total energy demand of a population is derived from its size, i.e. number of birds, and energy expenditure of free-living birds. Energy consumption of marine birds has been estimated using bioenergetic models (Wiens & Scott 1975, Furness 1978, Furness & Cooper 1982, Bourne 1983, Furness 1984, Wiens 1984, Duffy & Siegfried 1987, Duffy *et al.* 1987, Adams *et al.* 1993). These models vary in complexity, from simple equations with few parameters, to detailed energy budgets with lots of parameters. Here I develop a simple bioenergetic model of Cape gannets *Morus capensis* based on empirically determined daily energy budgets of chicks and energy expenditure of breeding birds. The objective of the study was to answer such questions as: (i) how are energy and food requirements partitioned according to reproductive status and chick growth? (ii) What are the energy requirements and food consumption of the different breeding colonies under varying feeding regimes? (iii) What is the foraging efficiency of Cape gannets at the population level in contrast with a similar measure at the individual level?

The doubly labelled water method applied to free-ranging birds gives a measure of their field metabolic rate, which is equivalent to the metabolized energy minus the tissue energy (Speakman 1997). If we assume that adults maintain constant body mass during chick rearing, then the tissue energy is close to zero. Also assuming that the energy expenditure of parent birds is independent of brood mass (see Chapter 7), then all excess energy consumed is invested into the brood. Therefore, an indirect way of estimating the energy investment of parents into their progeny is obtained by deriving an energy budget of the chicks from hatching to fledging (see Chapter 3). The energy expenditure of the parent birds from egg laying to fledging of the offspring, plus the brood's energy budget constitutes the family energy expenditure (Visser 2001). A full account of the bioenergetic models is given in Appendix 8.1.

The energy expenditure of a Cape gannet family unit was 2 947.9 kJ yr$^{-1}$ for a normal foraging year, and it was 7.5% higher and 5.3% lower in a lean and good foraging year respectively (Table 8.1). The energy invested into the chick in a normal foraging year represents 5.1% of the annual energy consumption, or 12.7% of the energy expenditure during the breeding period (Table 8.1). Food consumption calculated from the family energy expenditure varies greatly according to the prey taken (assuming a single-prey diet): sardine was the lowest (451 kg $yr^{-1}$) and hake the highest (952 kg $yr^{-1}$). Adams *et al.* (1991) estimated food consumption for a pair of Cape gannets from lay-to-fledge at 194.8 kg of anchovy *Engraulis encrasicolus* per pair, however this figure is not comparable to this study; recalculating for energy equivalent of $CO_2$ (27.33 J $ml^{-1}$) and energy content of anchovy (6.74 instead of 4.89 kJ $g^{-1}$) this figure becomes 150 kg $pair^{-1}$, 35% below the value obtained for a normal foraging period.

Food consumption of chicks, from hatching to fledging, was estimated at 26, 29 and 32 kg of anchovy (or 20, 23 and 25 kg of sardine *Sardinops sagax*) for a lean, normal and good year respectively (Table 8.1). Adams *et al.* (1991) estimated food consumption at 51 kg of anchovy, recalculating this value for an energy equivalent of 6.74 kJ $g^{-1}$ amounts to 37 kg, which is 27% over the value for a normal year. Northern gannet *Morus bassanus* chicks were estimated to consume about 24 kg of fish during a 91 d nesting (Monvetecchi *et al.* 1984); this figure is 17% below the estimate for a Cape gannet chick in a normal year.

Foraging efficiency of the parents is defined as the ratio of family energy expenditure divided by the parents' energy expenditure (modified from Visser 2001), which gives an indication of the energy collected as food per unit of energy expended. When calculated on a daily bases, foraging efficiency reaches its maximum at the time when the chick's daily metabolizable energy peaks (Visser 2001). The overall foraging efficiency in a normal foraging year was 1.187, and the peak foraging efficiency was 1.290, a value of 1.30 was reported by Visser (2001). The ratio overall/peak foraging efficiency is 0.920, which means that Cape gannets are operating just 8% below the peak efficiency throughout the breeding season in a normal foraging year; this figure is 6.6% and 9% for a lean and good foraging year respectively.

