The Swift Tern *Sterna bergii* in Southern Africa: Growth and Movement

by

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Abstract

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This project had two main objectives: to investigate the growth patterns of Swift Tern *Sterna bergii* chicks and to study the movement patterns of this species within southern Africa. The subspecies of the Swift Tern which breeds in southern Africa is the nominate race; the estimated population size is 20 000 birds; its conservation status is Least Concern. The Swift Tern is one of six tern species that are sometimes placed in the genus *Thalasseus*; one of the characteristics of this group of species is that they "crèche" their chicks, a behaviour exploited in this project to facilitate the capture and recapture of most chicks present in the study colony regularly.

In the autumn 2002 breeding season, the growth of Swift Tern chicks was investigated at a breeding colony on Robben Island, Western Cape, South Africa. 470 chicks were ringed on first encounter, and a total of 1232 recaptures were recorded. Masses were recorded and measurements of body structures (wing, bill and legs) were made at approximately weekly intervals, in order to generate a time series of observations on individual chicks from hatching to fledging. Mean hatchling mass was 39 g (10% of adult mass), and chicks fledged when their wing lengths reached c. 257 mm, when their mass averaged 329 g, 82% of adult mass. Leg growth was accomplished rapidly, with tarsus length reaching 85% adult size within 20 days of hatching. At this age, wing length was only 18% of adult size; fledging wing length was 70% of adult size. Bill length at fledging was 56% of adult size; assuming the bill to be conical in shape, it was estimated that approximately 69% of bill growth was deferred to the period after fledging. The ordering of the development of these three structures, legs–wings–bill, is consistent with the idea that the chick's first need is to participate in crèche

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formation, then to be able to fly so that it can move with its parents to better feeding areas, where bill development can be completed.

Novel statistical approaches to the analysis of growth were developed, which provided an index of growth that was, as far as possible, independent of the stage of growth. Using this method, no impact of weather variables on growth was found; however, growth rates were slower towards the end of the breeding season than at the start.

An analysis of growth in the suborder Lari was undertaken. The well-known patterns of a decrease in growth rates with asymptotic body size and an increase in growth rates with increasing latitude were confirmed. The most striking result was that the patterns of increase in growth rates towards the poles were different between the northern and southern hemispheres; the rate of increase in the southern hemisphere was not as large as that in the northern.

Because their crèching behaviour facilitates ringing studies, large numbers of Swift Tern near-fledglings have been ringed, particularly in the Western Cape, over nearly three decades. A preliminary analysis, conducted in 1999, made the recommendations that the database as a whole warranted more detailed study, and that there was an opportunity to undertake a study of the movement patterns of chicks marked with individually engraved colour rings. This project implemented these recommendations.

Most chicks which were reared in the Western Cape moved eastwards along the coastline towards KwaZulu-Natal. The fastest-moving bird covered a coastal distance of 849 km within 15 days of ringing, a minimum average speed of 57 km/day. It was established that Swift Tern juveniles have a nursery area, which takes them about 100 days to reach, and where they remain until about 18 months of age, between Plettenberg Bay, Western Cape, and the East London area of the Eastern Cape; 50% of the recoveries made during the "nursery period" were in this section of coastline. The nursery area extended to northern KwaZulu-Natal. Not all fledgings move to the nursery area, because birds were found within the breeding areas during the nursery period. Some Swift Terns from the Western Cape moved northward towards Namibia after fledging, but the

proportion cannot be estimated because the process that generates recoveries in this region is entirely different due to the fact that the diamond-mining areas are closed to people, and scavengers remove carcasses from beaches on an almost daily basis. The longest distance moved was of a chick ringed at Lüderitz, Namibia, which was recovered in KwaZulu-Natal at a coastal distance of 2072 km, at an age of 15 months, within the "nursery period".

From an age of 3–4 years onwards, the overall pattern of movement of young birds showed a trend towards being progressively closer to their natal areas during the breeding season. For birds aged five years and older (breeding adults), the median distance recovered from natal colonies during the breeding season was 36 km, and the upper quartile was 112 km, indicating that 75% of adults were within the breeding area.

The use of individually engraved colour bands resulted in a substantial increase in the proportion of birds from which information was obtained, from less than 2% in earlier years when metal rings only were used, to close to 10%. If this study is repeated in the future, its value could be enhanced by recruiting observers to be evenly spaced along the coastline.

The pattern of post-fledgling movement of the Swift Tern was compared and contrasted with that of the African Black Oystercatcher *Haematopus moquini*, a species which similarly breeds mainly in the Western Cape, and which has recently been discovered also to have a nursery area, beyond the breeding area of adults, where immatures remain for the first few years of their lives. The main nursery for the oystercatcher is in Namibia. The contrasting directions in which the two species move to their nursery areas is most likely to be a consequence of the availability of food resources accessible to inexperienced feeders. For the Swift Tern, the advantages of being along the coastline of the Eastern Cape and KwaZulu-Natal for the period from about July onwards when it has to learn to hunt, are hypothesized to be the relatively calm waters along the coastline and the presence of an abundance of sardines *Sardinops sagax* in the region.

Acknowledgements

Chapter 1: Introduction

Chapter 1: Introduction to Terns

The terns, *Sternidae*

According to the classification in the *Handbook of Birds of the World* (Gochfeld and Burger 1996), there are 44 species of terns in the family Sternidae, in 10 genera. More than half of these (25) are in the genus *Sterna* and these are all characterised by having 'black caps' of black feathers on their heads (Gochfeld and Burger 1996). The other genera are *Gelochelidon* (one species), *Hydroprogne* (one species), *Thalasseus* (six species), *Chlidonias* (three species), *Phaetusa* (one species), *Anous* (three species), *Procelesterna* (two species), *Gygis* (one species) and *Larosterna* (one species). Gochfeld and Burger (1996) pointed out that the species within the three genera *Gelochelidon*, *Hydroprogne* and *Thalasseus* are frequently placed within the genus *Sterna*; even though this thesis focuses mainly on one of the *Thalasseus* species, it follows this latter route.

The terns are one of four families in the suborder Lari: the others are the gulls (Laridae), 51 species in seven genera; the skuas (Stercorariidae), seven species in two genera; and the skimmers (Rynchopidae), three species in a single genus. The total number of species within the suborder is 105. The Lari are one of three suborders of the order Charadriiformes; the other suborders are the Charadrii (waders) (216 species in 13 families) and the Alcae (auks) (22 species in one family) (del Hoyo *et al.* 1996). The taxonomy of this large order (343 species) is not stable.

Terns are considered to be closely related to gulls (Laridae) but they are more specialised with regards to nesting, diet and in the air (Gochfeld and Burger 1996). Most terns are pale underneath and grey on top, with a lean, extended body, in contrast to the more full-bodied rounded shape of gulls . Terns are found throughout the world and breed on all continents, including Antarctica. Most occupy coastal regions, and only 11 of the species are found inland. They are

gregarious and diurnal, and breed, forage and migrate in flocks (Gochfeld and Burger 1996).

The species of the genus "*Thalasseus*"

Within the terns of the genus *Sterna* there is a distinct subgroup of six species, which is often classified as a separate genus, *Thalasseus* (Table 1). All are crested terns with a black cap of elongated crest feathers. They are larger then the typical *Sterna* terns and most have bright yellow, orange or orange-red bills. They have characteristic display patterns and breed in large colonies. The chicks of these species crèche together, especially when disturbed; this habit is not found in any other tern except the Sooty Tern *Sterna fuscata* (Gochfeld and Burger 1996).

Of the six species of "*Thalasseus*" terns, two are in threat categories: the Chinese Crested Tern *Sterna bernsteini* is classified as Critically Endangered, and the Elegant Tern *Sterna elegans* is classified as Near-Threatened species. The other four species are not known to have any unfavourable conservation status at the global level (BirdLife International 2004, Table 1).

This thesis focuses on the chick growth and movements of the nominate subspecies of one of these six species, the Swift Tern *Sterna bergii bergii*. The following sections review what is known about these aspects of the *Thalasseus* species.

Brief overview of the "*Thalasseus*" chicks

There is some information available about chick growth of these six tern species. Three out of the 6 species have more information available about the breeding biology. The 3 include the Swift tern, *Sterna bergii*, Royal Tern, *Sterna maxima* and Sandwich Tern, *Sterna sandvicensus*. Studies done at One Tree Island and Eagle Island in Australia showed that Swift Tern chicks hatch at 41.8–45 g

(Higgins and Davies 1996). They leave the nest at about two days and fledge at c. 38 to 40 days (Heydorn and Williams 1993). They are dependent on their adult parents for at least four months after fledging. Breeding first occurs at the age of three years (Crawford *et al.* 2002). The Royal Tern *Sterna maxima* hatches at a mass of 45–55 g, fledges at c. 30 days and parental care lasts for five to eight months (Buckley and Buckley 1972). Very little is known about the Chinese Crested Tern *Sterna bernsteini* (BirdLife International 2004). The Elegant Tern *Sterna Elegans* hatches at c. 26.4g (Burness *et al.* 1999) and fledges at c. 35 days, parental care takes place for longer than 6 months (Monroe 1956). The Sandwich Tern *Sterna sandvicensis* has a hatching mass of 22–25 g, forms a crèche within one to two weeks and fledges in 28 to 35 days (Gochfeld and Burger 1996).Chicks of the Lesser Crested Tern *Sterna bengalensis* form a crèche a few days after leaving the nest and fledge within a period of 32 -35 days (Cramp 1985).

Migratory movements of the *"Thalasseus"* terns

Most terns species are migratory and those reproducing in the northern temperate regions winter in the tropics or the southern hemisphere, whereas the south temperate breeders have a great deal more disparity and less well known movement patterns.

There are 6 subspecies in the *Sterna bergii* species. *Sterna bergii gwendolenae*, frequently referred to as the Greater Crested Tern, is found in Australia and disperses several hundred kilometres around the colonies after breeding, undertaking a partial migration, although the movement of *Sterna bergii* are poorly known (Higgins and Davies 1996). The Middle Eastern birds of the subspecies *velox* move south to East Africa after breeding, and winter mainly from Egypt to Kenya overlapping with subspecies *thalassinus*, undertaking a medium to long distance migration. The subspecies *thalassinus* breeds on offshore islands (Laytham Island, Dar-es-Salaam) off Tanzania, and in the Seychelles and Chagos Archipelagos, and probably remains within this region in

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the non-breeding season. The nominate subspecies *Sterna bergii bergii* breeds between Algoa Bay in the Eastern Cape, South Africa and central Namibia, and is a medium distance migrant (Gochfeld and Burger 1996). The known non-breeding distribution extends from Luanda, Angola, to Kosi Bay, KwaZulu-Natal, South Africa (Cooper *et al.* 1990, Crawford 1997, Underhill *et al.* 1999) but almost certainly extends to southern and central Mozambique (Cooper 1977, Parker 1999, 2005). The existence of the subspecies known as *enigma* (Clancey 1975, 1979), although recognized by Gochfeld and Burger (1996) and listed by Wetlands International (2002), was questioned by Underhill *et al.* (1999) and has been disregarded by Hockey *et al.* (2005).

The three populations of the Royal Tern *Sterna maxima* breed along the west and east coasts of the Americas, and along the west African coast from Mauritania to Guinea. The birds disperse north after breeding, followed by a southern migration. Chicks ringed in South Carolina colonies are recovered mainly along the Gulf Coast. The West African birds *Sterna maxima albididorsalis* disperse north to Morocco after breeding, then move south to winter from Senegal to Angola (Gochfeld and Burger 1996). This species is a long-distance migrant. A large number occurs in the Gulf of Guinea where immatures remain for at least two years (Cramp 1985). It occurs in southern Africa as an irregular vagrant to Namibia (Ryan 1997b, Komen and Paterson 1999).

The Chinese Crested Tern, *Sterna bernsteini* breeds on the East Coast of China and migrates to the tropics from Taiwan to South China, Indonesia and the Philippines (Gochfeld and Burger 1996). Little is known about this species. Specimens were collected in China in 1937; between then and 2000 there were only three sight records of non-breeding birds. In 2000, six adults were found breeding on an island off Taiwan in among a colony of other tern species (BirdLife International 2004)

The breeding distribution of the Elegant Tern *Sterna elegans* is limited to southern California and the northern Gulf of California, Mexico (Burness *et al.* 1999). There is a post breeding dispersal northwards from Mexico to North

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California, and in years of warm water intrusions, south to southern British Columbia (Burness *et al.* 1999). They then move south, leaving California, for a southern wintering range from Guatemala to central Chile (Howell and Webb 1995). It has been recorded as a vagrant in South Africa; the only record was of a sighting of a single bird near Cape Town in January-February 2006 (J. Graham *in litt.*). This species has a medium to long distance migratory pattern.

One population of the nominate subspecies of the Sandwich Tern *Sterna sandvicensis sandvicensis* breeds on the coasts of western and northern Europe and then migrates south along the west coast of Africa to winter in the tropics. Adults move farther south than the young; the young usually spend their second year in Africa (Gochfeld and Burger 1996). This subspecies is a long-distance migrant and occurs in the non-breeding season as far as the Western Cape, South Africa (Cramp 1985). The population which breeds at the Black Sea winters mainly in the eastern Black Sea, and central or southeast Mediterranean. The Caspian Sea population winters mainly in the Persian Gulf and Arabian Sea (Cramp 1985). These two populations are thus short-distance migrants. The three populations in the New World, breeding on the Atlantic coast of are each classified as subspecies. The North American subpopulation *acuflavidus* winters south in Caribbean and Peru making it a medium to long distance migratory bird. The other two subpopulations *eurygnatha* breed and winter in South America, making them short distance migrants (Cramp 1985).

Three of the four populations of the Lesser Crested Tern *Sterna bengalensis* breed in the Mediterranean Sea, Red Sea, Persian Gulf and the Maldives and Laccadives in the northern Indian Ocean. The movements of these populations are poorly studied; the species is considered a partial migrant, and some birds migrate to the east coast of Africa and Madagascar. It is common as far south as the coast of KwaZulu-Natal, South Africa, and a vagrant to the Western Cape (Cramp 1985, Gochfeld and Burger 1996, Ryan 1997a). Non-breeders often spend their first breeding season in the wintering regions in the south (Cramp 1985). The fourth subpopulation of the Lesser Crested Tern is the subspecies *torresii* which breeds in Sulawesi, New Guinea and north-eastern

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Australia. During non-breeding their range is throughout the South West Pacific Ocean. This population is possibly a medium distance migratory population although their movements are poorly known (Higgins and Davies 1996)

The Swift Tern *Sterna bergii bergii* of southern Africa

The biology of the nominate subspecies of the Swift Tern *Sterna bergii bergii*, the taxon studied in this thesis, is reviewed. Swift Terns are common in southern Africa and are found on marine shores and estuaries, frequently in flocks exceeding 50 birds, and often in association with other terns or gulls (Harrison 1983, Crawford 1997, Hockey *et al.* 2005).

Breeding in southern Africa has been recorded at 27 localities between Swakopmund (22° 30'S; 14°31'E), Namibia, and Stag Island (33° 50'S; 26° 17'E), Algoa Bay, South Africa (Cooper *et al.* 1990, Crawford and Dyer 2000). However, 80% of the breeding takes place in the Benguela upwelling ecosystem on islands between Saldanha Bay and Cape Town (Crawford and Dyer 1995). Usually, six to seven of the 27 known localities are occupied in any one breeding season; most of these are marine islands protected by conservation authorities (Cooper *et al.* 1990). Swift Terns are nomadic between these different sites and breeding usually peaks in February to March in the Western Cape. This period covers late summer and early autumn and most of the young fledge by April and May (Crawford 1997, Underhill *et al.* 1999).

Food availability is a factor that affects the number of birds breeding and where the birds are likely to breed (Crawford 2003). Counts during the years 1987 to 2000 have shown that the number of birds breeding in any one year can vary. There was a reduction in breeding pairs of 67% in a year when food was scarce (Crawford 2003). In one year there were 5 668 breeding pairs and in another 1 449 breeding pairs. This variability relates to food availability, because there are large inter-year fluctuations in the distribution and biomass of both Cape Anchovy *Engraulis japonicus* and Sardine *Sardinops sagax* off southern Africa (Barange *et al.* 1999). During the breeding season fish form 86% of all

prey items fed to chicks; 60% of this fish diet is pelagic shoaling fish of which the Cape Anchovy is the most abundant (Walter 1984, Walter *et al.* 1987). The size of the fish fed to chicks varies from 7 mm to 138 mm in length and from 0.1 g to 30.0 g in mass (Walter *et al.* 1987, Hulsman *et al.* 1989).

The Swift Tern's breeding biology has been relatively well described. Swift Terns breed in colonies, often in association with Hartlaub's Gulls *Larus hartlaubii* (Cooper *et al.* 1990). The nests are shallow scrapes in bare sand, rock or coral and usually on open flat ground (Gochfeld and Burger 1996, Crawford and Dyer 2000). Egg laying is synchronised within the Swift Tern breeding groups, with usually one egg per clutch, and the incubation period averages 28 days (Langham and Hulsman 1986, Heydorn and Williams 1993). The average time that chicks remain in the nest after hatching is two to four days, and chicks can fly when c. 56 days old (Heydorn and Williams 1993). Kelp Gulls *Larus dominicanus* have been observed feeding on eggs and nestlings of the Swift Tern, particularly as a result of human disturbance (Komen *et al.* 1986, Erwin 1989). Most fledglings leave the colony with at least one parent and within 19 days of fledging (Langham and Hulsman 1986). Parental recognition takes place by a 'kurriet call' when visual contact is not possible (Veen 1986). According to Burger (1980), quantitative data on post-fledging parental care of terns is extremely sparse, although the existence of post-fledging parental care has been mentioned for several species, including the Swift Tern (Ashmole and Tovar 1968, Dunn 1972, Buckley and Buckley 1974, Feare 1975). This long period of parental care is thought to be due to the juvenile birds requiring a long time to learn the skills necessary for feeding themselves. Swift Terns usually first breed when three years old or more (Buckley and Buckley 1974, Crawford *et al.* 2002). All tern species feed primarily by plunge diving for fish, the role of parents teaching and caring for their offspring during this period is unclear (Burger 1980). The fishing abilities of adult and juvenile Royal Terns *Sterna maxima* and Sandwich Terns *Sterna sandvicensis* has been investigated by Dunn (1972) and Buckley and Buckley (1974).