As in the case of the family energy budget, population energy expenditure has been calculated for three different food conditions

(Table 8.2). Energy expenditure for the total population was estimated to be 455 × $10^9$ kJ $yr^{-1}$, in a lean year it was 4.5% higher and in a good year it was 4.7% lower. The estimated number of chicks produced was 64 543 in a normal year, whereas in a lean year it was 16.6% lower and 19.8% higher in a good year. Adams *et al.* (1991) calculated a population energy budget for Bird Island–Lambert's Bay and Malgas Island, they reported a total EE for both localities of 101 × $10^9$ kJ. I have recalculated the energy budget for the population sizes used in their study and obtained a total EE for both islands 14% above their value, the difference could be accounted for by the lower energy expenditure attributed to breeding birds in their study.

### Conclusions

Fisheries catches of sardine and anchovy for South Africa (Marine and Coastal Management, unpublished data) for the years 2003–2006 averaged 2.8 × $10^8$ kg $year^{-1}$ and 2.0× $10^8$ kg $yr^{-1}$ respectively, a combined catch of 4.8 × $10^8$ kg $yr^{-1}$. The consumption of both anchovy and sardine, assuming a 1:1 diet, for the South African colonies was 73.8 × $10^6$ kg $year^{-1}$, which amounts to 15% of the annual catch; however the diet composition of Cape gannets includes a large proportion of fish discards. This represents an important fraction of the commercial catch, which coupled with significant overlap between the main foraging areas of Cape gannets with areas where purse-seine fisheries caught most fish (Pichegru *et al* 2009) suggests the potential for competition between purse-seine fisheries and Cape gannets. This competition could be particularly intense for the colonies in the southern Benguela (Bird Island, Lambert's Bay, and Malgas Islands) where the fisheries concentrate their effort during the gannets breeding season (Pichegru *et al.* 2009). Poor chick growth at Malgas Island could lend support to this hypothesis, but an alternative explanation can be found in the mismatch between anchovy and sardine distribution and the foraging areas of gannets (Grémillet *et al.* 2008, Pichegru *et al.* 2010).

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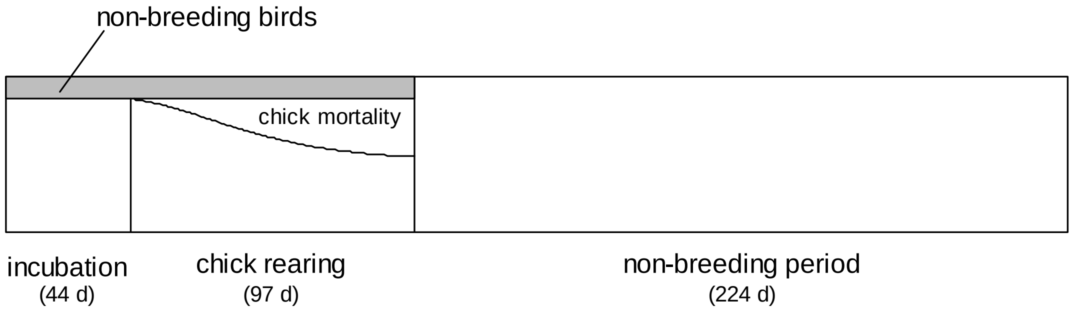

Fig. 8.1 Compartments of the population energy budget and activity pattern of Cape gannets. The simplified diagram is not a representation of the breeding phenology.