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Table 1: A description of the populations of the subspecies of the six species of '*Thalasseus*' terns (Cramp 1985, Olsen and Larsson 1995, Gochfeld and Burger 1996, Wetlands International 2002, BirdLife International 2004, Higgins and Davies 1996)

Sub species	Breeding range	Non-breeding range	Estimated population size	Mass (g)	Wing length (mm)	Clutch size	Conservation status
Sterna bergii (Swift Tern, Crested Tern, Great Crested Tern)							
bergii	Namibia to Western Cape South Africa	Angola to southern Mozambique	20000	402	365	1-2	Least concern
enigma (Validity of this subspecies is doubtful)	Madagascar, Juan de Nova, Mozambique	Zambezi Delta, Mozambique to KwaZulu-Natal South Africa	7500–10000				
thalassina	Tanzania, Seychelles, Chagos		1300–1700	320–350	322-356		
velox (Red Sea & NE Africa)	Red Sea and north-western Somalia	Red Sea & NW Somalia, South to Kenya		340–400	354-381		
velox (Arabian Gulf and Indian Ocean)	Arabian Gulf, east to Maldives, Sri Lanka, Myanmar	Indian Ocean, Kenya to Myanmar		340–400	354-381		
gwendolenae	Northern and north-western Australia			280	330-362	1	
cristata	Japan, Tai-wan, eastern China, Indonesia–Philippines, Eastern Australia, south-western Pacific Islands			325–383	325-365		

Table 1 continued

Sub species or population	Breeding range	Non-breeding range	Estimated population size	Mass (g)	Wing length (mm)	Clutch size	Conservation status
Sterna maxima (Royal tern)							
maxima (West Atlantic)	Coast of Maryland to Texas, West Indies, Guianas, southern Brazil, Uruguay, northern Patagonia	Coast of South Carolina to South Brazil	139 000	380–500	346-390	1	Least concern
maxima (East Pacific)	Coast of southern California to Sinaloa	Coast of California south to Peru	10 900	390–475	351-375	1	
albididorsalis	Coast of West Africa, Mauritania to Guinea	Coast of West Africa, Morocco to Angola, vagrant to Namibia	135 000–165 000	320–440	354–366	1	
Sterna bernsteini (Chinese Crested Tern)							
bernsteini	Poorly known, probably eastern Chinese Coast	Taiwan and southern China to Indonesia and Philippines	<50				Critically Endangered
Sterna elegans (Elegant Tern)							
elegans	Pacific coast, southern California and Gulf of California, Mexico	Pacific coast, from California to Chile	51 000–90 000	217–300	314	1	Near Threatened

Table 1 continued

Sub species	Breeding range	Non-breeding range	Estimated population size	Mass (g)	Wing length (mm)	Clutch size	Conservation status
Sterna sandvicensis (Sandwich Tern)							
sandvicensis (West Europe)	Coast of western and northern Europe	Western and north-western African coast, south to South Africa	159 000– 171 000	130– 285	283- 325	1-2	Least concern
sandvicensis (Black Sea)	Black Sea Coast	Mediterranean and Black Sea coasts	44 000– 73 000				
sandvicensis (Caspian Sea)	Caspian Sea	Coasts of Persian Gulf and southern Red Sea to Pakistan, India and Sri Lanka	110 000				
acuflavidus	Northern and central American coast, Virginia to Belize, and Caribbean	Caribbean to southern Peru and Uruguay	100 000	175– 202	275- 305		
eurygnatha (southern Caribbean)	Netherlands Antilles to Venezuela	Southern Caribbean, Atlantic coast of South America to Argentina	35 000– 37 000	250– 300	282- 310		
eurygnatha (Eastern Brazil to Argentina)	Eastern Brazil to Argentina	Southern Caribbean, Atlantic coast. South America to Argentina	10 000	170– 210	299- 327		

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Table 1 continued

Sub species	Breeding range	Non-breeding range	Estimated population size	Mass (g)	Wing length (mm)	Clutch size	Conservation status
Sterna bengalensis (Lesser Crested Tern)							
par (Mediterranean)	Libyan coast	Southern Mediterranean, North-west and western African coast	4 000	185–242	280-324	1	Least concern
par (Red Sea and Gulf of Aden)	Red Sea and Gulf of Aden	West Indian Ocean to South Africa and Madagascar	30 000				
bengalensis	Persian Gulf, Pakistani coast, Maldives and Laccadive Islands	Indian Ocean, south to Sri Lanka and possibly South Africa	150 000–180 000				
torresii	Sulawesi to New Guinea and northern and north-eastern Australia	South West Pacific Ocean		208-243	304		

Chapter 2: Growth

Chapter 2: Growth patterns of Swift Terns *Sterna bergii* on Robben Island in the 2002 breeding season

Abstract

In this chapter the growth patterns of Swift Tern chicks *Sterna bergii* was investigated. Chicks were ringed at a breeding colony on Robben Island in 2002, with a total of 470 chicks being ringed and 1232 recaptures. Masses were recorded, and measurements taken on a weekly basis to generate a time series of observations on individual chicks form hatching to fledging. Mean hatching mass was 39 g; chicks fledge when their wing length reaches c. 257 mm, when their mass is on average 329 g, which is 82% of the adult body mass.

Measurements were obtained for 22 breeding adult Swift Terns. Adult Swift Terns had a mean wing length of 365 mm, with a fledging wing length of c. 257 mm, most of the Swift Terns fledged when their wing length had reached 70% of adult wing length. Leg growth was accomplished rapidly, with tarsus length reaching 85% of adult mass within 20 days of hatching. At this age the wing length was only 18% of the adult size. Bill length at fledging was 56& of adult size, and if the bill was assumed to be conical in shape it was estimated that approximately 69% of the bill growth was deferred to the period after fledging. The ordering of the development of these three structures, legs-wing-bill, is consistent with the idea that the chicks first need to participate in a crèche, then they need to be able to fly to move with parents into better feeding areas, where bill development can be completed.

Novel statistical approaches were developed for the analysis of growth, which provided and index of growth that was, as far as possible, independent of the stage of growth. Using this method, no impact of weather variables on growth was found; however, growth rates were slower towards the end of the breeding season than at the start.

An analysis of growth in the suborder Lari was undertaken. The well-known patterns of a decrease in growth rates with asymptotic body size and an increase in growth rates with increasing latitude were confirmed. The most

striking result was that the patterns of increase in growth rates towards the poles were different between the northern and southern hemispheres; the rate of increase in the southern hemisphere was not as large as that in the northern.

Introduction

In birds, growth of chicks usually follows some form of sigmoidal curve, in which the initial rate of increase is slow, followed by a period of fairly rapid growth before the levelling off to an asymptote (Saffer *et al.* 2000). Within a species, growth rates vary around an average, and this variability can be correlated to explanatory variables operating at a local scale, such as timing of hatching within the breeding season, age and experience of the adults, and environmental factors including weather and short-term food availability (e.g. Robinson *et al.* 2002, Stienen and Brenninkmeijer 2002). Likewise, average growth rates vary between species and localities, and can be correlated to explanatory variables which are overall constraints operating on a wider scale, such as mean adult body mass, average length of the breeding season at the locality, latitude, average brood size and other physiological factors (e.g. Ricklefs 1973, Langham 1983, Klaassen 1994, Starck and Ricklefs 1998a, Visser 2001).

The growth of seabirds is likely to be particularly sensitive to these extrinsic factors. This sensitivity arises because most seabirds breed on land adjacent to the sea and chicks remain at or near the hatching site until they fledge; for many species, parents therefore need to cover long distances in search of food in the oceans, which represents a patchy, dynamic and unpredictable environment.

In this chapter, the growth of the Swift Tern *Sterna bergii* was studied at a single site during one breeding season. It was investigated whether or not environmental variables associated with weather were correlated with the growth rate (as done, for example, by Robinson *et al.* (2002) for two other species of terns). The variability in increase in mass was investigated in relation to the variability of growth of the wing, bill and legs. In particular, smaller fluctuations in the growth of wings than of mass was anticipated. Once chicks fledge they are mobile, enabling the family (consisting of the parent(s) and chick) to exploit feeding areas outside the range of the breeding site and reducing parental

foraging distances. In the closely related Sandwich Tern *Sterna sandvicensis*, studies have shown that chicks fledge at a wing length of approximately 190 mm, approximately 62% of the adult wing length of 305 mm (Stienen and Brenninkmeijer 1999, 2002). Because mobility is so important, attaining this wing length is probably a priority during the pre-fledging period.

Growth rates within the taxonomic context of the Swift Tern were compared. This inter-species comparison was made within the suborder Lari (as defined by Del Hoyo *et al.* 1996). Terns are one of four families within the Lari; this taxon was chosen because all species within it (skuas, gulls, terns and skimmers) are semi-precocial, having the same developmental mode within the so-called altricial-precocial spectrum. The other two suborders of the order Charadriiformes comprise of species with other developmental modes (del Hoyo *et al.* 1996): most of the Charadrii (waders and allies) are precocial, with mobile chicks feeding themselves from hatching; within the Alcae (auks and allies), the development modes ranges from semi-precocial to precocial, with chicks of several species leaving the nest and going to sea within days of hatching, enabling parents to reduce travelling time. By confining this investigation to a suborder which is uniform with regard to developmental mode, we were able to investigate the effects of latitude and adult size on growth rate more effectively. This analysis is motivated by Starck and Ricklefs's (1998a, b) overall review of growth rates in birds in relation to adult body mass. They assembled a database which contained 1117 estimates of the growth rates for 557 species of birds. They demonstrated the general overall trend of an inverse relationship between adult body mass A (g) and the growth rate of chicks. For logistic growth rates, K_L, their allometric relationship was $K_L = 0.962 \, A^{-0.316}$; the exponent of body mass was negative so larger species grow more slowly than did the smaller species. They also performed analyses within orders and found similar relationships for most orders, however the exponent of body mass varied considerably between orders and they showed that these differences were statistically significant. For the Laridae (defined by them as the gulls and terns), the exponent of body mass

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in the allometric relationship was –0.190, suggesting a flatter relationship for growth rates in relation to body size than for all species.

The aim of this paper is to estimate growth rates for Swift Terns. We achieved this estimation by devising a non-parametric approach to fitting growth curves, because we found that the standard growth models, such as logistic and Gompertz, did not describe the data particularly well. We also undertook a comparison of the growth rates of the suborder Lari, which includes the skuas, gulls, terns and skimmers.

Material and Methods

Fieldwork

In February 2002 Swift Terns bred on Dassen Island, Western Cape. The chicks that hatched in this breeding attempt were consumed by Great White Pelicans *Pelecanus onocrotalis* during March (per. obs). Presumably these breeding terns then relocated to Robben Island (33° 47'S, 18° 21'E) (see Crawford & Dyer (2000) and Underhill *et al.* (2001) for a description of the island and its seabirds and shorebirds). The terns established a breeding colony on the island in April 2002. Thus the breeding event during which this study took place was towards the end of the normal breeding period, described as February–April for Robben Island (Crawford *et al.* 2002). By 30 April 2002, a peak count of 485 nests was made at the colony on Robben Island.

Growth measurements of the Swift Tern chicks at this colony were made at approximately weekly intervals between May and July 2002. The objective was to catch individual chicks at regular intervals throughout the period between hatching and fledging. Swift Terns "crèche" their chicks and a pen was set up outside of the area where adults were still incubating eggs and small chicks. The chicks were herded into the pen by a team of about 10 people. On first capture, the chicks were ringed with a standard stainless steel ring (SAFRING 6 mm); most chicks were also fitted with an individually engraved Darvic colour bands

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(Pro-Touch, Saskatoon, Canada) prior to fledging, and an observer programme to resight these birds was established (Further description of colour bands on page 56 Chapter 3). The following measurements were taken, as described in Table 1: wing length, head length, culmen length, tarsus length and foot length were measured (mm). Chicks were weighed using Pesola spring balances of appropriate size for the mass of the chick. A sample of birds aged less than about three days was obtained by ringing and measuring chicks which were still in the nest cup; care was taken to minimize disturbance by moving slowly and carefully through the colony. The tarsus was sufficiently well developed that it was feasible to ring hatchlings with the standard stainless steel band. All measurements were made by a small group of people, who remained relatively constant on the weekly field trips; attempts were made to standardize measurements between observers. Even so, individual birds were measured by different people on each recapture. Given the large number of birds and the need to keep disturbance to a minimum, it would have been impossible for a single person to have done all the measurements on each particular bird. There are no values in the literature for head length or foot length of adult Swift Terns in southern Africa; thus a sample of breeding adults was trapped using noose mats, and their masses and measurements recorded (Table 5).

Statistical analysis for growth curves for Swift Terns

The growth patterns of most measurements did not conform to the standard growth curves, such as logistic or Gompertz (Reiss 1989). A new descriptive statistical approach was therefore devised. For all chicks that were captured more than once, growth rates were calculated between each pair of captures for mass and for each structure: wing length, head length, culmen length, tarsus length and foot length. The average of the pair of measurements was also calculated. For example if successive masses at times t and u were m_t and m_u, the growth rate over this time period is g = (change in size)/(time period) = $(m_t - m_u)/(t-u)$ and the average of the pair of measurements is $a = (m_t + m_u)/2$. All the

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pairs of values (*a*, *g*) were plotted. This was done for mass and for each length measurement. Identical "growth-rate vs size" plots were produced by Schoener and Schoener (1978) in their analysis of growth rates of lizards. These growth-rate vs size plot are referred to as "growth rate plots".

The initial focus was on growth in mass. For a set of target masses at small increments between hatching mass and fledging mass, the average growth rate at each of these masses was estimated. This estimation was achieved by using weighted regression. For the target mass at which growth rate needed to be estimated, weights for all the pairs of observations (*a*, *g*) were calculated in such a 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 8.0. This value is about 2 % of the adult mass (see below). This formula results in weights attached to observations 8 g distant from the target mass being substantial (weight 0.37), at 12 g distant the weight (0.105) is small, and at 16 g distant the weight (0.018) is tiny. Observations more than 16 g distant from the target mass thus have negligible weights within the regression calculations. The weighted linear regression was fitted to predict growth rate from mass using these weights, and this regression line, fitted by GenStat8 (Payne 2005) was used to predict the growth rate g^* at the target mass. Using this weighted approach, the estimated growth rate then depends on observed growth rates in the neighbourhood of the target mass.

By varying σ, the length of the influential neighbourhood can be modified. The smaller the value of σ, the shorter the neighbourhood, the fewer the observations that are effectively included, and the estimated growth rates at the target masses are based on small samples and tend to be unstable. The larger the value of σ, the wider the neighbourhood and the more stable the estimates; however, the inclusion of growth rates distant from the target mass can result in biases. There is thus a trade-off between values of σ which are large enough to prevent instability of the estimates and values which are small enough that the estimate refers to a small neighbourhood of the target mass. A similar

compromise has to be made in various statistical smoothing methods (Silverman 1986), where the amount of smoothing depends on the size of the smoothing window (frequently referred to as "bandwidth"); too small a window results in little smoothing, too large a window results in over-smoothing, with important aspects of the data being obscured. There are automatic methods to choose the width of the smoothing window, but the best approach remains visual inspection of the results (Silverman 1986). The visual inspection approach was used to choose $\sigma = 8$; however, the results do not depend critically on the choice of a particular value for σ. Experimentation showed that if a chosen value was twice as large or half as small, the results would have been nearly identical.

An approximate standard deviation of mass at each target mass was estimated. The same weights used for the regression were used to estimate a weighted standard deviation s_{m^*}; the formula $s_{m^*}=(1/\sum w)((w(g{-}g^*)^2)$ was used. An approximate coefficient of variation for each target mass was calculated as $CV^*= 100 \times (s_{m^*}/m^*)$. This coefficient of variation provides a measure of the variability of the growth rate for each target mass.

The estimated growth rates at each target mass were plotted, and the points were linked using an interpolated line. Likewise, approximate lower and upper confidence limits for the growth rates were plotted. A normal distribution was assumed, so that the lower and upper confidence limits were $g^*{-}1.96\ s_{m^*}$ and $g^* + 1.96\ s_{m^*}$ respectively. Using hatchling mass as the starting value on day 0, the growth rate curve was integrated to produce a plot of mass against time. This provides a non-parametric growth curve which 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.

For each successive pair of measurements on a chick, a comparison was made between the observed growth rate and the expected growth rate in the interval between the two measurements. The expected growth rate was computed at the average of the two measurements, and its approximate standard deviation calculated as described above. The standardized growth rate was then computed using the conventional approach to standardization –

dividing the difference between the observed and expected growth rate by the standard deviation. In symbols, if the observed growth rate is g, the predicted growth rate is g^* and the estimated standard deviation at this growth rate is s^*, then the standardized growth rate z is defined to be $z = (g-g^*)/s^*$. 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. The z-values can be interpreted as an index of the extent to which growth in the interval is above or below expected; through the mechanism of dividing by the standard deviation, the index is independent of the stage of growth. In other words, the z-values, which are dimensionless. They represent a common currency to measure departures from "average" growth, which are independent of the size when the measurement is made. In other words, the z-score are comparable across chicks of all sizes.

If the analyst is prepared to make the assumption of normality (which to a first approximation is probably reasonable), the magnitudes of z-scores can be expected to be in keeping with the standard normal distribution; for example, approximately 95% of the z-scores can be anticipated to lie between the values −1.96 and +1.96; less than 0.5% of the values can be anticipated to be smaller than −2.58 or larger than +2.58. These large values should be screened to consider the possibility that one or other of the measurements were erroneous.

Because the index is independent of growth stage, it becomes possible to investigate the effect of explanatory variables on growth rates. Frequently required comparisons are between arrays of growth rate deviations for birds of different periods (e.g. comparing early breeders vs late breeders), sites, years, hatch orders (e.g. comparing growth rates of A-, B- and C-chicks) and clutch sizes (e.g. comparing growth rates of chicks from one-egg and two-egg clutches). Making the assumption of normality, analysis of variance can be used to test these differences; alternatively either the Kruskal-Wallis test or permutation tests (such as the one devised by Oatley and Underhill 2001) can be used to compare groups. It is also possible to relate the standardized growth rate to explanatory variables in multiple regression analyses (e.g. the growth

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rates can be related to contemporaneous explanatory variables such as temperature, wind-speed, provisioning rate, etc). In this study, the only available explanatory variables were hourly weather data for Robben Island obtained from the South African Weather Service, from 1 May to 8 July 2002, covering the entire period of the study.

Although the description of the statistical method above is in terms of mass, it also applies to the 5 length measurements of structures such as wing length, head length, bill length, foot length and tarsus size.

Analysis of growth rates of the suborder Lari

To undertake the study of growth for species within the suborder Lari, as defined by Del Hoyo *et al.* (1996), standard Gompertz growth rates were used because this growth function is the one which most frequently is a reasonable approximation to the growth patterns of seabirds (Ricklefs 1973). Growth rates and adult body mass were collated from the literature, using mainly Starck and Ricklefs (1998b) as a source. The original papers were consulted to provide information on the latitude and longitude of each study site. If the published growth rates were logistic, they were converted to Gompertz growth rates, using the relationship between the growth parameters of these curves: $k_L = 0.68\ k_G$ (Ricklefs 1973). Note that many of the source papers do not include the growth rates; the data in the papers were digitized by Starck and Ricklefs (1998b), and the growth curve fitted to the observations. The growth rates were modelled with a series of multiple linear regression models using body mass and latitude, and transformations thereof, as explanatory variables. To use the data for the Swift Tern from this chapter in the analysis, Gompertz growth models were fitted to the data for each of the chicks for which we had more than one mass measurement separated by at least 10 days. The median of these values (K_G=0.044) was used as the growth rate in the analysis.

Results

Swift Tern chicks were caught on a series of dates from 3 May 2002 to 8 July 2002 (Table 2). Steel rings were placed on a total of 88 nestlings (chicks still in the nest cup) and 382 runners (chicks that had left the nest cup but not yet fledged). No chicks were recaptured in the nest cup after initially being ringed, so all recaptures were of runners. In total there were 1232 recaptures of the 470 chicks ringed (Table 2).

Of the 88 chicks measured, weighed and ringed while still in the nest cup, 77 were hatchlings (still wet or with a conspicuous egg tooth). The mean mass of hatchlings was 39 g (SD 4.8 g) (Table 3). The mass of hatchlings showed a coefficient of variation (CV) of 12.3%; head length (CV 4.2%) and foot length (CV 4.9%) showed the least variability of the structures measured (Table 3).

The histogram of wing lengths showed that when they were last captured, most chicks had wing lengths were between 250 mm and 270 mm; few birds with larger wing lengths were retrapped (Fig. 1). We therefore infer that most chicks fledged when their wing lengths were in this interval. Assuming that attaining a wing length in this interval is the key fledging criterion, we computed the average sizes of the structures for chicks with wing lengths in this interval (Table 4). We used these size values for mass, wing, head, bill, foot and tarsus (Table 4) to provide guidelines for the upper limits of the growth rate plots and the growth curves (Figs 2–7). The mean wing length within this sample was 257 mm, and this was taken as fledging wing length. This approach suggested that the mean fledging mass is 329 g. Likewise, the mean size values for hatchlings (Table 2) were used as the initial values on day 0 for growth rate plots and the growth curves (Figs 2–7)

Measurements were obtained from 22 breeding adult Swift Terns (Table 5). The mean wing length was 365 mm, similar to the mean wing length of 357 mm, based on a sample of 18 birds, in Hockey et al. (2005). This information indicated that fledging wing length is c. 70% of the wing length of breeding adults (Tables 4 and 5). Fledging mass was 82% of adult mass. Foot

length and tarsus length of fledglings and adults were similar. The head length of the fledglings was 76% of adult head length, but the bill length at fledging was only 56% of adult bill length (Tables 4 and 5). By subtraction, the mean skull length (ie the distance from the base of the bill to the back of the skull) of the adults was 57.0 mm, and that of the fledglings was 56.7 mm, indicating that it was the bill rather than the skull which had not attained adult dimension at fledging.

Statistical analysis for growth curves for Swift Terns

The growth rate plot for mass showed that the growth rate from a mass of c. 75 g to a mass of c. 225 g was fairly constant at 7.5 g/day (Fig. 2A). The peak growth rate occurred at 136 g, when the growth rate was 8.5 g/day (Table 6). At fledging mass, the mean growth rate was 2.1 g/day. The rate of growth in mass showed a large scatter (Fig. 2A); at 200 g, the mean growth rate was 6.7 g/day, (standard deviation 3.9 g/day), producing an approximate 95% prediction interval for growth rate increases which stretched from −1.0 g/day to 14.3 g/day. Thus the coefficient of variation of growth rates at 200 g was 58%. The coefficient of variation of growth rate at the peak growth rate was 35.2% (Table 6). The transformation of the growth rate curve into the plot showing average mass in relation to age indicates nearly linear growth in mass from 10 to 30 days (Fig. 2B).

The growth rate of the wing length showed a steady increase from 1.0 mm/day at hatching to a peak of 6.9 mm/day when the wing length was 109 mm (Table 6, Fig. 3A). The growth rate then remained relatively constant until the wing length was c. 170 mm, and then decreased slowly, until at fledging wing-length (c. 257 mm), the wing length was increasing at a rate of 4.3 mm/day. The growth curve for wing length against age reflects this pattern (Fig. 3B); the wing length growth rate increases slowly until an age of c. 20 days is reached, and then shows almost linear increase until the rate of increase starts to decrease just prior to fledging. At 20 days, wing length is 64 mm, 18% of adult

size. The rate of growth for wing length shows less scatter than that for mass (Figs 2A and 3A). At the point when wing length was increasing most rapidly (6.9 mm/day), the standard deviation of the rate of increase was 1.2 mm/day, with a coefficient of variation of 17.7%, approximately half the size of the coefficient of variation for mass at the equivalent point (Table 6). If the rate of growth of wing length at fledging were to remain constant, about one month would be needed for the fledglings to reach adult wing length.

The growth patterns through time for bill length and head length were similar (Figs 4B and 5B). There were relatively few observations of rate of increase on head length for head lengths less than 55 mm (Fig. 5A), and the suggestion of initial slow rate of head growth in Fig. 5B is probably an artifact of the small sample size. The growth rates of both bill length and head length decreased at c. 20 days. At the time of fledging bill length increased at a rate of 0.3 mm/day. If this growth rate were maintained after fledging, the remaining 28.3 mm required to attain adult bill length would take approximately three months to achieve.

The initial growth rates of the foot and tarsus were poorly determined because of small sample sizes (Figs 6A and 7A). However, it is clear that the growth rates of the foot and tarsus at fledging were small (0.1 mm/day), indicating that most birds had reached adult dimensions. In fact, the lengths of foot and tarsus had reached 87% and 85% of adult size, respectively, by age 20 days (Figs 6A and 7A).

The manner in which growth rates varied through time was explored. Specifically, we investigated whether there were patterns in growth rates between successive capture dates (Table 2). In order to compare growth rates of chicks at various stages of growth, the z-values were computed for each bird captured on successive capture dates and these values were averaged to provide an overall index of growth over the time period. These averages were computed for mass, wing length and head length (Table 7). The mean growth index for mass for the first time period (10–17 May) was positive at 1.07, and for the last time period (1–8 July) was negative at –0.97 (Table 7); the overall trend

was negative (Spearman's rank correlation coefficient = -0.929, P <0.005). There were similar significant trends for wing length and head length (Table 7).

The hourly weather data from Robben Island were summarized into daily values (Table 8). A variety of explanatory variables were derived from these data, using functions of mean, maximum and minimum temperatures, mean and maximum wind speeds and rainfall. We computed these variables both for the entire period between captures and for various shorter periods before the second capture date (for example maximum wind speed one day, two days and three days before the second capture date). We found no relationships even approaching statistical significance between any weather explanatory variable and the growth index between capture dates. There were no extreme weather conditions during the study period (Table 8) in spite of the fact that the months May to July covered the midwinter period when storms are frequently prevalent in this winter rainfall region with its Mediterranean climate.

We tested whether chicks which were found dead in the colony had previously shown slower growth rates than the surviving chicks, and whether chicks which had definitely fledged and left the breeding colony (i.e. which had been resighted alive, i.e. engraved colour rings reported by the observer programme, or had been recovered dead, i.e. metal ring number reported to SAFRING) had previously grown more rapidly than average. The average growth index for all chicks with two or more mass measurements was computed. Average growth indices were available for 12 of the 14 chicks that were known to have died before fledging, and it was tested whether these were smaller than the growth indices of all the remaining chicks. The median growth index for chicks which were found dead was -0.52, whereas that for the remaining chicks was 0.32; this difference was significant (Mann-Whitney U=1287, n_1=12, n_2=404, P=0.003, one-sided test). Growth indices were available for 37 chicks that were known to have fledged. The growth rate of these successful birds was not significantly different from those of the remaining birds (one-sided Mann-Whitney U test, P=0.63). The median growth index for the 37 resighted fledglings was 0.20, unexpectedly slightly smaller than the value of 0.27 for the remaining 379

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birds. In addition there was no significant difference between the growth rates of the 12 fledglings which were recovered dead (median 0.07) and the 25 which were resighted (median 0.23) (one-sided Mann-Whitney U, P = 0.45), justifying the decision to consider all birds which fledged as a single group.

Growth rates within the suborder Lari

The assembled set of growth rates included information from 121 studies of 40 species of Lari. The latitude of the study site was available for 83 studies. The data set included species from each the four families within the Lari: Stercorariidae (skuas), seven species, data for three species; Laridae (gulls), 51 species, data for 15 species , Sternidae (terns), 44 species data for 21 species; and Rynchopidae (skimmers), three species, data for one (Table 9).

There was a strong negative relationship between growth rate and mass; more strictly, the relationship was calculated in log-log space, using both the logarithm of growth rate and the logarithm of mass (r = –0.46, P < 0.001, n = 121,) Expressed using the standard allometric formulation, the relationship was K_G = 0.346 $A^{-0.189}$. This analysis suggested that mass alone accounted for 20.8% of the variance in growth rates in the Lari.

In the next model, the logarithms of both mass and latitude were considered as explanatory variables for growth rates. The sample size was smaller; there were now 84 sets of summary data. Both variables were significant predictors of growth rate, and the new relationship was

$$K_G = 0.164\,A^{-0.235} \times L^{0.2667}$$

where L is latitude in degrees, regardless of north or south. The standard error of the exponent of adult mass was 0.035 (t_{82}=–6.82, P<0.001) and that of latitude was 0.047 (t_{82}=5.64, P<0.001); this model accounted for 42.8% of the variance in growth rates. This model suggests that growth rates increase with increasing latitudes, i.e. that they increase from the equator towards the poles. By including an interaction term, we tested whether the rate of increase towards the poles was the same in both the northern and southern hemispheres; the inclusion of this

interaction marginally improved the fit of the model, accounting for 43.3% of the variance:

$$K_G = 0.182\, A^{-0.238} \times L^{0.223 \text{ (if S) or } 0.250 \text{ (if N)}}$$

where the exponent of latitude was 0.223 (SE 0.058, $t_{81}=-3.83$, $P<0.001$) for latitudes in the southern hemisphere and 0.250 (SE 0.049, $t_{81}=-5.13$, $P<0.001$) for latitudes in the northern hemisphere. This suggests that the rate of increase in growth rates towards the poles is slightly less in the southern hemisphere than in the northern hemisphere.

We next considered whether the families within the Lari showed similar patterns. We excluded the Rynchopidae (the skimmers), because we had growth rates for only one species within this family. We first considered whether the exponent of body mass was the same, so that the differences between families consisted of parallel lines in the log-log space. We also considered whether each family should have its own exponent, so that each family would have its own slope in log-log space. We both included and excluded the effects of latitude, and of differences between the northern and southern hemispheres in this analysis. The best fitting model was

$$K_G = 0.634\, A^{-0.370 \text{ (if Skua) or } -0.409 \text{ (if Gull) or } -0.473 \text{ (if Tern)}} \times L^{0.189 \text{ (if S) or } 0.209 \text{ (if N)}}$$

which accounted for 52.0% of the variance in growth rates. All terms were significant ($P < 0.002$). This model suggests that the growth rates of the terns decrease more rapidly with increases in size than is the case for skuas. The model also confirms the small difference in the pattern of growth rate increases towards the poles in the northern and southern hemispheres.

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Discussion

This study was made feasible by the convenient size of the colony – small enough to be manageable, so that the weekly capture and recapture operation could be completed within four hours, yet large enough (470 chicks ringed and 1232 recaptures made) to produce adequate sample sizes to enable fine-scale analyses to be performed.

One of the most striking results was the difference in percentages of adult dimensions attained at fledging. The legs were virtually fully-grown, whereas the wing length had reached 70% of adult size and the bill length was only 56% of adult size. At hatching, mean foot length was already 65% of adult length whereas wing length was only 6% of adult size. For this semi-precocial species, resources are clearly channeled into leg growth; this channeling is appropriate because chicks are required to be mobile within days of hatching, so as to be able to participate in the "creching" system that provides a measure of security against predators.

Although the attainment of flight is a critical stage in the chick's development, the development of wing length is postponed until the legs are well-developed. At approximately age 20 days, wing length was 18% of adult size whereas the foot length was 87% of adult size. From age 20 days onwards, the development of wings and the associated ability to fly received allocation of resources. Flight affords two advantages: the parents are able to take the chick to localities where food is abundant, and feed them more efficiently which has energetic advantages both for the parents and for the chick. Furthermore, dangers from predators which take chicks on the ground are reduced.

The Swift Tern is a surface plunge-feeder, seldom reaching depths exceeding 1 m (Hockey *et al.* 2005). The bill is therefore critical to hunting success; however, development of the bill lags behind that of the other structures. Swift Terns, when they fledge, are most likely to be unable to feed for themselves. Given the roughly conical bill shape, and the fact that it is the base of the bill that is grown after fledging, it is apparent that a large proportion of bill

growth must take place after fledging. To quantify this approximately, the bill was assumed to be a cone with basal diameter 15 mm (unpubl. data). The surface area of the adult bill is then given by $A = \pi \times r \times l = 1500$ mm^2 where the radius is $r = 7.5$ mm and the bill length is $l = 63.6$ mm. At fledging, when the bill length and radius are 56% of adult size, the surface area of the bill is 462 mm^2. If the bill is of uniform thickness, this means that only 31% of the bill material will have been grown at fledging, and that 69% is grown subsequently. It is also possible that the slow growth of the bill ensures that the structure is strong and efficient; Serra (2002) showed that rapidly-grown feathers are of poorer quality and wear more rapidly than feathers that are grown slowly. It should be investigated whether the same principle applies to the growth of the bill.

The ordering of the development of legs, wing and bill is explicable. Leg development is the first priority, so that the chicks can crèche and avoid predators. Wing development is the next priority, so that chicks can fly and move to better feeding areas with their parents. Because parents are still feeding the fledglings at this stage, it is possible to have the "luxury" of delaying the major component of bill growth until this time.

The shapes of the non-parametric growth curves for mass and the various structures measured showed considerable variation (Figs 2B–7B). The two most commonly used parametric growth model are the logistic and Gompertz growth curves, which have their maximum growth rates at 50% and 37% of the asymptote, respectively. The growth rate curve associated with logistic model is a quadratic function (growth rate proportional to $m(A-m)$. The growth rate curve for the Gompertz model has a growth rate proportional to $-m \times \log_e(m/A)$. The wing length of Swift Tern chicks had its peak growth rate at 36% of the asymptote (Table 6, Fig. 3A) and it would therefore appear that the Gompertz growth curve would provide a suitable model. However, the growth rate curve associated with the Gompertz function does not capture the "plateau" seen in Fig. 3A and therefore fails to provide a good fit to the data. The observed growth rate curves for bill length and head length (Figs 4A and 5A) differ from those of

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any of those of the more flexible families of standard growth curves, including the Richard's family (Reiss 1989).

The growth rate curves provide a visual impression of variability of growth of the five structures measured and of mass (Figs 2A–7A). The approximate standard deviations, and the 95% confidence intervals plotted onto these scatter diagrams formalize the visual impression. It is instructive to compare the overall impressions of variability of growth in mass, wing length and head length (Figs 2A, 3A and 5A). The relative scatter was clearly largest for mass, and appeared to be least for head length. This impression was captured by considering the coefficient of variation of growth when the growth rate was at its largest (Table 6). The coefficient of variation, the ratio of the standard deviation and the mean, quantifies the required concept. The coefficient of variation for mass was 35%, whereas those for wing length and head length were 18% and 15%, respectively. This quantifies the impression that the mass of a chick fluctuates more widely than do the lengths of the legs, wing and bill, partly because the observed mass depends on weighing time in relation to when the chick was last fed (a short-term effect, operating on a scale of hours) but also because of overall food availability (a longer-term effect, operating on a scale of between days and breeding seasons).

It was therefore unexpected that the coefficients of variation for the growth of bill length, foot length and tarsus length were comparable with that of mass (Table 6). The reason for this CV comparability appears to hinge on the difficulty of measuring these structures precisely. Although negative growth rates are acceptable for mass (Fig 2A), they are impossible for the body structures. Wing length and head length show no negative growth rates (Figs 3A and 5A). In contrast, there were large numbers of pairs of successive observations of bill length, foot length and tarsus length for which the second observation was smaller than the first (Figs 4A, 6A and 7A). Bill length appears to be difficult to measure because the demarcation of the line of feathers on the forehead is not stable and may be interpreted differently by different observers. Tarsus length is difficult to measure consistently, and this difficulty is reflected in it having the

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largest coefficient of variation (Table 6). In addition, both tarsus length and foot length grew slowly (less than 0.5 mm per day for much of the fledging period, Figs 6A and 7A), and small measurement errors result in "noise" that swamps the "signal". The foot is regarded as a structure that is easily defined and can be measured consistently and without bias by different observers; unfortunately, we measured this slow-growing structure to the nearest 1 mm. This lack of precision is the explanation of the patterning observed in Fig 7A. We recommend that futures studies of growth measure foot length to the nearest 0.1 mm.

Unlike Robinson *et al.* (2002) and the studies reviewed by them, we failed to detect any influence of weather variables on growth rates of Swift Terns on Robben Island during the 2002 breeding season. This outcome was probably because the weather was relatively benign throughout this period, and there were no particularly stormy periods (Table 8). However, there was a generally decreasing trend in growth rates towards the end of the breeding season. This trend can be attributed to the observation that the last birds to fledge were those that were slowest growing.

Chicks that were found dead within the colony tended to be those that had earlier displayed slow growth rates. However, we would have anticipated that the sample of birds which definitely fledged, and were seen away from the breeding colony, would have exhibited higher-than-average growth rates. This was not observed. Klaassen *et al.* (1992), working on Sandwich Terns *Sterna sandvicensis* speculated that because parents could move their chicks closer to food resources after fledging, there was an opportunity for a compensation for earlier food shortages which had reduced growth rates. Terns chicks are known to display considerable flexibility in being able to match growth rates to variations in food availability (reviewed by Robinson *et al.* 2002).

Growth rates of the suborder Lari

Our results for the relationship between body mass and growth rate parallel those of earlier studies, in particular the major review by Starck and Ricklefs (1998a). The additional contribution of this study is the deeper exploration on the effect of latitude on growth rates. The growth rates underpinning this study come from a wide range of sources, and have been computed by a variety of methods. In addition, use has been made of conversion factors between Gompertz and logistic growth rates which, though approximately correct, need to be subjected to further scrutiny (L.G. Underhill pers. comm.). Given the range of sources of errors for the growth rates of Table 9, it is not surprising that there are striking differences between studies for several species, even at a single locality (e.g. the range of growth rates for the Common Tern *Sterna hirundo* in Table 9). More detailed studies of the variability of growth rates in relation to, for example, climate change, will almost certainly be examining small relative differences, which are unlikely to be detectable from current data sets of this type, such as provided by Table 9. To perform such analysis, it will be necessary to use a standard statistical method to estimate growth rates from the original raw data from each study.

The most extensive review of growth rates in relation to latitude is that of Klaassen and Drent (1991). As they point out, it is not latitude *per se* that influences growth rates, but latitude operates as a proxy for a variety of environmental variables that are largely latitude dependent. For example, ambient temperatures in general decrease towards the poles. Also, seasonality is more pronounced towards the poles. This has two important effects. Firstly, it shortens the period when conditions are suitable for breeding. Secondly, and consequently, this results in a synchronization of breeding activities so that, throughout the food web, additional resources are available for a short period; this effect is most extreme in the tundra regions of the Arctic (Chernov 1985). In combination, these effects tend to drive more rapid growth rates at higher latitudes. At comparable latitudes, seasonality is more pronounced in the

northern latitudes than in the southern hemisphere; this is attributable to the uneven distribution of land mass between the hemispheres, and the associated continental climate of much of the north temperate zone and as far north as the tundra, especially in Siberia (Chernov 1985). This study is the first to consider whether the impact of latitude on growth rates may differ between the two hemispheres. Because the relative sizes of ocean and continent is dramatically different between the hemispheres, seasonality is less pronounced in the southern than in the northern hemisphere. It is therefore not surprising that the influence of latitude on growth rate is smaller in the southern hemisphere. It would be instructive to include a fuller suite of seabirds of other orders in this analysis. Inclusion of seabirds of the orders Sphenisciformes, Procellariiformes and Pelecaniformes would provide a data set with a wide latitudinal range, with many species breeding in all climate zones, from the tropics to both polar regions. It would also be useful to refine the explanatory variables related to latitude, and use, for example, variables such as ambient air temperatures and day length during the breeding season. It is unlikely that these variables operate linearly.

It is also worth commenting on the statistical approach used here. Earlier studies (e.g. Klaassen and Drent 1991, Visser 2002) have computed relative residuals, calculated as (observed growth rate – predicted growth rate)/(predicted growth rate), where the predicted growth rate is obtained from an allometric relationship of the form growth rate = a × mass^b. The main disadvantage of this approach is that it becomes impossible to disentangle the relative importance of the various explanatory variables. In this study, mass and latitude were of approximately equal importance in predicting growth rates.

Table 1: Measurements taken of Swift Tern chicks on Robben Island.

Measurement	Method
Mass	Measured to nearest 1 g or 2 g with Pesola spring balance
Wing	Flattened chord to the tip of the longest growing primary (mm), measured to 1 mm with an aluminium wing rule (Evans 1986)
Culmen	Tip of the upper beak to the edge of the forehead feathers (mm) measured to 0.1 mm with dial Vernier calipers (Green 1980)
Head	Tip of the upper beak to the back of skull (mm) measured to 0.1 mm with dial Vernier calipers
Tarsus	Measured to 0.1 mm with dial calipers (mm)
Foot	Standard "tarsus-toe" measurement (mm) from "heel" to the end of the longest toe, excluding the claw, measured to 1 mm with wing rule

Table 2: Number of Swift Tern chicks caught, recaptured (alive) and recovered (dead) on Robben Island, May–July 2002. Nestlings refers to chicks still in the nest cup.

Date	Total	New Rings		Recaptures	Recoveries
		Nestlings	Runners	Runners	
3 May 2002	30	30			
10 May 2002	29		28	1	
17 May 2002	129	26	80	23	
18 May 2002	32	32			
27 May 2002	297		186	111	
3 Jun 2002	361		69	292	
10 Jun 2002	391		18	373	
18 Jun 2002	229			229	1
24 Jun 2002	145		1	144	5
1 Jul 2002	49			49	6
8 Jul 2002	10			10	2
TOTAL	1702	88	382	1232	14

Table 3: Summary statistics of mass (g) and measurements (mm) of Swift Tern hatchlings (within one day of having hatched) on Robben Island. The tarsus length of one hatchling was not measured.

	Sample Size	Mean	Standard Deviation	Min	Lower Quartile	Median	Upper Quartile	Max
Mass	77	39	4.8	29	36	39	43	48
Wing	77	23	2.1	19	22	23	25	32
Bill	77	15	0.9	13	14	15	15	17
Head	77	45	1.9	40	43	45	46	51
Foot	77	43	2.1	40	41	43	45	47
Tarsus	76	21	1.9	18	20	21	23	27

Table 4: Summary statistics of mass (g) and measurements (mm) of Swift Tern fledglings on Robben Island. The sample is restricted to those chicks with wing-lengths between 250 mm and 270 mm; see text for details. All measurements were not made on all birds.

	Sample Size	Mean	Standard Deviation	Min	Lower Quartile	Median	Upper Quartile	Max
Mass	85	329	21.4	272	375	328	345	375
Wing	85	257	4.7	251	253	255	260	269
Bill	64	35.3	2.7	27.4	33.5	35	37.2	43.8
Head	82	92	3.0	85	90	92	95	98
Foot	82	66	2.2	62	65	66	68	73
Tarsus	62	35.5	3.0	31.0	33	34.6	38.4	40.5

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Table 5: Masses (g) and measurements (mm) and summary statistics for 22 breeding Swift Tern adults trapped on Robben Island.