Table 8.1. Energy expenditure (EE), foraging efficiency (FE) and food consumption estimated for a Cape gannet family unit, including the non-breeding period of both adults (224 d), the energy expenditure during the breeding period (141 d), plus the chick's energy expenditure (97 d). The EE for different feeding conditions as well as the fish equivalent of single species diet are also given (see text for details).

| | Foraging conditions | | |
|---|---|---|---|
| | Lean | Normal | Good |
| **Energy expenditure (MJ)** | | | |
| breeding period (pair) | 1 280.1 | 1 040.5 | 869.9 |
| non-breeding period (pair) | 1 756.5 | 1 756.5 | 1 756.5 |
| chick | 132.3 | 150.8 | 162.7 |
| total | 3 168.9 | 2 947.9 | 2 789.1 |
| **Proportion of total EE** | | | |
| breeding pair | 0.404 | 0.353 | 0.312 |
| non-breeding pair | 0.554 | 0.596 | 0.630 |
| chick | 0.042 | 0.051 | 0.058 |
| chick (prop. of total breeding EE) | 0.094 | 0.127 | 0.158 |
| FE (peak) | 1.208 | 1.290 | 1.373 |
| FE (overall) | 1.128 | 1.187 | 1.250 |
| FE ratio (overall/peak) | 0.934 | 0.920 | 0.910 |
| **Food consumption (kg)** | | | |
| **Breeding period (pair)** | | | |
| anchovy | 250 | 203 | 170 |
| sardine | 196 | 159 | 133 |
| saury | 271 | 221 | 184 |
| hake | 413 | 336 | 281 |
| **Non-breeding period (pair)** | | | |
| anchovy | 342 | 342 | 342 |
| sardine | 269 | 269 | 269 |
| saury | 372 | 372 | 372 |
| hake | 567 | 567 | 567 |
| **Chick** | | | |
| anchovy | 26 | 29 | 32 |
| sardine | 20 | 23 | 25 |
| saury | 28 | 32 | 34 |
| hake | 43 | 49 | 53 |
| **Total** | | | |
| anchovy | 618 | 575 | 544 |
| sardine | 485 | 451 | 427 |
| saury | 672 | 625 | 591 |
| hake | 1 023 | 952 | 901 |

Table 8.2. Estimated annual energy expenditure and food consumption for each Cape gannet colony during tree different foraging conditions (see text for details).