Ring number	Mass	Wing	Bill	Head	Tarsus	Foot	Tail	Tail Short	Tail Fork
529147	465.0	350.0	66.3	131.0	39.4	76.0	179.0	107.0	72.0
529148	455.0	360.0	60.9	115.3	36.5	76.0	178.0	98.0	80.0
589783	390.0	367.5	60.5	117.5	35.0	66.0	167.0	99.0	68.0
5H00318	400.0	382.0	62.4	119.7	34.9	65.0	202.0	126.0	76.0
5H02096	380.0	370.0	67.2	123.7	36.5	68.0	165.0	93.0	72.0
5H02261	400.0	378.0	65.6	122.5	35.0	65.0	181.0	102.0	79.0
5H25802	370.0	350.0	61.1	119.9	34.5	66.0	152.0	92.0	60.0
5H25803	390.0	363.0	60.5	115.9	31.0	68.0	160.0		
5H25804	395.0	371.0	65.4	123.1	32.6	67.0	180.0	108.0	72.0
5H25805	365.0	360.0	64.3	118.6	36.9	65.0	159.0	100.0	59.0
5H25806	380.0	363.0	63.0	116.6	34.9	66.0	165.0	98.0	67.0
5H25807	410.0	363.0	64.6	119.8	34.5	67.0	180.0	95.0	85.0
5H25808	390.0	365.0	63.0	119.0	33.5	65.0	185.0	100.0	85.0
5H25809	420.0	359.0	64.6	123.2	32.7	65.0	186.0	98.0	88.0
5H25810	350.0	352.0	59.5	113.4	35.5	63.0	162.0	98.0	64.0
5H25811	400.0	357.0	67.0	126.7	36.0	66.0	153.0	102.0	51.0
5H25837	435.0	380.0	65.1	124.1	33.9	68.0	165.0	97.0	68.0
5H25843	405.0	376.5	62.5	120.2	37.8	65.0	185.0	124.0	61.0
5H25844	435.0	360.0	68.4	124.2	36.4	70.0	179.0	90.0	89.0
5H25845	400.0	371.0	63.8	122.5	33.8	65.0	178.0	100.0	78.0
5H25846	445.0	383.0	61.4	118.5	35.4	69.0	177.0	103.0	74.0
5H25847	355.0	352.0	61.9	117.4	35.6	66.0	166.	94.0	72.0
Mean	401.6	365.2	63.6	120.6	35.1	67.14	172.9	101.2	72.4
Min	350.0	350.0	59.5	113.4	31.0	63.0	152.0	90.0	51.0
Max	465.0	383.0	68.4	131.0	39.4	76.0	202.0	126.0	89.0
SD	30.8	10.3	2.5	4.1	1.8	3.3	12.4	9.1	10.1
Mean adult measurements in Hockey *et al.* (2005)	394	357	61.2	-	33	-	175		78

Table 6: Maximum daily growth rates of Swift Terns on Robben Island (see text for details). Mean adult size taken from Table 5.

Structure	Size at maximum growth rate	Percentage of mean adult size	Mean maximum growth rate per day	Standard deviation of maximum growth rate	CV
Mass (g)	136	40%	8.5	3.0	35.2%
Wing (mm)	109	36%	6.9	1.2	17.7%
Bill (mm)	19.3	31%	0.64	0.23	35.3%
Head (mm)	53.7	45%	1.78	0.27	15.3%
Foot (mm)	48.1	71%	1.14	0.40	35.1%
Tarsus (mm)	24.4	70%	0.85	0.36	42.8%

Table 7: Average z-scores for each recapture period of Swift Terns on Robben Island (see text for details).

	Mass (g)			Wing (mm)			Head (mm)		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
10 to 17 May 2002	1.07	1.63	6	0.75	0.93	6	0.65	1.80	6
17 to 27 May 2002	0.24	0.82	61	0.09	0.62	60	0.28	0.84	60
27 May to 3 Jun 2002	0.61	0.92	241	0.28	0.76	238	0.15	1.02	121
3 to 10 Jun 2002	-0.33	0.89	323	0.19	0.84	322	0.31	0.99	178
10 to 18 Jun 2002	0.09	0.92	219	-0.33	1.02	219	-0.31	0.79	218
18 to 24 Jun 2002	-0.56	0.95	138	-0.10	1.18	138	-0.10	1.09	138
24 Jun to 1 Jul 2002	-0.49	0.79	47	-0.77	1.49	47	-0.51	1.16	47
1 Jul to 8 Jul 2002	-0.97	0.89	10	-0.30	1.85	10	-0.55	0.86	9

Table 8: Daily weather variables for Robben Island during the study period in May–July 2002.

Date	Rainfall (mm)	Mean temp- erature (°C)	Maximum temp- erature (°C)	Minimum temp- erature (°C)	Mean wind speed (m/sec)	Maximum wind speed (m/sec)	Wind Direction degrees
1 May 2002	0.0	14.9	19.1	10.7	2.4	7.2	330
2 May 2002	0.0	16.6	19.1	14.0	3.2	8.0	290
3 May 2002	0.0	16.9	20.2	13.6	1.3	7.5	120
4 May 2002	0.2	14.3	18.8	9.8	1.7	6.3	210
5 May 2002	8.6	14.9	17.6	12.1	2.6	12.1	220
6 May 2002	5.2	13.2	15.7	10.6	3.4	15.7	200
7 May 2002	0.0	13.1	16.2	9.9	1.7	7.2	130
8 May 2002	0.0	14.3	19.1	9.5	1.7	7.2	130
9 May 2002	0.0	13.4	19.2	7.7	1.5	10.5	110
10 May 2002	0.0	12.7	18.4	7.0	1.9	9.4	120
11 May 2002	0.0	14.9	19.3	10.4	1.7	5.7	050
12 May 2002	0.0	15.8	20.0	11.6	1.6	5.7	300
13 May 2002	0.8	14.4	17.2	11.7	1.3	5.5	320
14 May 2002	0.0	16.6	18.9	14.2	5.0	13.0	130
15 May 2002	0.0	15.8	19.2	12.4	2.5	7.7	110
16 May 2002	0.0	15.4	17.7	13.2	4.2	9.8	320
17 May 2002	0.0	16.3	18.3	14.2	1.8	5.6	280
18 May 2002	0.0	14.3	19.4	9.2	0.9	6.2	220
19 May 2002	0.0	15.0	22.0	8.0	1.7	4.7	190
20 May 2002	0.0	19.4	27.6	11.3	2.1	8.6	290
21 May 2002	0.4	15.5	19.7	11.3	1.7	7.6	040
22 May 2002	3.8	14.6	16.9	12.2	3.9	12.2	290
23 May 2002	3.6	15.4	17.2	13.6	3.8	11.9	260
24 May 2002	2.4	15.0	16.7	13.3	6.7	19.2	320
25 May 2002	4.2	15.1	17.3	12.8	2.8	10.0	280
26 May 2002	0.2	14.0	17.5	10.5	1.6	5.3	110
27 May 2002	0.0	11.2	16.9	5.5	0.8	4.9	210
28 May 2002	6.0	12.9	15.4	10.4	4.0	13.3	330
29 May 2002	1.4	13.1	15.2	11.0	2.3	15.4	210
30 May 2002	0.0	10.4	15.5	5.2	2.4	5.9	350
31 May 2002	3.2	13.2	16.1	10.2	4.3	11.0	320
1 Jun 2002	6.4	13.1	15.0	11.1	4.6	13.4	140
2 Jun 2002	0.0	12.8	15.4	10.1	1.7	8.9	110
3 Jun 2002	0.0	10.5	17.3	3.7	2.2	8.3	120

Date	Rainfall (mm)	Mean temp- erature (°C)	Maximum temp- erature (°C)	Minimum temp- erature (°C)	Mean wind speed (m/sec)	Maximum wind speed (m/sec)	Wind Direction degrees
4 Jun 2002	0.0	15.2	21.4	9.0	2.5	6.4	080
5 Jun 2002	0.0	13.8	17.7	9.8	2.3	6.9	300
6 Jun 2002	5.0	14.1	15.6	12.5	3.1	13.7	210
7 Jun 2002	11.0	11.2	15.1	7.2	3.9	12.0	330
8 Jun 2002	1.4	13.5	16.7	10.3	3.1	13.2	210
9 Jun 2002	0.0	14.2	15.4	12.9	4.3	9.4	330
10 Jun 2002	0.0	14.1	16.8	11.3	2.0	5.2	010
11 Jun 2002	0.0	13.8	16.0	11.6	1.8	9.0	100
12 Jun 2002	0.2	13.3	15.1	11.5	2.8	9.1	320
13 Jun 2002	2.6	11.9	13.3	10.4	2.8	6.8	010
14 Jun 2002	0.0	13.8	15.2	12.3	2.8	7.4	350
15 Jun 2002	0.8	13.7	15.0	12.4	2.9	11.5	170
16 Jun 2002	0.2	11.8	16.3	7.2	1.4	4.8	270
17 Jun 2002	1.2	12.7	16.4	9.0	4.4	12.1	310
18 Jun 2002	0.8	15.4	17.4	13.5	2.5	9.2	240
19 Jun 2002	0.0	11.5	15.9	7.1	2.8	13.5	130
20 Jun 2002	0.0	15.1	17.9	12.3	4.9	15.1	130
21 Jun 2002	0.0	18.1	23.9	12.2	1.6	5.9	100
22 Jun 2002	0.0	13.1	17.8	8.3	2.7	12.2	200
23 Jun 2002	0.4	14.6	17.2	12.0	4.5	13.0	190
24 Jun 2002	0.0	12.1	15.5	8.7	1.3	5.9	200
25 Jun 2002	0.0	11.1	15.1	7.0	2.5	5.7	360
26 Jun 2002	9.6	12.4	13.5	11.2	4.2	15.1	200
27 Jun 2002	1.0	10.0	13.0	7.0	2.8	8.5	340
28 Jun 2002	11.2	12.8	15.2	10.4	3.9	10.6	330
29 Jun 2002	4.2	13.9	15.5	12.4	2.4	10.8	270
30 Jun 2002	0.0	12.2	15.6	8.7	2.0	5.7	120
1 Jul 2002	0.0	11.1	16.6	5.6	1.3	7.6	120
2 Jul 2002	0.0	11.7	16.2	7.1	2.1	8.7	110
3 Jul 2002	0.0	11.8	16.6	7.0	2.1	7.4	090
4 Jul 2002	0.0	13.4	16.9	9.8	1.6	8.4	100
5 Jul 2002	0.0	12.4	16.6	8.1	2.2	10.5	130
6 Jul 2002	0.0	12.3	16.6	7.9	1.9	7.8	110
7 Jul 2002	0.0	13.4	16.3	10.4	3.2	7.9	320
8 Jul 2002	0.0	12.6	15.3	9.9	2.5	15.0	320

Table 9: Gompertz growth rates K_G for Lari. See text for details.

Species	Body Mass	K_G	Locality	Lat	Long	Reference
Family Stercorariidae						
Catharacta maccormicki (South Polar Skua)	1250.0	0.086	Signy Island, South Orkney Islands	60.43 S	45.38 W	Hemmings 1984
	1277.6	0.092	Foula, Shetland	60.10 N	2.05 W	Furness 1987
Catharacta skua (Great skua)	1167.1	0.120	Foula, Shetland	60.10 N	2.05 W	Furness 1987
	1250.0	0.092	Cape Hallet, Antarctica	72.19 S	170.18 E	Reid 1966 (in Ricklefs 1968, 1973)
ssp. lönnbergi	1560.0	0.099	Bird Island, South Georgia	54.00 S	34.02 W	Osborne 1985
	1703.9	0.126				Stonehouse 1956
	1706.8	0.097				Stonehouse 1956
Stercorarius longicaudus (Long-tailed Skua)	242.8	0.225	Foula, Shetland	60.10 N	2.05 W	Furness 1987
Family: Laridae						
Creagrus furcatus (Swallow-tailed Gull)	652.4	0.073	Plaza, Galapagos	1.0 S	91.0 W	Harris 1970
Larus argentatus (Herring Gull)	866.6	0.111				Heinroth and Heinroth 1928
	1012.0	0.109	Skomer Island, Wales	51.44 N	5.17 W	Harris 1964 (in Ricklefs 1973)
	1012.0	0.140				Belopolskii (in Ricklefs 1973)
	1050.0	0.097	Gray's Rock, Salem, Massachusets	42.31 N	70.55 W	Kadlec et al. 1969

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Species	Body Mass	K_G	Locality	Lat	Long	Reference
	1080.0	0.070				Brisbin, unpublished data (in Ricklefs 1973)
	1150.0	0.083	Terschelling	53.24 N	5.20 E	Spaans 1971
Larus audonii (Audouin's Gull)	510.0	0.122	Mediterranean	34-42 N	3-36 E	Witt 1977
Larus californicus (California Gull)	600.0	0.109	Bamforth Lake, Wyoming			Smith and Diem 1972
Larus canus (Mew Gull)	400.0	0.130				Belopolskii 1957 (in Ricklefs 1973)
Larus fuscus (Lesser Black-backed Gull)	806.0	0.109	Skomer Island, Wales	51.44 N	5.17 W	Harris 1964 (in Ricklefs 1973) Dunning 1993
	650.1	0.064				Belpolskii 1957 (in Ricklefs 1973)
	850.0	0.067	Farne Island, Northumberland	55.38 N	1.38 W	Pearson 1968 (in Ricklefs 1973)
	700.0	0.123				Heinroth and Heinroth 1928
	810.0	0.092				Heinroth and Heinroth 1928
Larus glaucescens (Glaucous-winged Gull)	885.0	0.091	Mandarte Island, British Columbia	48.39 N	123.24 W	Vermeer 1963 (in Ricklefs 1968, 1973)
Larus marinus (Great Black-backed Gull)	1650.0	0.069	Skomer Island, Wales	51.44 N	5.17 W	Harris 1964 (in Ricklefs 1973)
	1700.0	0.108				Heinroth and Heinroth 1928
Larus minutus (Little Gull)	110.0	0.186				Heinroth and Heinroth 1928
Larus occidentalis (Western Gull)	800.0	0.105	San Nicholas Island, California	33.14 N	119.32 W	Schreiber 1970

Species	Body Mass	K_G	Locality	Lat	Long	Reference
	900.0	0.080	San Nicholas Island, California	33.14 N	119.32 W	Schreiber, unpublished data (in Ricklefs 1973)
Larus occidentali	900.0	0.080		29		Ricklefs 1973
Larus ridibundus (Black-headed Gull)	270.0	0.169				Heinroth and Heinroth 1928
	281.0	0.115		61		Glutz 1982
	350.0	0.088	San Nicholas Island, California	33.14 N	119.32 W	Schreiber *et al.* 1980
Larus atricilla (Laughing Gull)						
Larus dominicanus vetula (Kelp Gull)	1084.0	0.081	Robben Island	33.47 S	18.21 E	Bakker 2004
Larus delawarensis (Ring-billed Gull)	403.0	0.099		45		Glutz 1982
Rissa tridactyla (Black-legged Kittiwake)	335.0	0.114	Western Norway	62.25 N	5.38 E	Barrett and Runde 1980
	350.0	0.146				Coulson and White 1958 (in Barrett and Runde 1980)
	350.0	0.156	North Shields, England	55.10 N	1.26 W	Coulson and Porter 1985
	363.0	0.122	Helgoland	54.12 N	7.53 E	Voss *et al.* 1987
	375.0	0.133	Farne Island, Northumberland	55.38 N	1.38 W	Pearson 1968 (in Barrett and Runde 1980)
	380.0	0.095				Belpolskii 1957 (in Ricklefs 1973)
	400.0	0.131	Gull Island, Newfoundland	47.15 N	52.46 W	Maunder and Threfall 1972 (in Barrett and Runde 1980)
	402.2	0.133	Bleiksøy	69.17 N	15.53 E	Barrett 1989
	405.0	0.135	Northern Norway	69.35 N	17.50 E	Barrett and Runde 1980

Species	Body Mass	K_G	Locality	Lat	Long	Reference
	410.0	0.144	Northern Norway	69.35 N	17.50 E	Barrett and Runde 1980
	410.0	0.111	Kongsfjorden, Svalbard	79 N	12 E	Gabrielsen et al. 1992
	414.0	0.123	Northern Norway	69.35 N	17.50 E	Barrett and Runde 1980
	421.0	0.120	Gull Island, Newfoundland	47.15 N	52.46 W	Maunder and Threfall 1972
	449.0	0.097		79		Klaassen et al. 1987
Family: Sternidae						
Anous minutus (Black Noddy)	101.0	0.129	Heron Island, Barrier Reef	23.26 S	151.51 E	Congdon 1990
	101.0	0.136	Heron Island, Barrier Reef	23.26 S	151.51 E	Congdon 1990
	101.0	0.156	Heron Island, Barrier Reef	23.26 S	151.51 E	Congdon 1990
	101.0	0.163	Heron Island, Barrier Reef	23.26 S	151.51 E	Congdon 1990
	101.0	0.170	Heron Island, Barrier Reef	23.26 S	151.51 E	Congdon 1990
	115.0	0.107	Tern Island	23.52 N	151.55 E	Pettit et al. 1984
	117.0	0.103	One Tree Island, Barrier Reef	23.27 S	151.55 E	Langham 1986
	117.0	0.152	One Tree Island, Barrier Reef	23.27 S	151.55 E	Langham 1983
	126.0	0.078				Congdong 1984 (in Hulsman and Smith 1988)
Anous stolidus (Brown Noddy)	190.0	0.070				Fleet, unpublished data (in Ricklefs 1973)
	190.0	0.103		23		Ricklefs 1973

| Species	Body Mass	K_G	Locality	Lat	Long	Reference
Chlidonias niger (Black Tern)	63.0	0.248	Port Rowan, Ontario	42.35 N	80.24 W	Dunn 1979
Gelochelidon nilotica (Gull-billed Tern)	250.0	0.067				Heinroth and Heinroth 1928
	100.0	0.065	Midway Atoll	28.13 N	177.23 W	Pettit *et al.* 1984
Gygis alba (Fairy Tern)						
	115.0	0.064	Ascension Island	7.57 S	14.22 W	Dorward 1963
Hydroprogne caspia (Caspian Tern)	540.0	0.197				Heinroth and Heinroth 1928
Sterna albifrons (Little Tern)	45.0	0.124				Heinroth and Heinroth 1928
Sterna anaethetus (Bridled Tern)	82.5	0.097	Cousin Island, Seychelles	4.20 S	55.40 E	Diamond 1976
	126.0	0.075	One Tree Island, Barrier Reef	23.31 S	152.06 E	Hulsman and Langham 1985
	128.5	0.078	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham 1986
Sterna dougallii (Roseate Tern)	106.0	0.159	Great Gull Island, New York	41.11 N	72.12 W	LeCroy and Collins 1972
	98.9	0.201				Nisbet *et al.* 1995
	95.6	0.176				Nisbet *et al.* 1995
Sterna forsteri (Forster's Tern)	175.0	0.085	Midway Islands	28.13 N	177.22 W	Shea and Ricklefs 1985
Sterna fuscata (Sooty Tern)	187.2	0.073				Brown 1976
	190.0	0.086	Dry Tortugas, Florida	24.38 N	82.55 W	Ricklefs and White 1981, Shea and Ricklefs 1985
	205.0	0.073	Dry Tortugas, Florida	24.38 N	82.55 W	Ricklefs 1973, Ricklefs and White 1981

Species	Body Mass	K_G	Locality	Lat	Long	Reference
	205.0	0.073	Dry Tortugas, Florida	24.38 N	82.55 W	Ricklefs 1973
Sterna hirundo (Common Tern)	100.0	0.115	Great Gull Island, New York	41.11 N	72.12 W	LeCroy and Collins 1972
	105.0	0.163				Nisbet *et al.* 1995
	107.1	0.132				Klassen *et al.* 1992
	110.0	0.180	Great Gull Island, New York	41.11 N	72.12 W	Ricklefs 1979, Ricklefs and White 1981
	110.0	0.179	Great Gull Island, New York		72.12 W	LeCroy and Collins 1972
	114.0	0.165	Griend	53.14 N	5.15 E	Klaassen 1994
	120.0	0.184				Klassen *et al.* 1992
	121.2	0.105	Minsener Oldeoog Island	53.46 N	8.00 E	Mlody and Becker 1991
	122.0	0.169	Great Gull Island, New York	41.11 N	72.12 W	Ricklefs 1979, Ricklefs and White 1981
	122.3	0.192				Uttley *et al.* 1989
	123.6	0.161	Haren, Groningen	53.10 N	6.35 E	Drent *et al.* 1992
	125.0	0.173	Great Gull Island, New York	41.11 N	72.12 W	Ricklefs 1979, Ricklefs and White 1981
	126.0	0.211				Langham 1983 (in Hulsman and Smith 1988)
	127.8	0.207	Minsener Oldeoog Island	53.46 N	8.00 E	Mlody and Becker 1991
	130.0	0.204	Midway Islands	28.13 N	177.22 W	Shea and Ricklefs 1985
	130.0	0.204		54		Ricklefs 1973, Klaassen *et al.* 1987

| Species	Body Mass	K_G	Locality	Lat	Long	Reference
	133.0	0.242				Ricklefs 1973
	139.0	0.107	Midway Islands	28.13 N	177.22 W	Shea and Ricklefs 1985
Sterna lunata (Grey-backed Tern)						
Sterna paradisea (Arctic Tern)	102.5	0.153	Haren, Groningen	53.10 N	6.35 E	Drent *et al.* 1992
	105.0	0.230				Ricklefs 1973
	105.0	0.230		79		Ricklefs 1973, Klaassen *et al.* 1987
	107.0	0.190	Spitsbergen	78.55 N	12.00 E	Klaassen 1994
	110.0	0.133				Ricklefs 1973
	110.0	0.196		54		Ricklefs 1973, Klaassen *et al.* 1987
	113.0	0.197				Klaassen *et al.* 1989
	115.0	0.179	Spitsbergen	78.55 N	12.00 E	Klaassen *et al.* 1989 , Klaassen 1994
	115.0	0.205				Langham 1983 (in Hulsman and Smith 1988)
Sterna sumatrana (Black-naped Tern)	100.0	0.196				Hulsman and Smith 1988
	133.0	0.147	Arctowski	62.09 S	58.28 W	Klaassen 1994
Sterna vittata (Antarctic Tern)						
Sterna balaenarum (Damara Tern)	51.8	0.149	Möwe Bay, Namibia	19.20 S	12.40 W	J. Paterson *in litt.*
Sterna bergii gwendolenae (Crested Tern)	233.5	0.082	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham and Hulsman 1986

Species	Body Mass	K_G	Locality	Lat	Long	Reference
	279.0	0.064	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham 1986
	279.3	0.073	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham and Hulsman 1986
	279.3	0.083	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham and Hulsman 1986
	318.0	0.116	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham 1986
Sterna bergii bergii (Swift Tern)	399.0	0.044	Robben Island	33.47 S	18.21 E	This chapter
Sterna sandvicensis (Sandwich Tern)	172.8	0.111				Klassen *et al.* 1992
	180.0	0.119	Farne Island, Newfoundland	55.38 N	1.38 W	Pearson 1986 (in Ricklefs
	180.0	0.175		54		Ricklefs 1973, Klaassen *et al.* 1987
	189.0	0.112	One Tree Island, Barrier Reef	23.31 S	152.05 E	Langham and Hulsman 1986
	219.4	0.183	Haren, Groningen	53.10 N	6.35 E	Drent *et al.* 1992, Klaassen 1994
	220.0	0.188				Klassen *et al.* 1992
Family: Rynchopidae						
Rynchops nigra (Black Skimmer)	264.4	0.228	Virginia USA	37.50 N		Erwin 1977
	295.2	0.228				Erwin 1977
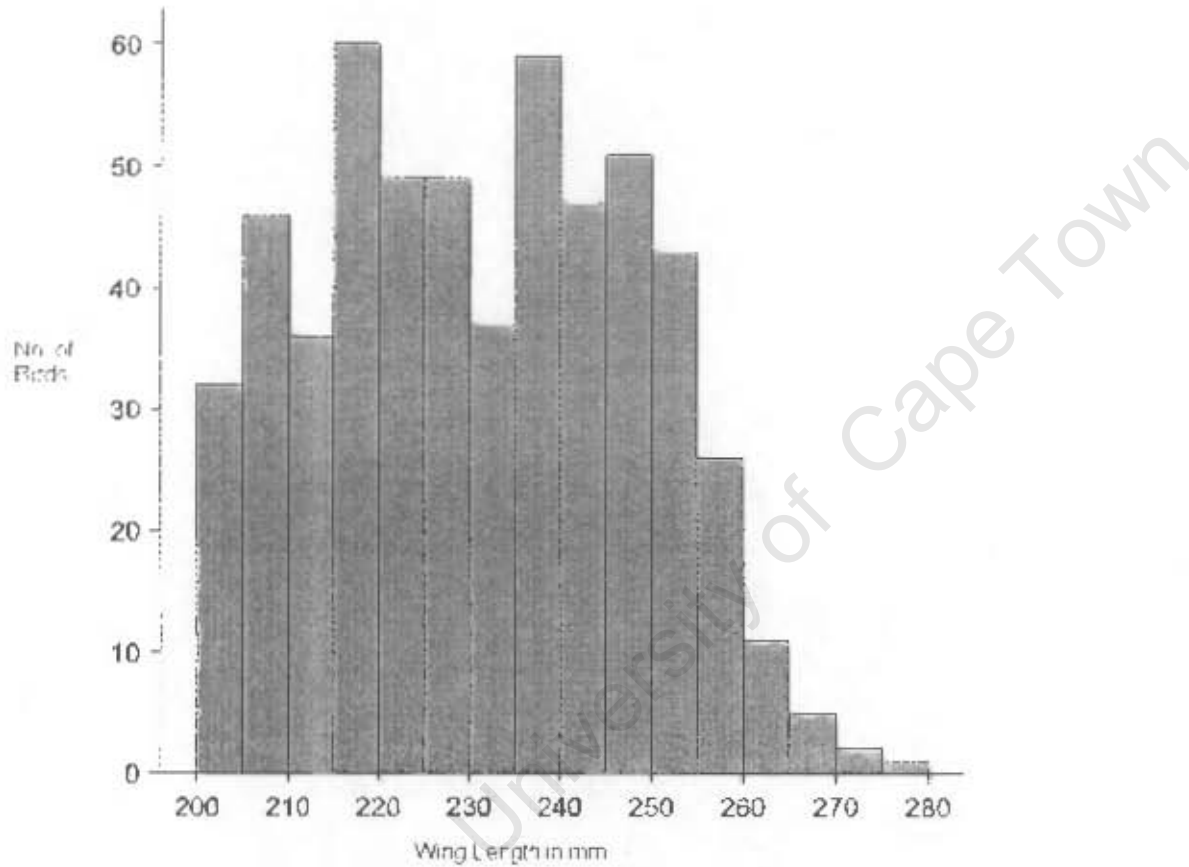
Figure 1: Histogram of wing length (mm) showing number of Swift Tern chicks captured on Robben Island. The plot is restricted to chicks with wing length above 200 mm in order to demonstrate that fledging wing lengths are mostly in range of 250 mm to 270 mm. See text for detail
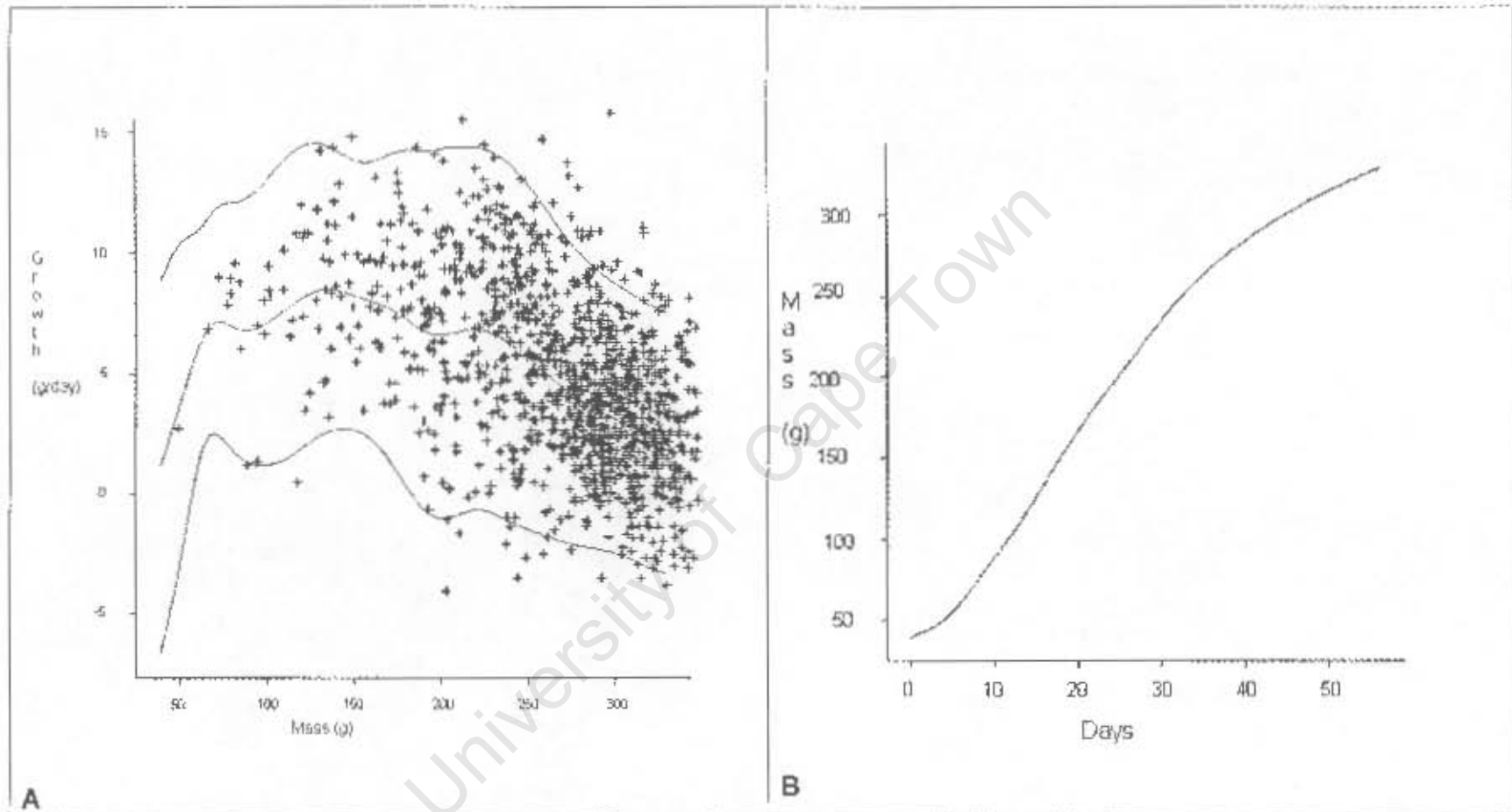
Figure 2: A: Growth rates (g/day) of the mass (g) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). **B:** Growth curve of mass (g) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching mass from Table 3 as mass on day 0.
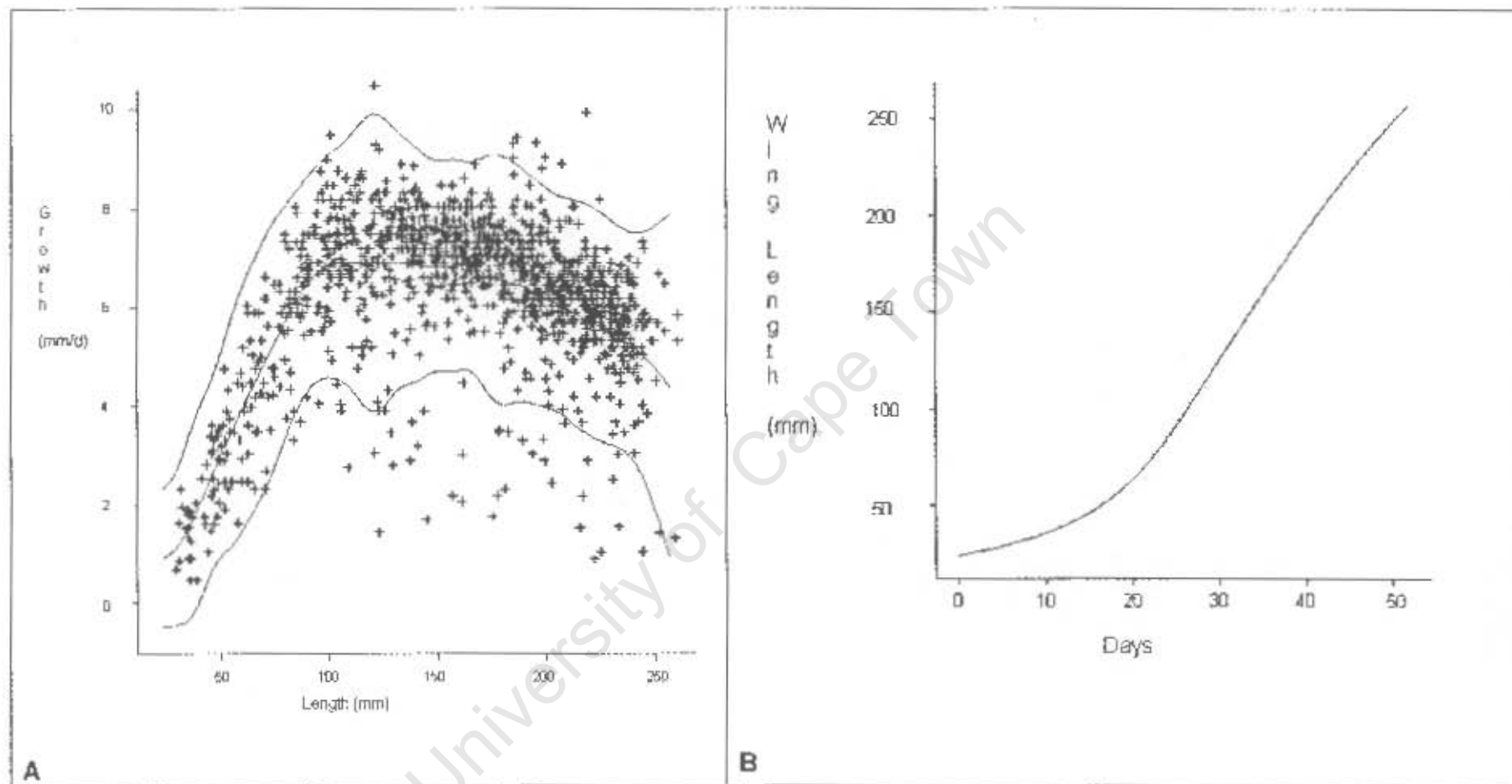
Figure 3: A: Growth rates (mm/day) of the wing length (mm) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). **B:** Growth curve of wing length (mm) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching wing length from Table 3 as length of wing on day 0.
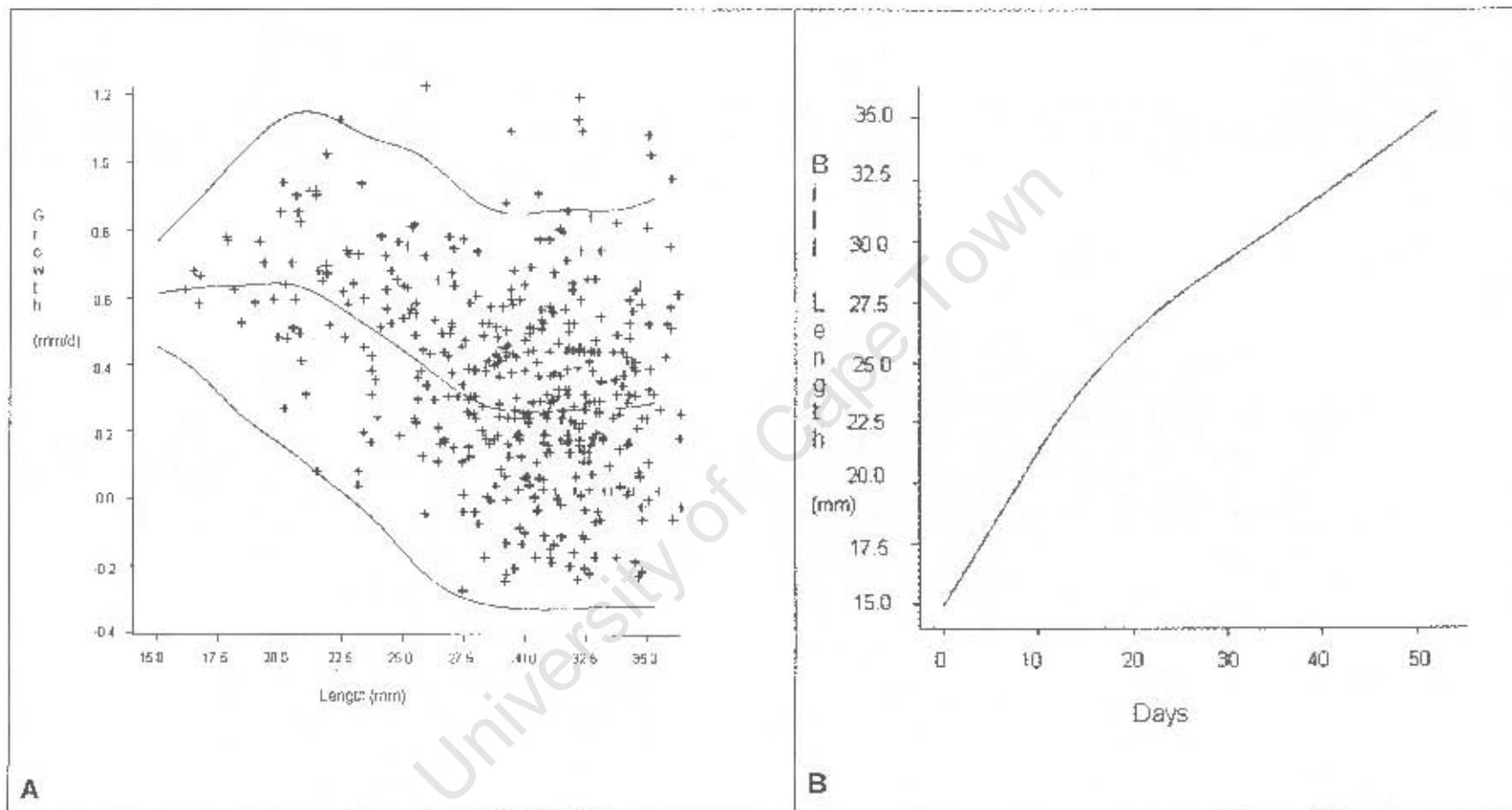
Figure 4: A: Growth rates (mm/day) of the bill length (mm) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). **B:** Growth curve of bill length (mm) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching bill length from Table 3 as bill length on day 0.