| | | | | Energy expenditure (kJ x $10^9$) | | | | Fish consumption [a] ( x 1000 kg) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Food condition / island | number of pairs[b] | chicks fledged | proportion fledged | breeding birds | chicks | non-breeding birds | total | Anchovy | Sardine | Saury | Hake |
| **(1) lean year** | | | | | | | | | | | |
| Possession | 351 | 125 | 0.375 | 0.29 | 0.02 | 0.77 | 1.08 | 210 | 165 | 228 | 348 |
| Mercury | 1 414 | 488 | 0.363 | 1.17 | 0.08 | 3.09 | 4.34 | 846 | 664 | 920 | 1 401 |
| Ichaboe | 8 669 | 3 006 | 0.365 | 7.15 | 0.49 | 18.96 | 26.61 | 5 188 | 4 071 | 5 640 | 8 592 |
| Lambert's Bay | 10 529 | 3 649 | 0.365 | 8.69 | 0.60 | 23.03 | 32.32 | 6 301 | 4 944 | 6 850 | 10 435 |
| Malgas | 36 156 | 12 535 | 0.365 | 29.84 | 2.06 | 79.09 | 110.99 | 21 639 | 16 978 | 23 523 | 35 834 |
| Bird Is. P.E. | 98 149 | 34 021 | 0.365 | 81.00 | 5.59 | 214.69 | 301.29 | 58 740 | 46 089 | 63 856 | 97 275 |
| **Total** | **155 268** | **53 824** | **0.365** | **128.14** | **8.84** | **339.63** | **476.63** | **92 925** | **72 912** | **101 018** | **153 885** |
| **(2) normal year** | | | | | | | | | | | |
| Possession | 351 | 153 | 0.459 | 0.25 | 0.03 | 0.75 | 1.03 | 201 | 157 | 218 | 332 |
| Mercury | 1 414 | 586 | 0.436 | 1.00 | 0.11 | 3.04 | 4.14 | 808 | 634 | 878 | 1 338 |
| Ichaboe | 8 669 | 3 600 | 0.437 | 6.13 | 0.65 | 18.62 | 25.4 | 4 953 | 3 886 | 5 384 | 8 202 |
| Lambert's Bay | 10 529 | 4 377 | 0.438 | 7.45 | 0.78 | 22.62 | 30.85 | 6 015 | 4 720 | 6 539 | 9 962 |
| Malgas | 36 156 | 15 029 | 0.438 | 25.59 | 2.69 | 77.67 | 105.95 | 20 657 | 16 208 | 22 456 | 34 208 |
| Bird Is. P.E. | 98 149 | 40 798 | 0.438 | 69.47 | 7.31 | 210.84 | 287.62 | 56 075 | 43 998 | 60 959 | 92 861 |
| **Total** | **155 268** | **64 543** | **0.438** | **109.89** | **11.57** | **333.54** | **454.99** | **88 709** | **69 604** | **96 435** | **146 903** |
| **(3) good year** | | | | | | | | | | | |
| Possession | 351 | 178 | 0.534 | 0.22 | 0.03 | 0.74 | 0.99 | 193 | 152 | 210 | 320 |
| Mercury | 1 414 | 705 | 0.525 | 0.89 | 0.13 | 2.97 | 3.99 | 778 | 611 | 846 | 1 289 |
| Ichaboe | 8 669 | 4 320 | 0.525 | 5.44 | 0.80 | 18.23 | 24.47 | 4 770 | 3 743 | 5 186 | 7 900 |
| Lambert's Bay | 10 529 | 5 240 | 0.524 | 6.60 | 0.97 | 22.14 | 29.72 | 5 794 | 4 546 | 6 299 | 9 595 |
| Malgas | 36 156 | 18 013 | 0.524 | 22.68 | 3.34 | 76.03 | 102.05 | 19 896 | 15 611 | 21 629 | 32 948 |
| Bird Is. P.E. | 98 149 | 48 894 | 0.524 | 61.56 | 9.06 | 206.4 | 277.02 | 54 010 | 42 378 | 58 714 | 89 441 |
| **Total** | **155 268** | **77 350** | **0.525** | **97.39** | **14.33** | **326.51** | **438.24** | **85 441** | **67 040** | **92 883** | **141 492** |

[a] Assuming a diet composed 100% for each prey species

[b] From Crawford *et al.* (2007), figures correspond to 2005/2006 censuses, except for Lambert's Bay for which the 2003/2004 value was used

# Appendix 8.1

## I. Family unit model

For the purpose of modelling the energy requirements of a family unit the energy expenditure (EE) has been divided in the following components: EE during the incubation period; EE of the chick; and EE of the parents during chick rearing.

**Energetic costs**

The EE of an adult at the nest, either incubating an egg or brooding a chick, is taken as 36.03 kJ $kg^{-1}$ $h^{-1}$. This was calculated from the value of 25.8 J $ml^{-1}$ given by Adams *et al.* (2001), and corrected for an energy equivalent of $CO_2$ production of 27.33 J $ml^{-1}$ instead of the value of 25.8 J $ml^{-1}$ used in their study' therefore daily EE at the nest (kJ $d^{-1}$) is:

$$EE_{nest} = 36.03 \times 24 \times M \qquad (8.1),$$

where $M = 2.6$ kg, corresponds to the mean adult mass.