Figure 5: A: Growth rates (mm/day) of the head length (mm) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). **B**: Growth curve of head length (mm) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching head length from Table 3 as head length on day 0.
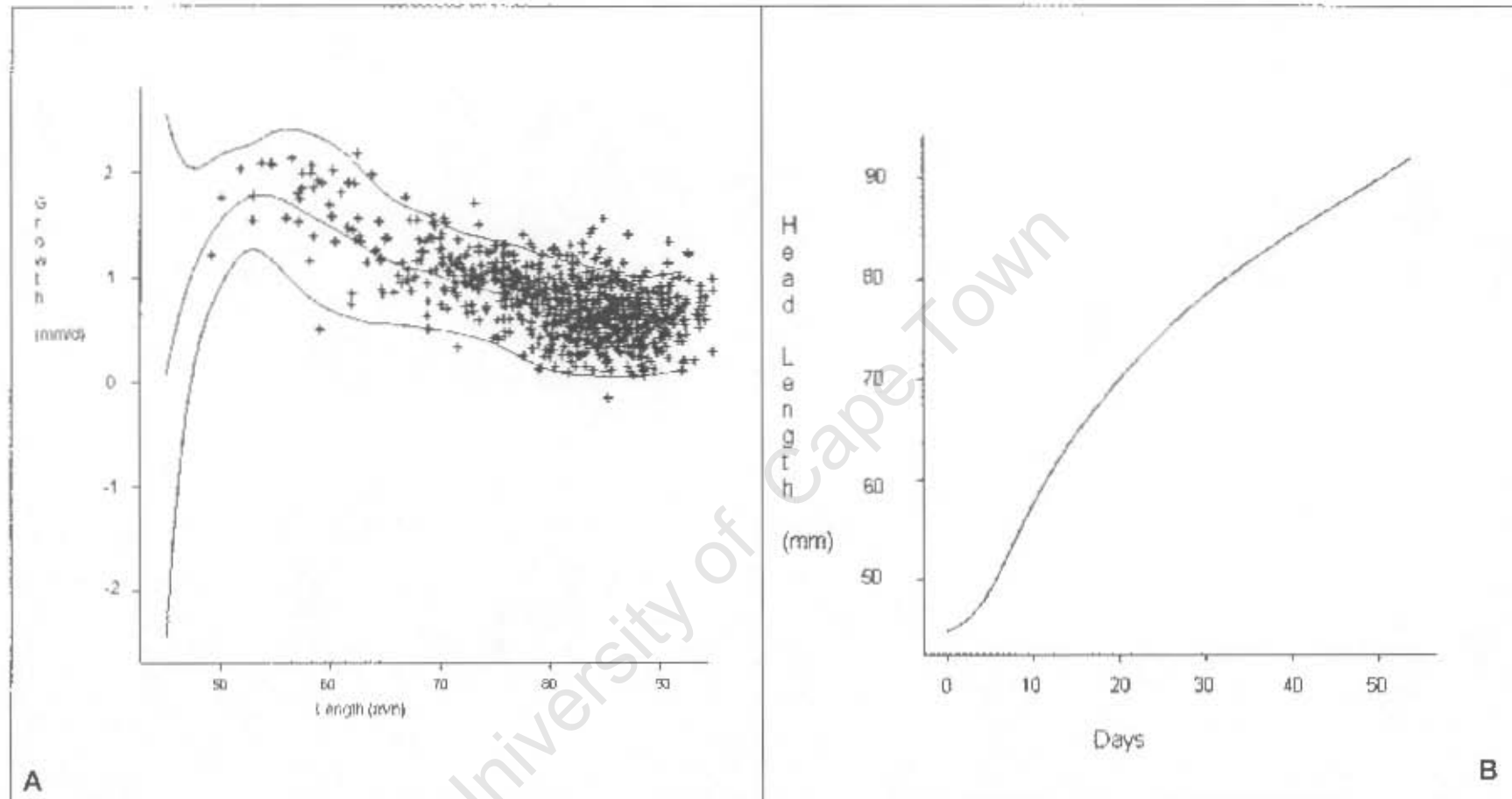
Figure 6: A: Growth rates (mm/day) of the foot length (mm) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). B: Growth curve of foot length (mm) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching foot length from Table 3 as foot length on day 0.
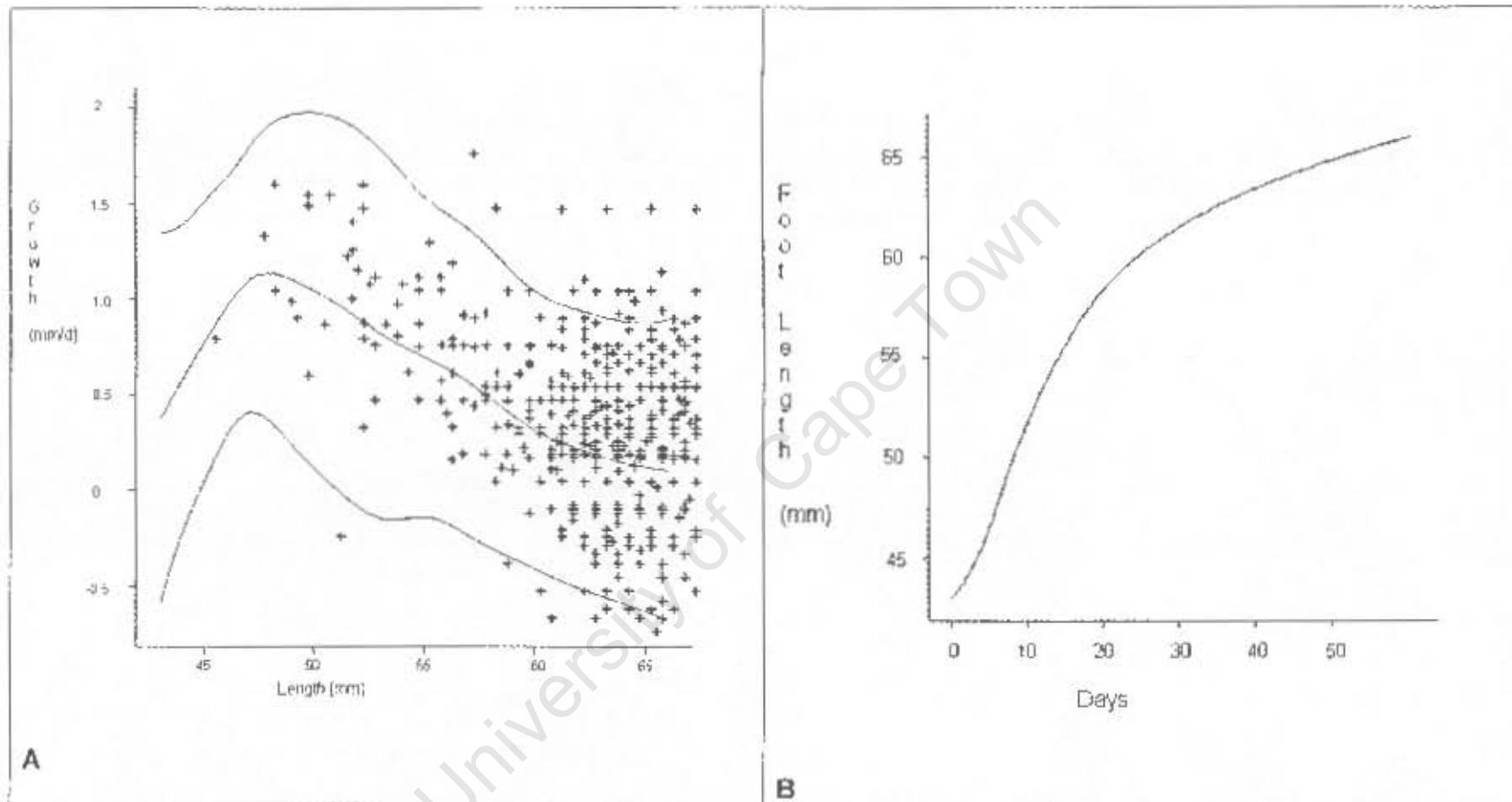
Figure 7: A: Growth rates (mm/day) of the tarsus length (mm) of Swift Tern chicks on Robben Island. Smoothed curve gives the trajectory of the mean, and upper and lower 95% prediction intervals are shown (see text). **B:** Growth curve of tarsus length (mm) of Swift Tern chicks in relation to age in days, transformed from the trajectory of the mean in A. Using the hatching length of the tarsus from Table 3 as tarsus length on day 0.
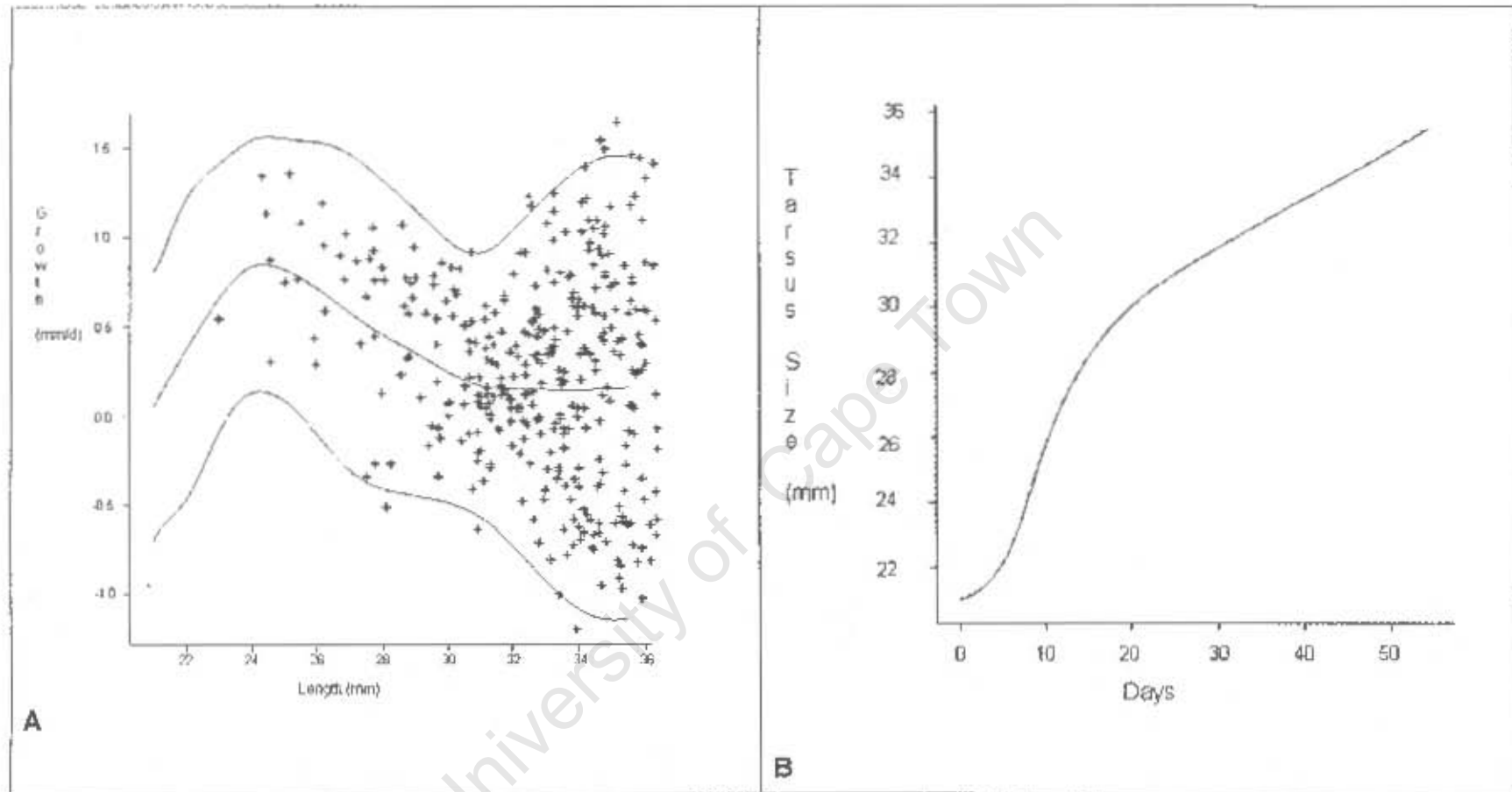
Chapter 3: Movement

Chapter 3: Movements of Swift Terns Sterna bergii in southern Africa based on recoveries of birds ringed as pre-fledglings

Abstract

Because their crèching behaviour facilitates ringing studies, large numbers of Swift Tern near-fledglings have been ringed, particularly in the Western Cape, over nearly three decades. A preliminary analysis, conducted in 1999, made the recommendations that the database as a whole warranted more detailed study, and that there was an opportunity to undertake a study of the movement patterns of chicks marked with individually engraved colour rings. This chapter implemented these recommendations.

Most chicks which were reared in the Western Cape moved eastwards along the coastline towards KwaZulu-Natal. The fastest-moving bird covered a coastal distance of 849 km within 15 days of ringing, a minimum average speed of 57 km/day. It was established that Swift Tern juveniles have a nursery area, which takes them about 100 days to reach, and where they remain until about 18 months of age, between Plettenberg Bay, Western Cape, and the East London area of the Eastern Cape; 50% of the recoveries made during the "nursery period" were in this section of coastline. The nursery area extended to northern KwaZulu-Natal. Not all fledgings move to the nursery area, because birds were found within the breeding areas during the nursery period. Some Swift Terns from the Western Cape moved northward towards Namibia after fledging, but the proportion cannot be estimated because the process that generates recoveries in this region is entirely different due to the fact that the diamond-mining areas are closed to people, and scavengers remove carcasses from beaches on an almost daily basis. The longest distance moved was of a chick ringed at Lüderitz, Namibia, which was recovered in KwaZulu-Natal at a coastal distance of 2072 km, at an age of 15 months, within the "nursery period".

From an age of 3–4 years onwards, the overall pattern of movement of young birds showed a trend towards being progressively closer to their natal areas during the breeding season. For birds aged five years and older (breeding adults), the median distance recovered from natal colonies during the breeding season was 36 km, and the upper quartile was 112 km, indicating that 75% of adults were within the breeding area.

The use of individually engraved colour bands resulted in a substantial increase in the proportion of birds from which information was obtained, from less than 2% in earlier years when metal rings only were used, to close to 10%. If this study is repeated in the future, its value could be enhanced by recruiting observers to be evenly spaced along the coastline.

The pattern of post-fledgling movement of the Swift Tern was compared and contrasted with that of the African Black Oystercatcher *Haematopus moquini*, a species which similarly breeds mainly in the Western Cape, and which has recently been discovered also to have a nursery area, beyond the breeding area of adults, where immatures remain for the first few years of their lives. The main nursery for the oystercatcher is in Namibia. The contrasting directions in which the two species move to their nursery areas is most likely to be a consequence of the availability of food resources accessible to inexperienced feeders. For the Swift Tern, the advantages of being along the coastline of the Eastern Cape and KwaZulu-Natal for the period from about July onwards when it has to learn to hunt, are hypothesized to be the relatively calm waters along the coastline and the presence of an abundance of sardines *Sardinops sagax* in the region.

Introduction

The Swift Tern *Sterna bergii* (also known as the Greater Crested Tern) occurs on coastlines in the south-east Atlantic Ocean, the Indian Ocean and the western Pacific Ocean (Del Hoyo *et al.* 1996; Crawford 1997). In southern Africa the nominate subspecies *Sterna bergii bergii* occurs, with an estimated overall population size as *c.* 6100 breeding pairs (Cooper *et al.* 1990; du Toit *et al.* 2003). Chapter 1 contains a fuller description of the biology of the species, and provides an overview of the migration systems of the closely related tern species.

Underhill *et al.* (1999) undertook a cursory analysis of the Swift Tern database of ringing recoveries as part of a review of the results of waterbird ringing in southern Africa. A total of 19 322 Swift Terns, mostly ringed as pre-fledglings, had been ringed between 1968 and 1999; by the latter date, 447 recoveries had been recorded on the South African Bird Ringing Unit (SAFRING) database. The preliminary investigation of these data by Underhill *et al.* (1999) showed that Swift Terns breed within the Benguela upwelling ecosystem, on the western coastline of southern Africa, mainly from February to May and then most migrate along the Indian Ocean coastline during the non-breeding season. This migration raised further questions about their post-breeding dispersal and whether or not juveniles move into nursery areas, and whether or not they would remain there during the subsequent breeding seasons. Underhill *et al.* (1999) recommended that the movement patterns of this species could be further elucidated by enabling the individual identification of individuals through the use of engraved colour rings which could be read from a distance with telescope or binoculars.

This chapter aims to provide a more detailed investigation of the movement patterns of Swift Terns than that provided by Underhill *et al.* (1999) and reports on the results of a study in which fledglings were individually colour-marked with engraved plastic rings.

Materials and Methods:

Methods for investigating post-breeding dispersal

By March 2005 the number of recoveries and resightings of Swift Terns ringed as chicks recorded in the SAFRING database had increased from the 447 reviewed by Underhill *et al*. (1999) to 654. Information included in the data set were date and place of ringing, date and place of ring recovery, age and distance moved. Chicks which were deemed not to have fledged (i.e. were recovered within a few weeks of ringing at the site where they had been ringed) were excluded from all analyses. Age was calculated as the elapsed time between ringing (which was close to fledging) and recovery in days. Distance between the site of ringing and recovery was calculated using software developed by SAFRING (Underhill *et al*. 1999), which incorporates the distances between headlands along the coastline to estimate the minimum distance using the route flown by a coastal seabird, rather than the conventional "great circle distance", which, for example would be entirely overland for a tern ringed in Namibia and recovered in KwaZulu-Natal (Underhill *et al*. 1999).

In order to investigate the movement patterns of individual Swift Terns, 738 fledglings were ringed with individually engraved Darvic colour bands (Pro-Touch, Saskatoon, Canada) in the 2002 breeding season. A total of 434 fledglings was colour-banded at the Koeberg Nuclear Power Station (33°40'S 18°25'E) on 13 May 2002, and 304 were colour banded at Robben Island (33°47'S 18°21'E) during a series of 11 ringing sessions between 3 May and 8 July 2002. The colour bands were red and had two white engraved letters or digits, repeated three times around the ring. The numbers on the bands were conspicuously visible to observers with telescopes or binoculars, and could be read to a distance of *c*. 65 m without having to re-trap the bird. Observers were alerted to the presence of these birds and requested to report them to SAFRING (see http://web.uct.ac.za/depts/stats/adu/sterna_project.htm). Individual birds could therefore be monitored as they moved along the coastline of southern Africa. For individuals resighted from the 2002 cohort the final retrap date before fledging was taken as the date of ringing so that the elapsed time would start from as close to the

fledging date as possible. Data from birds from this cohort, which were resighted more than once, were tabulated to elucidate patterns of movement of individual birds.

In the main detailed analysis in this paper, birds that had been ringed as pre-fledglings in the Western Cape were included. These constituted a large proportion of the database. From Underhill *et al.* (1999), it was known that the bulk of these birds move along the southern and eastern coast of South Africa shortly after fledging. These birds ringed as pre-fledglings were considered as a homogeneous sample and analysed quantitatively. Two small samples of birds, those that had moved north from the Western Cape, and those that had been ringed in Namibia, were considered qualitatively.

For the pre-fledglings ringed in the Western Cape and which had moved south and east, ages at recovery or resighting were divided into 20-day intervals for birds younger than 200 days old, and after that into wider intervals so that the sample sizes per interval were approximately uniform. For each of these age-class intervals five-number summaries (minimum, lower quartile, median, upper quartile and maximum) of the distance moved were computed (Tukey 1977). Genstat 8 (Payne 2005) was used to compute the five-number summaries and to produce box-and-whisker plots (Tukey 1977).

Five-number summaries and box-and-whisker plots for distance moved were also produced for birds up to one year old (birds recovered up to 365 days from date of ringing), then one to two years old (i.e. 366 to 730 days), two to three years old, three to four years old, four to five years old and then from five years old and upwards (1826 days and older). This choice of categories was based on the knowledge that Swift Terns start breeding from the age of three years and most are breeding at age five years (Crawford *et al.* 2002).

In order to examine the annual pattern of movements of breeding adults monthly five-number summaries and box-and-whisker plots for distance moved were produced. For this analysis, we used only birds recovered when five years and older.

The breeding season for the Swift Tern in southern Africa is February to April (Crawford *et al.* 2002). Five-number summaries and box-and-whisker plots of distances moved were produced for birds recovered inside and outside the breeding season for

four age groups: two–three years, three–four years, four–five years and five years and older. These plots enabled us to compare the patterns of movement of younger birds with breeding birds during the breeding season.

Fast-moving fledglings were identified, by calculating average speed moved as kilometres per day from date of ringing to date of recovery, to illustrate the minimum speeds with which fledglings can move. Those with the highest daily speeds were tabulated.

Results

Of the 654 available recoveries of Swift Terns ringed as near-fledglings, 607 had moved from breeding colonies in the Western Cape southward around Cape Point and then eastward towards Cape Agulhas, the Eastern Cape and KwaZulu-Natal. Sixteen fledglings had moved northwards from the Western Cape towards the Northern Cape and Namibia, and 31 had been ringed in Namibia and moved either north or south. The following statistical analysis relates to the 607 (97.4%) of the recoveries of terns ringed in the Western Cape and which had moved southward and eastward.

Swift Terns fledglings, which moved southwards and eastwards from their breeding colonies in the Western Cape to the Eastern Cape and KwaZulu-Natal, did so rapidly, with substantial numbers of recoveries away from the natal colonies within months of fledging (Table 1, Figure 1). The median distances moved during the 15 age-class intervals up to 24 months were significantly different from each other (Kruskal-Wallis one-way analysis of variance, H=75.7, 14 df, P<0.001). However, the median distances moved during the period 100 days to the end of the first half of the second year were not significantly different from each other (Kruskal-Wallis, H=12.22, 8 df, P=0.142). This contrast suggested that young Swift Terns take approximately 100 days to reach their "nursery" destinations, and remain there until about 18 months of age (Fig. 1). This interval is considered the nursery period.

Eight fledglings were recovered away from their ringing sites within 20 days of ringing; the median distance which these birds had moved was 225 km. The farthest distance covered was 849 km (Table 1), this bird, 565149, had been ringed on the 26 May 1977 at Jutten Island, Saldanha, and was found dead at Bird Island, Eastern Cape,

15 days later. It had moved the coastal distance of 849 km at a minimum average speed of 57 km/day (Table 2). Bird 582796, ringed on 10 June 2002 at Robben Island, was resighted 20 days later having moved 832 km to Riet River Point, Eastern Cape, (Tables 2, Figure 1). This movement was at an average minimum speed of 42 km/day (Table 2). These values (57 km/day and 42 km/day) were the two fastest average speeds for those birds recovered within the first 55 days after fledging.

For a dataset of 27 fledglings recovered 21 to 40 days after ringing the median distance moved was 708 km, with a maximum of 832 km (Table 1, Figure 1). Two birds ringed at Robben Island on 10 June 2002, birds 571995 and 5H31664, were both resighted 25 days later at Riet River, Eastern Cape, having moved a distance of 832 km, at a minimum average speed of 33 km/day (Table 2). Bird 582662 ringed at Robben Island on the 18 June 2002 was resighted 37 days later at Cape Recife Point having moved 708 km, at a minimum average speed of 19 km/day (Table 2).

Between days 41 and 60 days after fledging the median distance moved for 45 Swift Tern juveniles was 719 km, with a maximum distance of 1068 km (Table 1, Figure 1). Bird 515396 ringed at Robben Island on 16 May 1970 was recovered 41 days later at Umngazi having moved 1068 km at an average speed of 26 km/day (Table 2). Bird 5H31387 ringed at Koeberg on 13 May 2002 was resighted 45 days later at Riet River having moved 843 km at an average speed of 19 km/day (Table 2).

Between 100 days and 18 months after ringing, the period for which young Swift Terns remain in their "nursery" areas, the median distances moved ranged between 843 km and 1385 km (Table 1, Figure 1). For this period, the overall median of the 192 recoveries of Swift Terns which had been ringed as near fledglings in the Western Cape and which had moved eastwards, was 1015 km, with quartiles 582 km and 1015 km. This places the main nursery area, within which 50% of recoveries were made, for those Swift Terns which moved eastwards between Plettenberg Bay, Western Cape, and East London, Eastern Cape.

The outer limits of the nursery area was in northern KwaZulu-Natal; six recoveries were made at Sodwana Bay and St Lucia during the nursery period. Not all birds moved away from their natal colonies in the Western Cape after fledging. The inner limit of the nursery area clearly covered the breeding areas (Table 1, Figure 1).

During the nursery period, 123 recoveries were made in the Western Cape. In the first 365 days, the minimum distances moved ranged from 0 km to 115 km (Table 1, Figure 1). Many which were found close to the ringing site were discovered as dead birds, 72% of those recovered within 499 km of the ringing site were dead birds. Of the birds resighted between 500 km to 999 km away from ringing site, 35% were recovered dead.

Many birds moved rapidly away from their ringing site after fledging (Table 2). Among the fast-moving birds, the longest movement was bird 63502368, which covered 1701 km, from Robben Island to Sodwana Bay, KwaZulu-Natal, within 79 days after ringing, at 21.5 km/day (Table 2). The fastest was bird 565149, which was mentioned earlier, covered 849 km in 15 days, an average speed of 57 km/day. Of the 29 fastest moving birds, 22 had been individually colour marked in the 2002 cohort (Table 2). Because the probabilities of a dead bird being found with a ring and reported to SAFRING vary along the coastline (see Discussion), the data do not enable us to estimate the proportions of birds which moved different distance classes in given periods.

After the nursery period, the median distances moved decreased: for the remaining six months of the second year the median was 506 km, 50% of the value during the nursery period; for birds aged 2–3 years it was 408 km, for 3–4 years, it was 106 km, with similar medians for older birds (Table 1, Figure 1). The farthest distance travelled from the Western Cape colonies was by a tern aged 2–3 years; bird 527227 was ringed at Marcus Island in Saldanha Bay on 9 April 1983 and recovered on 25 February 1986, aged 2.9 years, at Kosi Bay Estuary in KwaZulu-Natal, 1886 km from the place of ringing.

Of the individually colour marked 2002 cohort, 20 birds had been resighted more than once by March 2005 (Table 3). Four birds (571995, 5H31036, 5H31045 and 5H31141) were resighted away from their natal grounds and then resighted in March 2003 close to their original ringing site (Table 3). Bird 5H31042 was resighted in March 2003 aged 10 months near its ringing site, but then resighted at Cape Recife in the Eastern Cape, about one year later. Bird 5H31491 was resighted 53 days after being ringed at Koeberg, at Riet River, Eastern Cape, having moved 843 km (Table 3). It was resighted 251 days after ringing at the same place on the 19 January 2003. Bird

582654 was resighted at locations spread over 139 km of coastline in the Eastern Cape over a period of six days in June-July 2002. These two records and others in Table 3 that suggest that birds remained within a fairly short section of coastline within their chosen nursery area during their first year after fledging. Of the 20 birds that were resighted more than once, the median distance moved was 708 km, inside the nursery area.

Adult Swift Terns in the Western Cape breed on offshore islands during February, March and April. Birds aged five years and older (1826 days upwards) should all be of breeding age. The sample size available for analysis in this age class was 160: 110 were recovered dead, 29 were reported as sick and 21 were resighted alive. Monthly sample sizes ranged from six to 23. For these adult birds, the median distance away from their natal sites was the smallest (23 km) in March (Table 4, Figure 2). During the breeding season, February, March and April, the minimum and maximum distances ranged from 0 km to 1380 km, indicating a spread of mature adults along the coastline, even during the peak of the breeding season. The month with the largest median (1036 km) was July (Table 4, Figure 2). The most interesting set of summary statistics is that of the upper quartiles; these ranged from 74 km to 189 km during the three-month peak breeding season, and from 452 km to 1312 km during the remainder of the year (Table 4, Figure 2).

This result motivated a comparison of movements during the peak breeding season (February, March and April) with the remainder of the year. This comparison was done within each age group from birds aged two years old and older (731 days and older) (Table 5, Figure 3). In Year 2 (731 days to 1095 days) the median distance was 212 km during the breeding season and 432 km outside of it. This distance was successively smaller in years 3 and 4, being 72 km and 52 km, respectively, and was 36 km for adult birds aged five years and older (Table 5, Figure 3). In spite of the small sample sizes, this reduction in distance suggests a trend of an increasing proportion of birds returning to their natal areas from year 2 onwards. The median distances moved outside the breeding season showed a less noticeable trend, but were consistently larger than the medians during the breeding season (Table 5, Figure 3).

Only 16 recoveries (2.6% of the Swift Tern fledglings ringed in the Western Cape) were of birds which moved northward and were recovered in the Northern Cape and Namibia (Table 6). The distances moved ranged from 434 km (Port Nolloth, Northern Cape) to 1299 km (Swakopmund, Namibia) from the site of ringing (Table 6). The fastest moving tern, bird 589057, moved at an average speed of 14.7 km/day; it had been ringed on Robben Island on 7 April 1994, and was recovered 61 days later at Ichaboe Island, Namibia. Four birds from the colour-marked 2002 cohort were resighted at Mile 4 Saltworks, Swakopmund, Namibia, between 10 and 13 months after ringing, suggesting that birds which move northwards from the Western Cape also remain at their nursery areas. These four birds had moved 1299 km northwards in their first year (Table 6); their dates of recoveries were about one year after ringing, and it is therefore inferred that they had not returned to their original breeding site during the breeding season immediately subsequent to fledging.

Fourteen birds ringed in Namibia were recovered there (Table 7). Seventeen birds ringed in Namibia were recovered in South Africa, along the coastlines of the Western Cape (seven birds), Eastern Cape (seven) and KwaZulu-Natal (three) (Table 8). Within the first 100 days after ringing, the time taken by fledglings in the Western Cape to reach their nursery areas, nine terns were recovered. Seven were within 107 km of their ringing sites, and two had moved south to South Africa – one 678 km to Lambert's Bay, Western Cape, and one 1830 km, to Mazeppa Bay, Eastern Cape. This latter tern, bird 567131, covered this distance in 64 days (Table 8), a average speed of 28.6 km/day, and if it had been ringed in the Western Cape would have featured in Table 2 in 12th place.

From 100 days to 18 months, the nursery period for fledglings from the Western Cape, 14 birds were recovered, five in northern Namibia (north of Swakopmund), and nine in South Africa, between Lambert's Bay and Umzumbe, KwaZulu-Natal (Table 8). The bird which moved the farthest was bird 567080, ringed on the 18 May 1977 in Lüderitz, Namibia, and recovered on 9 August 1978; at 2072 km it is the longest recorded movement for a Swift Tern within the SAFRING database.

Two Namibian-ringed birds recovered in South Africa were five years of age or older, and were therefore old enough to be breeding adults (5H08307, 567148) (Table

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8). These three birds were found in November and December, outside the breeding season and during what could be considered the nursery period, suggesting that Namibian-breeding birds show a similar pattern to those breeding in the Western Cape, i.e. they migrate with their offspring to the nursery area, and are then assumed return to Namibia to breed again. One tern, bird 5H08724 (Table 8), ringed at Lüderitz on 6 April 1999, was found incapacitated on Robben Island on 15 December 2003, rehabilitated at the Southern African Foundation for the Conservation of Coastal Birds (SANCCOB) and released on 30 December (Parsons *et al.* 2006). Given that its age was 4.7 years, it is possible that it was on passage towards breeding in its natal area when incapacitated.

Although some Swift Terns were ringed before 1977, no major efforts were made to ring at that time. Between 1977 and 1986, and again since 1993 to 2002, birds have been ringed each year (Table 9). Up to 2001, the percentage recovered in each year varied from 0% to 2.77%. The largest recovery made was for the 2002 cohort when engraved colour rings were used; the recovery rate increased dramatically to 9.37% of birds resighted or recovered within the first year after ringing; the percentage of birds recovered dead from this cohort was 1.87%, within the range of for all previous years (Table 9).

Discussion

Potential biases

We cannot infer from the recovery data that 97.4% of fledgling Swift Terns from the Western Cape move eastward towards KwaZulu-Natal and 2.6% move northward towards Namibia. The probability that a dead Swift Tern with a ring is both found and reported is far larger on the populous coast of the Eastern Cape and KwaZulu-Natal, where there are numerous recreational users of the coastline, than along the coastline of the Northern Cape and Namibia, where much of the coastline is diamond mining concessions, and are closed to the public. The coastline of the Northern Cape and Namibia is adjacent to the arid Karoo and Namib Desert, and is patrolled regularly by Black-backed Jackals *Canis mesomelas* and, in parts, by Brown Hyaenas *Parahyaena*

brunnea which scavenge dead animals including terns, further reducing the probability of recovery of a dead ringed Swift Tern (L.G. Underhill pers. comm.). The recoveries made in Namibia are mostly from the small number of localities where there is human access to the coastline: Port Nolloth, the vicinity of Lüderitz, and the coastline of central Namibia from Walvis Bay northwards, although in this region the number of people on the coastline decreases rapidly north of Cape Cross and is minimal in the Skeleton Coast Park, which stretches to the border of Namibia with Angola.

Even along the coastline of the Western Cape south and east of the Swift Tern breeding colonies, the Eastern Cape and KwaZulu-Natal, the number of people "searching" each kilometer of shoreline for dead seabirds varies through several orders of magnitude. Many sections of coastline are rarely visited, either because they are inaccessible or because they are effectively closed to the public. In addition, even if a person finds a bird with a ring, the probability that it is reported to SAFRING depends on socio-economic factors such as education (an insight that it is scientifically valuable to make the effort to report the information and a knowledge of what is the relevant data) and financial resources (communicating the information costs money, either in stamps, telephone calls or internet connections). Thus it is not feasible, even for the large sample of recoveries of birds in this region, to describe the "nursery area" using more sophisticated analytical approaches than used in this chapter. Although it would be desirable to make statements such as "at least 50% of birds have passed Locality X by Date Y", the biases within the ring recovery process are likely to invalidate such analyses. The level of analysis to which these data have been subjected in this chapter is appropriate to their reliability.

Although the colour-ringing project of 2002 resulted in a substantial increase in the proportion of birds for which information subsequent to ringing was obtained (Table 9), it introduced a further bias. The distribution of birders willing to participate in the resighting program was even more non-random than the distribution of members of the public who report ring recoveries; for this project, the most intensive efforts were made in the Eastern Cape. Although this effort in the Eastern Cape is unlikely to have influenced the overall results, because the 2002 resightings comprised a small component of the overall data set, it is recommended that future projects of this nature

address the issue of the distribution of participants in ring resighting programs. The amount of effort put into resightings, measured most effectively as total number of birds scanned for rings, should be recorded. The primary objective should be to make the distribution of effort as uniform as possible.

Swift Tern vs African Black Oystercatcher

It is instructive to compare the post fledging movements of the Swift Tern with those of the African Black Oystercatcher *Haematopus moquini*. The oystercatcher has a breeding range similar to that of the nominate subspecies of the Swift Tern; both species have the bulk of their breeding populations concentrated on the offshore islands of the Western Cape. The oystercatcher feeds almost exclusively in the intertidal zone, mainly on limpets and mussels; the tern feeds mostly within a few kilometres of the shore, and mainly on fish (Hockey *et al.* 2005). Ultimately, while breeding in the Western Cape, both species are dependent on the Benguela upwelling system.

The terns breed in colonies numbering up to thousands of pairs; in contrast, oystercatchers are territorial defending linear territories. On the mainland territories are often about 1 km in length, but on the offshore islands where populations are densest nests of neighbours are frequently within 50 m of each other, and nests as close as 1.5 m apart have been observed. There are similarities in the breeding biology of the tern and the oystercatcher; for both species the chicks are fed by the parents, a single item at a time. The food is gathered within the breeding territory by the oystercatcher, and probably within about 10 km of the nest for the tern. In the tern and the oystercatcher, flight is attained before the chick is fully grown; for oystercatchers fledging takes place at about two-thirds of adult mass (Hockey 1984) and for Swift Terns at about 86% of adult mass (Chapter 2); for both species the wings and bill are not fully grown at fledging.

There are two key factors on which this comparison among the two species is based. Firstly, for the tern and the oystercatcher, the feeding techniques involve complex sets of skills, and chicks are fed by the parents for an extended period of several months before they are able to forage for themselves (Hockey *et al.* 2005).

Secondly, the immatures undertake a dispersal/migration to "nursery areas" which lie beyond the normal breeding range of the species. However, there are sharp contrasts in the nature of this dispersal between the two species.

The post breeding dispersal of Swift Terns from the Western Cape is mainly eastwards, into the Agulhas Current, where the main nursery area lies along the shore of the Eastern Cape and KwaZulu-Natal, although some juveniles do disperse northwards to Namibia. For the oystercatcher the post breeding dispersal is northwards, towards Namibia and southern Angola, into the northern Benguela upwelling system. For the oystercatcher, the main nursery areas are discrete localities at sheltered embayments north of Lüderitz, especially Walvis Bay and Sandwich Harbour (Hockey *et al*. 2003). A minority of oystercatchers disperse eastwards (Hockey *et al*. 2003, 2005). For the oystercatcher, there is a minor nursery area beyond the eastern limit of the breeding area in KwaZulu-Natal. For both species there are breeding localities within the nursery areas: oystercatchers breed on the islands and adjacent mainland near Lüderitz, Namibia; Swift Terns breed in some years on the Algoa Bay islands, Eastern Cape. The juvenile dispersal is partial in both species, with some juveniles remaining within the breeding range. In both species, maturity is delayed and birds tend to return from the nursery areas to their natal areas within two to five years (Hockey *et al*. 2005).

There is a striking difference between the two species. The oystercatcher chicks are fed within the natal territory after fledging, and are driven out of it by the adults after two–three months and travel without their parents to the nursery areas. In contrast, the tern chicks rapidly move away from their breeding colonies with at least one parent, and are fed by that parent even within the nursery area for periods of at least four months (Hockey *et al*. 2005, pers. obs).

Why do the nursery areas lie beyond the breeding range of the adults? Why is the main nursery area of the Swift Terns in the Agulhas ecosystem, and why is the main nursery area of the African Black Oystercatchers in the Benguela Ecosystem? The most likely explanation for these questions is food availability. For both species, migration to nursery areas confers the advantage of feeding in the absence of competition from conspecific adults. For the oystercatcher, the diet at the Namibian

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nurseries consists of prey species which are abundant and easier to handle than the mussels and limpets which are the main prey species within the breeding areas (Leseberg 2001, Hockey *et al.* 2003, 2005). The availability of intertidal resources which provide suitable food for oystercatchers is far higher in the northern Benguela ecosystem than in the Agulhas ecosystem (Branch *et al.* 1994). Thus the preference of oystercatchers for a nursery area in Namibia is understandable.

The prey of the Swift Tern in its nursery areas is not known; however, it is predicted that the prey species available in the Agulhas ecosystem are slower-moving, closer to the surface and easier to hunt by plunge-diving than are the shoaling fish such as Anchovies *Engraulis capensis* and Sardines *Sardinops sagax* which are the main food of adult Swift Terns in the Benguela upwelling system (Walter 1984, Walter *et al.* 1987). Given that Swift Tern fledglings are fed by adults for about four months, the main period in which juvenile Swift Terns need to learn to hunt will start in July. This is generally the period of winter storms in the Western Cape. In addition, it is therefore predicted that, at this time of the year, learning to hunt by plunge diving is easier in the relatively calm waters of the nursery area (east of Plettenberg Bay, Western Cape, through the Eastern Cape to KwaZulu-Natal) than in the rough seas of the southern Benguela upwelling system. A further factor favouring eastwards migration by the fledgling Swift Terns is the presence of spawning sardines in winter offshore of the Eastern Cape and the so-called "Sardine Run" in midwinter along the coast of KwaZulu-Natal (Baird 1971, Armstrong and Thomas 1989). This predictable food abundance within their nursery is synchronised with the period when immature Swift Terns start to hunt fish for themselves.

Table 1: Five number summaries of distances (km) moved eastward by Swift Terns ringed as fledglings at various breeding locations in the Western Cape. The distances are coastal distances from the natal site; see text. Data are classified according to intervals of days from date of ringing as pre-fledglings to date of recovery/resighting. See Figure 1.

Days	Sample size	Min	Lower Quartile	Median	Upper Quartile	Max
1 to 20 days	8	4	72	225	736	849
21 to 40 days	27	11	198	708	708	832
41 to 60 days	45	32	642	719	798	1068
61 to 80 days	38	32	147	512	719	1701
81 to 100 days	20	36	189	419	1048	1725
101 to 120 days	20	45	776	1049	1384	1527
121 to 140 days	20	465	1014	1148	1389	1720
141 to 160 days	19	76	297	1149	1396	1661
161 to 180 days	16	0	1009	1385	1408	1479
181 to 200 days	12	48	796	1346	1400	1545
201 to 250 days	19	36	351	843	1276	1721
251 to 300 days	28	27	530	1000	1274	1412
301 to 365 days	18	115	600	1000	1224	1575
366 to 547 days (1 to 1.5 years)	40	32	582	1012	1398	1729
548 to 730 days (1.5 to 2 years old)	34	99	191	506	804	1405
731 to 1095 days (2 to 3 years)	28	48	128	408	829	1886
1096 to 1460 days (3 to 4 years)	21	0	49	106	470	1403
1461 to 1825 days (4 to 5 years)	20	2	50	99	675	1708
1826 days upwards (5 years and older)	160	0	42	116	608	1724
Total	607					

Table 2: Fast-moving Swift Tern juveniles, ringed in the Western Cape, which were recovered within 55 days of date of ringing as a pre-fledging and which had moved more than 800km

Ring	Ringing date	Ringing locality	Recovery date	Recovery locality	Days	Dist-ance (km)	Speed (km/day)
565149	26 May 1977	Jutten Island, Western Cape	10 Jun 1977	Bird Island, Algoa Bay, Eastern Cape	15	849	56.6
582796	10 Jun 2002	Robben Island, Western Cape	30 Jun 2002	Riet River Point, Eastern Cape	20	832	41.6
571995	10 Jun 2002	Robben Island, Western Cape	5 Jul 2002	Riet River Point, Eastern Cape	25	832	33.3
5H31664	10 Jun 2002	Robben Island, Western Cape	5 Jul 2002	Riet River Point, Eastern Cape	25	832	33.3
582580	18 Jun 2002	Robben Island, Western Cape	8 Jul 2002	Cape St Francis, Eastern Cape	20	641	32.1
5H31133	13 May 2002	Koeberg Nuclear Power Station, Western Cape	5 Jun 2002	Cape Recife Point, Eastern Cape	23	719	31.3
5H31712	10 Jun 2002	Robben Island, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	23	708	30.8
582796	10 Jun 2002	Robben Island, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	23	708	30.8
5H25812	10 Jun 2002	Robben Island, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	23	708	30.8
5H31663	10 Jun 2002	Robben Island, Western Cape	8 Jul 2002	Riet River Point, Eastern Cape	28	832	29.7
5H31802	18 Jun 2002	Robben Island, Western Cape	12 Jul 2002	Cape Recife Point, Eastern Cape	24	708	29.5
5H31802	18 Jun 2002	Robben Island, Western Cape	13 Jul 2002	Cape Recife Point, Eastern Cape	25	708	28.3
582796	10 Jun 2002	Robben Island, Western Cape	5 Jul 2002	Schoenmakerskop, Eastern Cape	25	693	27.7
5H31830	10 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	26	708	27.2
5H25815	10 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	26	708	27.2
5H25812	10 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	26	708	27.2
5H31712	10 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Schoenmakerskop, Eastern Cape	26	693	26.7
515396	16 May 1970	Robben Island, Western Cape	26 Jun 1970	Umngazi Mouth, Eastern Cape	41	1068	26.0
565203	30 Apr 1977	Jutten Island, Western Cape	6 Jul 1977	Richards Bay, KwaZulu-Natal	67	1661	24.8
582654	10 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Cape St.Francis, Eastern Cape	26	631	24.3
5H31893	24 Jun 2002	Robben Island, Western Cape	25 Jul 2002	Cape Recife Point, Eastern Cape	31	708	22.8
63502368	25 May 1968	Robben Island, Western Cape	12 Aug 1968	Sodwana Bay, KwaZulu-Natal	79	1701	21.5

Ring	Ringing date	Ringing locality	Recovery date	Recovery locality	Days	Dist-ance (km)	Speed (km/day)
582654	10 Jun 2002	Robben Island, Western Cape	13 Jul 2002	Cape Recife Point, Eastern Cape	33	708	21.5
570883	19 Apr 1980	Saldanha	29 Jun 1980	Amanzimtoti, KwaZulu-Natal	71	1375	19.4
582662	18 Jun 2002	Robben Island, Western Cape	25 Jul 2002	Cape Recife Point, Eastern Cape	37	708	19.1
5H31387	13 May 2002	Koeberg Nuclear Power Station, Western Cape	27 Jun 2002	Riet River Point, Eastern Cape	45	843	18.7
5H31018	13 May 2002	Koeberg Nuclear Power Station, Western Cape	3 Jul 2002	Gonubie Point, East London	51	950	18.6
565999	30 Apr 1977	Jutten Island, Western Cape	24 Jun 1977	Orient Beach, East London	55	1011	18.4
565723	30 Apr 1977	Jutten Island, Western Cape	24 Jun 1977	Orient Beach, East London	55	1011	18.4