The daily EE of foraging during the breeding period, assuming that the foraging trip lasts 24 h (from Table 7.1), is given by

$$EE_{sea} = h_f \times EE_f \times M + (24 - h_f) \times EE_{drift} \times M \qquad (8.2),$$

where $h_f$ is the time spent flying (h); $EE_f = 227.3$ kJ $kg^{-1}$ $h^{-1}$, is the overall cost of flying (from Table 7.4); $EE_{drift} = 23.1$ kJ $kg^{-1}$ $h^{-1}$, is the cost of drifting or swimming (from Table 7.4). The value of $h_f$ was varied according to foraging conditions: good year $h_{f\,=}$ 4.67 hours; normal year $h_{f\,=}$ 6.95 hours; and lean year $h_{f\,=}$ 10.15 ; these values correspond to the 1st, 2nd and 3rd quantiles of flying time (calculated from data in Table 7.1). Therefore the mean EE per bird during the breeding season is $(EE_{nest} + EE_{sea}) / 2$, which amounts to 4 539, 3 690, and 3 085 kJ $d^{-1}$ for a lean, normal, and good food supply year respectively.

The daily EE during the non-breeding period, and that of failed breeders, was estimated as:

$$EE_{nonbr} = h_{f.q1} \times EE_f \times M + (24 - h_{f.q1}) \times EE_{drift} \times M \qquad (8.3),$$

where $h_{f.q1} = 6.95$ (h) corresponds to the first quantile of the time spent flying (h). It is assumed that during the non-breeding period gannets can reduce the time spent flying by remaining at sea for long periods of time because they are no longer central-place foragers. This is corroborated by the emptying of the colony as the birds that have failed or successfully fledged chicks no longer return to their nesting sites (pers. obs).

The chick energy budgets derived in Chapter 3 are used here to estimate total $EE_{chick}$ during chick growth; three different energy budgets were used to simulate $EE_{chick}$ at low, normal and good foraging conditions. These corresponded to chicks growing along the 25%, 50%, and 75% growth percentiles (see Chapter 3 for details). Total EE of chicks were 132.3, 150.8, and 162.7 MJ per fledging for low, normal and good foraging conditions respectively. The mean daily EE for chicks was: 1 364, 1 555 and 1 678 kJ $d^{-1}$ for a lean, normal, and good year respectively.

### Activity pattern

The activity pattern of a pair successfully fledging a chick was considered to be the same throughout the breeding season: that is, one adult always in attendance at the nest while the partner is foraging. During periods of poor food availability large chicks are often left unattended (pers. obs), but for simplicity of the calculations, this factor is not considered in the formulation of the model. Incubation and chick rearing periods of Cape gannets are 44 and 97 days respectively (Adams *et al.* 1991), total nest attendance is therefore 141 days.

### Family energy budget

The energy budget for a family unit is estimated as:

$$EE_{fam} = 141 \times (EE_{nest} + EE_{sea}) + 448 \times EE_{nonbr} + EE_{chick} \qquad (8.4),$$

which amounts to 2 947.9 MJ per family unit per year for a normal foraging year (Table 8.1), in a lean year it increases to 107.5% and decreases to 94.6% in a good year.

### Food consumption

Food consumption (Table 8.1) was calculated assuming a single-species diet. The metabolizable energy content of anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, saury *Scomberesox saurus* and hake *Merluccius* spp. are 6.74, 8.59, 6.20 and 4.07 kJ $g^{-1}$ respectively (Batchelor & Ross 1984). Fish consumption derived from these energy equivalents was further adjusted assuming Cooper's (1978) assimilation coefficient of 0.761. Although Cooper estimated assimilation for anchovy only, I have used this value for all prey species considered here because no other estimates are available for this species; this value is however comparable to values for the African penguin *Spheniscus demersus* and shorebirds (Cooper 1977, Klaassen *et al.* 1990). The amount of food delivered to chicks has not been modelled separately, but it is included in the chicks' energy budget.

### Limitations of the energetic model

An important limitation of this energy budget is that I have ignored seasonal changes in the weight of birds, which can be a potentially important source of inaccuracy because energy expenditure is a power function of body mass. Weight of Cape gannets is usually high at the start of the breeding season, and decreases during chick rearing (unpubl. data). The cost of egg production by females and the cost of nest establishment and defence by males, as well as nest building by both sexes have been ignored in these models because no estimates for the energetic costs of these activities are available. Walsberg (1983) gave a model to predict the energy content of reproductive organs coincidentally with yolk deposition of the first egg. The predicted value for a 2.6 kg Cape gannet is 3 576 kJ, which represents about 0.3% of the EE during a yearly cycle. So, ignoring this cost has a negligible effect on the overall energy budget.

Another assumption of the energy budget is that metabolic rates measured during the breeding season are representative of energetic costs throughout the non-breeding season, when costs are assumed to be lower. The likely overestimation of yearly energy expenditure may be offset, at least in part, by assuming shorter foraging trips during the non-breeding season (see equation 8.3 below).

With regard to the estimation of food consumption, seasonal changes in the energy content of prey have not been considered: for example Adams *et al.* (1991) measured energy content of anchovy at 4.89 kJ $g^{-1}$, whereas Batchelor & Ross (1984) measured 6.74 kJ $g^{-1}$ for the same species, although no details are given in either study, the difference could be attributed to seasonal changes, particularly related to the condition of the fish (Schülein *et al.* 1995).

## II. Whole population model

The population energy budget was built using the family energy budget as a basis, but taking into consideration the effect of chick mortality throughout the chick rearing period. Chick energy budget were truncated by mortality, and parents of failed chicks joined the non-breeding population for the remainder of the season. The juvenile population, i.e. from the time of fledging until the birds are 4–5 years old, is largely absent from the breeding colonies and it is excluded from the model.

### Chick mortality and breeding success

The rate of chick mortality in relation to chick age has not been reported previously, therefore the details briefly follow. During the breeding seasons of 2004/05 and 2005/06 I assessed chick survival and fledging success in 10 areas of the Cape gannet colony at Malgas Island, South Africa. Areas chosen were at least 3 m from the edge of the colony; a single marker was placed and all nests within a radius of 2–3 m were mapped and their content noted; mean number of nests per area was 42 ± 6 ($n = 20$). The content of the nests were monitored fortnightly from October to February, when most of the birds have fledged. Nest content was assigned one of the following categories: empty; prospecting adult; incubating; naked chick; small chick; small downy; medium downy; large downy; very large downy; feathered downy; feathered chick. Mean age for these chick categories were 8; 15; 20; 30; 50; 65; 75; and 90 d respectively. Chick mortality in relation to age approached a parabolic distribution, and was best described by the polynomial model:

$$M_t = 1.159 \times 10^{-3} \times t - 2.766 \times 10^{-5} \times t^2 + 1.662 \times 10^{-7} \times t^3 \quad (8.5),$$

where $M_t$ is the rate of chick mortality at age $t$ (days) ($r^2 = 0.841$, $p < 0.01$, $n = 16$).

### Population parameters

The data described above also provided the following population parameters: overall nesting success = 0.799 (0.816 in 2004/2005, $n$ = 412; 0.783 in 2005/2006, $n$ = 428); overall hatching success = 0.824 (0.866 in 2004/2005, $n$ = 373; 0.785 in 2005/2006, $n$ = 396); overall fledging success = 0.382 (0.283 in 2004/2005, $n$ = 286; 0.496 in 2005/2006, $n$ = 250); and overall breeding success = 0.306 (0.241 in 2004/2005, $n$ = 336; 0.370 in 2005/2006, $n$ = 335). Makhado *et al.* (2006) reported breeding success at Malgas Island for these two seasons: 0.42 fledglings per nest in 2004/2005 ($n$ = 55) and 0.02 fledglings per nest in 2005/2006 ($n$ = 201). The first figure is almost double the one reported in this study; however the figure for 2005/2006, which was measured in a small group of nests isolated from the core of the colony, was not representative of rest of the colony (Makhado *et al.* 2006). The overall breeding success of 0.306 chicks per pair reported in this study was below the threshold value of 0.32 necessary to maintain a population of Cape gannets at equilibrium (Makhado *et al.* 2006).

Population size for all six breeding colonies (Namibia: Possession, Mercury and Ichaboe Islands; South Africa: Bird Island–Lambert's Bay, Malgas Island and Bird Island–Port Elizabeth) correspond to the 2005/06 breeding season, except for Bird Island–Lambert's Bay for which the 2003/04 value was used (Crawford *et al.* 2007).

### Energy budget model

Calculations for the population energy budget have been partitioned according to Fig. 8.1. The number of incubating pairs is $N_{\mathrm{inc}} = N \times ns$, where $N$ is the number of breeding pairs in the population and $ns$ is the nesting success, therefore the number of non-breeding pairs is $N_{\mathrm{nonbr}} = N - N_{\mathrm{inc}}$. From equation 8.1 and 8.2 the population energy expenditure (PEE) of the breeding pairs during the incubation period is:

$$\mathrm{PEE}_{\mathrm{inc}} = 44 \times N_{\mathrm{inc}} \times (\mathrm{EE}_{\mathrm{nest}} + \mathrm{EE}_{\mathrm{sea}}) \qquad (8.6),$$

assuming a 1:1 ratio between time spent attending the nest and foraging. The energy expenditure of the non-breeding fraction of the population during the breeding period, plus the whole population during the non-breeding period is:

$$\mathrm{PEE}_{\mathrm{nonbr}} = 2 \times (141 \times N_{\mathrm{nonbr}} \times \mathrm{EE}_{\mathrm{nonbr}} + 365 \times N \times \mathrm{EE}_{\mathrm{nonbr}}) \qquad (8.7).$$

The energy expenditure during the chick rearing period of breeders, failed breeders and chicks can only be calculated in an iterative way.
The number of breeding pairs, which equals the number of chicks at age $t$ (days), is $N_{\mathrm{chk}[t]}$. The initial condition is given by $N_{\mathrm{chk}[1]} = N_{\mathrm{inc}} \times hs$, where $hs$ is the hatching success. From $t = 2$ to 97 (fledging), $N_{\mathrm{chk}[t]} = N_{\mathrm{chk}[t-1]} \times (1 - M_t)$, where $M_{\mathrm{t}}$ is the chick mortality according to equation 8.5. It follows that the number of failed breeders is $N_{\mathrm{fail.br}[t]} = N_{\mathrm{inc}} - N_{\mathrm{chk}[t]}$. We can now estimate the energy expenditure of the chick rearing pairs:

$$\mathrm{PEE}_{\mathrm{br}} = \sum N_{\mathrm{chk}[t]} \times (\mathrm{EE}_{\mathrm{nest}} + \mathrm{EE}_{\mathrm{sea}}) \qquad (8.8),$$

similarly, the energy expenditure of failed breeders is:

$$\mathrm{PEE}_{\mathrm{fail}} = 2 \times \sum N_{\mathrm{fail.br}[t]} \times \mathrm{EE}_{\mathrm{nonbr}} \qquad (8.9),$$

and the energy expenditure of chicks is:

$$\mathrm{PEE}_{\mathrm{chk}} = \sum (N_{\mathrm{chk}[t]} \times \mathrm{DME}_t) \qquad (8.10),$$

where $\mathrm{DME}_t$ is the chicks daily metabolizable energy (seen Chapter 3 for details); all summations are over $t = 1, \ldots, 97$.

The population energy budget then is defined by:

$$\mathrm{PEE}_{\mathrm{total}} = \mathrm{PEE}_{\mathrm{inc}} + \mathrm{PEE}_{\mathrm{nonbr}} + \mathrm{PEE}_{\mathrm{br}} + \mathrm{PEE}_{\mathrm{fail.br}} + \mathrm{PEE}_{\mathrm{chk}} \quad (8.11).$$

Population energy expenditure was converted into feeding rates for single prey according to the energy content given in the family energy budget.

All calculations have been done with R-statistical software (R Development Core Team 2009).