Table 3: Swift Terns ringed as pre-fledglings in the Western Cape in 2002 and re-sighted more than once up until March 2005

Ring	Ringing date	Ringing locality	Resighting Date	Resighting locality	Days	Distance (km)
571995	3 Jun 2002	Robben Island, Western Cape	5 Jul 2002	Riet River Point, Eastern Cape	32	832
571995			2 Mar 2003	Buffels Bay, Western Cape	272	60
582654	3 Jun 2002	Robben Island, Western Cape	6 Jul 2002	Cape St. Francis, Eastern Cape	33	631
582654			13 Jul 2002	Cape Recife Point, Eastern Cape	40	708
582796	10 May 2002	Robben Island, Western Cape	30 Jun 2002	Riet River Point, Eastern Cape	51	832
582796			3 Jul 2002	Cape Recife Point, Eastern Cape	54	708
582796			5 Jul 2002	Schoenmakerskop, Eastern Cape	56	693
5H25812	3 May 2002	Robben Island, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	61	708
5H25812			6 Jul 2002	Cape Recife Point, Eastern Cape	64	708
5H30766	13 May 2002	Koeberg, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	54	719
5H30766			28 Jul 2005	Cape St Francis, Eastern Cape	76	652
5H31036	13 May 2002	Koeberg, Western Cape	29 Jun 2002	Cape Recife Point, Eastern Cape	47	719
5H31036			3 Jul 2002	Cape Recife Point, Eastern Cape	51	719
5H31036			2 Mar 2003	Buffels Bay, Western Cape	293	70
5H31042	13 May 2002	Koeberg, Western Cape	2 Mar 2003	Buffels Bay, Western Cape	293	72
5H31042			23 Apr 2004	Cape Recife Point, Eastern Cape	711	724
5H31045	13 May 2002	Koeberg, Western Cape	25 Jun 2002	Cape Recife Point, Eastern Cape	43	719
5H31045			25 Jul 2002	Cape Recife Point, Eastern Cape	73	719
5H31045			2 Mar 2003	Buffels Bay, Western Cape	293	70
5H31127	13 May 2002	Koeberg, Western Cape	25 Jun 2002	Cape Recife Point, Eastern Cape	43	719
5H31127			7 Jul 2002	St Francis Point, Eastern Cape	55	642
5H31141	13 May 2002	Koeberg, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	51	719
5H31141			2 Mar 2003	Buffels Bay, Western Cape	293	72
5H31151	13 May 2002	Koeberg, Western Cape	28 Jul 2002	Cape St Francis, Eastern Cape	76	652
5H31151			16 Jun 2003	Cape St Francis, Eastern Cape	399	652
5H31164	13 May 2002	Koeberg, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	54	719

Ring	Ringing date	Ringing locality	Resighting Date	Resighting locality	Days	Distance (km)
5H31164			8 Jul 2002	Cape St Francis	56	652
5H31191	13 May 2002	Koeberg, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	54	719
5H31191			25 Jul 2002	Cape Recife Point, Eastern Cape	73	719
5H31314	13 May 2002	Koeberg, Western Cape	8 Jul 2002	Cape St Francis, Eastern Cape	56	652
5H31314			28 Jul 2004	Dyer Island, Western Cape	807	157
5H31324	13 May 2002	Koeberg, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	51	719
5H31324			6 Jul 2002	Cape Recife Point, Eastern Cape	54	719
5H31491	13 May 2002	Koeberg, Western Cape	5 Jul 2002	Riet River Point, Eastern Cape	53	843
5H31491			19 Jan 2003	Riet River Point, Eastern Cape	251	843
5H31493	13 May 2002	Koeberg, Western Cape	6 Jul 2002	Cape Recife Point, Eastern Cape	54	719
5H31493			9 Jan 2003	Riet River Point, Eastern Cape	241	843
5H31712	27 May 2002	Robben Island, Western Cape	3 Jul 2002	Cape Recife Point, Eastern Cape	37	708
5H31712			6 Jul 2002	Schoenmakerskop, Eastern Cape	40	693
5H31802	27 May 2002	Robben Island, Western Cape	12 Jul 2002	Cape Recife Point, Eastern Cape	46	708
5H31802			13 Jul 2002	Cape Recife Point, Eastern Cape	47	708
5H31893	27 May 2002	Robben Island, Western Cape	25 Jul 2002	Cape Recife Point, Eastern Cape	59	708
5H31893			12 Apr 2004	Kasoega River mouth, Eastern Cape	686	804

Table 4: Five number summaries of distances (km) moved eastward by Swift Terns which were at least five years old when recovered, which were ringed as fledglings at various breeding locations in the Western Cape. The distances are coastal distances from the natal site; see text. See Figure 2

Month	Sample size	Minimum	Lower Quartile	Median	Upper Quartile	Maximum
January	18	2	8	108	1005	1436
February	8	0	11	46	128	232
March	15	2	8.5	23	74	584
April	13	9	29	63	189	1380
May	9	2	41	89	500	1335
June	11	12	53	90	590	1329
July	14	5	141	1036	1274	1479
August	10	14	112	280.5	791	1352
September	6	36	91	213.5	478	783
October	13	21	128	236	1312	1717
November	23	78	112	122	557	1724
December	20	0	27	108.5	452	1723
TOTAL	160					

Table 5: Five-number summaries of distances (km) moved eastward by Swift Terns aged two years and older, ringed in the Western Cape and recovered during the breeding season (February, March and April) and during the non-breeding season (May to January). The distances are coastal distances from the natal site; see text. See Figure 3

Age	Sample Size	Minimum	Lower Quartile	Median	Upper Quartile	Maximum
Year 2 (Non-breeding season)	21	63	138	432	794	1390
Year 2 (Breeding season)	7	48	103	212	962	1886
Year 3 (Non-breeding season)	17	0	49	106	470	1403
Year 3 (Breeding season)	4	49	54	72	573	1060
Year 4 (Non-breeding season)	10	49	112	388	1281	1708
Year 4 (Breeding season)	10	2	36	52	61	712
Year 5 plus (Non-breeding season)	124	0	87	144	824	1724
Year 5 plus (Breeding season)	36	0	14	36	112	1380

Table 6: Ringing and recovery details of Swift Terns ringed in the Western Cape which moved northwards to the Northern Cape and Namibia

Ring	Date	Ringing Location	Recovery Date	Recovery Location	Days	Dist ance
568721	16 Apr 1979	Marcus Island	9 Nov 1986	McDougalls Bay, Port Nolloth, Northern Cape	2764	434
572587	17 Apr 1982	Marcus Island	9 Nov 1986	McDougalls Bay	1667	434
527220	9 Apr 1983	Marcus Island	9 Nov 1986	McDougalls Bay	1310	434
569458	16 Apr 1979	Marcus Island	24 Nov 1983	Orange River mouth, Northern Cape/Namibia	1683	519
5H29511	24 Mar 2004	Dassen Island	23 Nov 2004	Orange River mouth	244	560
529821	20 Apr 1985	Marcus Island	15 Jun 1994	Radford Lagoon, Lüderitz	3343	762
589057	7 Apr 1994	Robben Island	7 Jun 1994	Ichaboe Island	61	896
529903	20 Apr 1985	Marcus Island	4 Jul 1994	Walvis Bay	3362	1172
5H12549	20 Mar 1997	Marcus Island	1 Mar 1999	Mile 4 Saltworks, Swakopmund	711	1209
5H12024	20 Mar 1997	Marcus Island	20 Mar 1999	Mile 4 Saltworks	730	1209
575944	17 Apr 1982	Marcus Island	5 Nov 1994	Henties Bay	4585	1269
5H30717	13 May 2002	Koeberg	9 Jun 2003	Mile 4 Saltworks	392	1288
5H31637	10 Jun 2002	Robben Island	29 April 2003	Mile 4 Saltworks	323	1299
5H00335	1 Jun 1999	Robben Island	7 May 2001	Mile 4 Saltworks	706	1299
582602	10 Jun 2002	Robben Island	9 Jun 2003	Mile 4 Saltworks	364	1299
5H31651	10 Jun 2002	Robben Island	9 Jun 2003	Mile 4 Saltworks	364	1299

Table 7: Ringing and recovery details of Swift Terns ringed and recovered in Namibia

| Ring	Date	Ringing Location	Recovery Date	Recovery Location	Days	Distance
5H03551	28 Apr 1994	Dias Point, Lüderitz	16 Jun 1994	Ichaboe Island	49	44
5H03636	28 Apr 1994	Dias Point	16 Jun 1994	Ichaboe Island	49	44
5H04463	29 Apr 1994	Dias Point	16 Jun 1994	Ichaboe Island	48	44
5H04719	29 Apr 1994	Dias Point	16 Jun 1994	Ichaboe Island	48	44
5H04850	28 Apr 1994	Dias Point	9 Jun 1994	Mercury Island	42	107
5H04666	29 Apr 1994	Dias Point	7 Jun 1994	Mercury Island	39	107
5H05230	18 Apr 1995	Dias Point	7 Jun 1995	Mercury Island	50	107
5H05125	18 Apr 1995	Dias Point	6 Oct 1995	Mile 4 Saltworks, Swakopmund	171	449
5H15448	4 Apr 1999	Dias Point	30 Sep 1999	Mile 4 Saltworks	179	451
5H08121	26 Apr 1995	Dias Point	15 Jun 1999	Mile 4 Saltworks	1603	453
580853	1 May 1998	Dias Point	20 Feb 1999	Mile 4 Saltworks	295	453
5H04551	29 Apr 1994	Dias Point	15 Nov 1994	Henties Bay, north of Swakopmund	200	510
556653	11 Apr 1994	Dias Point	2 Jan 1995	Terrace Bay, Skeleton Coast	266	768
5H08547	26 Apr 1995	Penguin Island, Lüderitz	27 Nov 199	Möwe Bay Beach, Skeleton Coast	1676	844

Table 8: Ringing and recovery details of Swift Terns ringed in Namibia and recovered in South Africa

Ring	Date	Ringing location	Recovery date	Recovery location	Days	Distance
587697	12 Jul 2001	Possession Island	18 Nov 2003	Bird Island, Lambert's Bay, Western Cape	859	638
5H08285	16 May 1995	Dias Point	4 Aug 1995	Bird Island, Lambert's Bay, Western Cape	80	678
5H08612	16 May 1995	Dias Point	1 Dec 1995	Bird Island, Lambert's Bay, Western Cape	199	678
5H08724	6 Apr 1999	Dias Point	30 Dec 2003	Robben Island, Western Cape	1729	855
5H05323	18 Apr 1995	Dias Point	20 Dec1995	Kommetjie, Western Cape	246	887
5H08307	16 May 1995	Dias Point	3 Dec 2001	Kommetjie, Western Cape	2393	892
5H08051	26 Apr 1995	Dias Point	17 Nov 1996	Sedgefield, Western Cape	571	1292
567058	18 May 1977	Sinclair Farm	17 Sep 1977	Swartkops River Mouth, Eastern Cape	122	1551
567331	16 May 1980	Sinclair Farm	20 Nov 1982	Colchester, Eastern Cape	918	1568
5H08417	16 May 1995	Dias Point	3 Nov 1995	Christmas Rocks, Eastern Cape	171	1749
5H04094	18 Apr 1995	Dias Point	23 Aug 1995	Orient Beach, Eastern Cape	127	1778
567148	18 May 1977	Dias Point	2 Nov 1996	Morgans Bay, Eastern Cape	7108	1824
567131	18 May 1977	Sinclair Farm	21 Jul 1977	Qolora River Mouth Transkei, Eastern Cape	64	1830
567266	16 May 1980	Sinclair Farm	23 Sep 1980	Mazeppa Bay, Transkei, Eastern Cape	130	1854
5H15168	5 Apr 1999	Dias Point	6 Sep 1999	Port St. Johns, Eastern Cape	154	1901
5H08484	26 Apr 1995	Dias Point	25 Aug 1996	Port St. Johns, Eastern Cape	487	1930
567080	18 May 1977	Sinclair Farm	9 Aug 1978	Umzumbe, KwaZulu-Natal	448	2072

Table 9: Numbers of Swift Terns ringed annually as near-fledglings in the Western Cape from 1977 to 2002, along with the numbers of recoveries made within the first year. The number of birds ringed in 1983 is unknown (H.D. Oschadleus, SAFRING pers. comm.).

Year	Island	Number Ringed	Number Recover within 12 months of ringing	% Recovered within 12 months
1977	Jutten	1336	37	2.77%
1978	Marcus	271	0	0.00%
1979	Marcus	742	3	0.40%
1980	Jutten/Malgas	1729	23	1.33%
1981	Vondeling/Robben	415	2	0.48%
1982	Marcus	2671	27	1.01%
1983	Marcus		34	
1984	Marcus	2145	25	1.17%
1985	Marcus	748	5	0.67%
1986	Marcus	470	3	0.64%
1993	Dassen Island/Robben Island	400	3	0.75%
1994	Dassen Island/Robben Island	351	7	1.99%
1995	Robben Island	500	5	1.00%
1996	Robben Island	497	7	1.41%
1997	Malgas Island	500	4	0.80%
1998	Marcus Island	500	2	0.40%
1999	Dassen Island	500	2	0.40%
2002	Robben Island/Koeberg	907	85 Total	9.37%
			17 Dead	1.87%

81
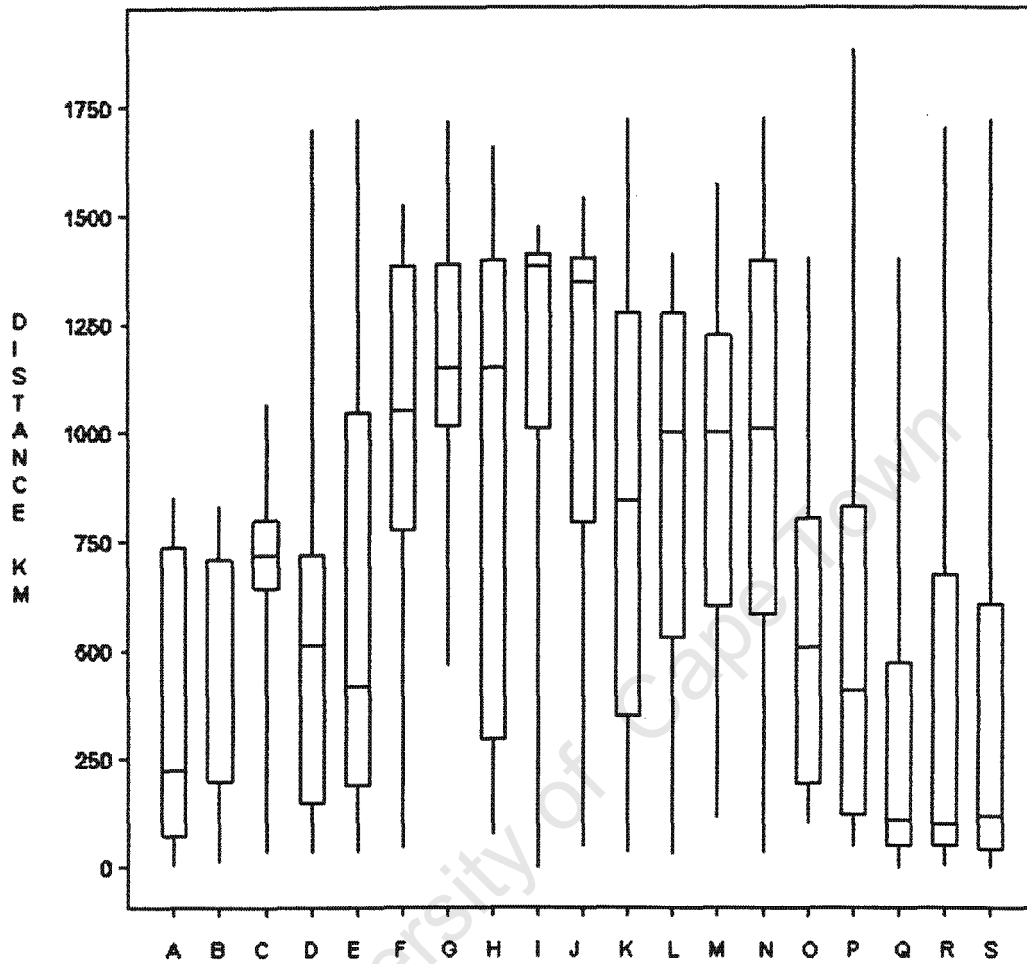
Figure 1: Movements of Swift Terns which moved eastwards from breeding colonies in the Western Cape represented as box-and-whisker plots for age groups. The movement was calculated as coastal distances (km) from the natal colony. Data are tabulated in Table 1. A 1 to 20 days old, B 21 to 40 days old, C 41 to 60 days old, D 61 to 80 days old, E 81 to 100 days old, F 101 to 120 days old, G 121 to 140 days old, H 141 to 160 days old, I 161 to 180 days old, J 181 to 200 days old, K 201 to 250 days old, L 251 to 300 days old, M 301 to 365 days old, N 366 to 548 days old (12–18 months), 0 548 to 730 days old (18–24 months), P 731 to 1095 days old (2–3 years old), Q 1096 days to 1460 days old (3–4 years old), R 1461 to 1825 days old (4–5 years old), S 1826 days upwards (older than 5 years, considered breeding adults)
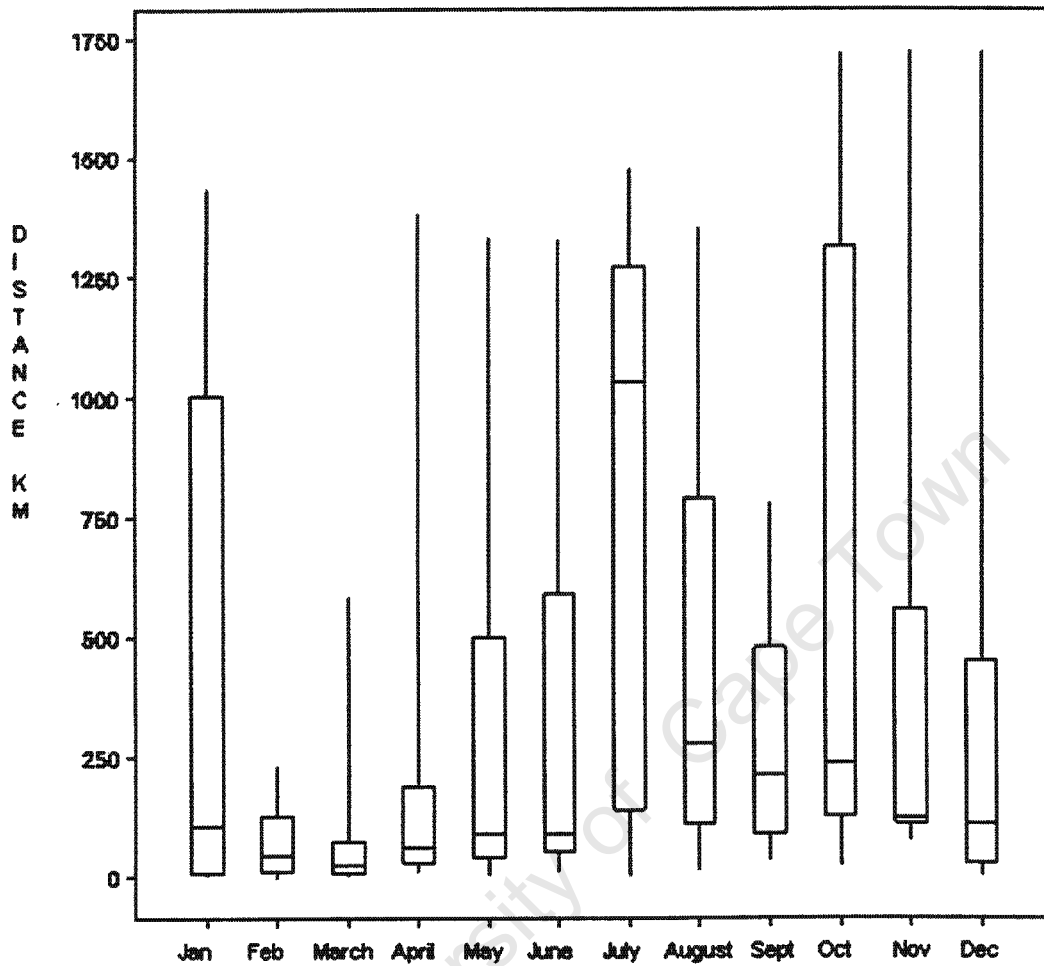
Figure 2: Monthly movements of adult Swift Terns aged five years and upwards represented as box-and-whisker plots. The distances were calculated as coastal distances (km) from the natal colony and the plot is restricted to birds which moved eastwards from the Western Cape. Data are tabulated in Table 4
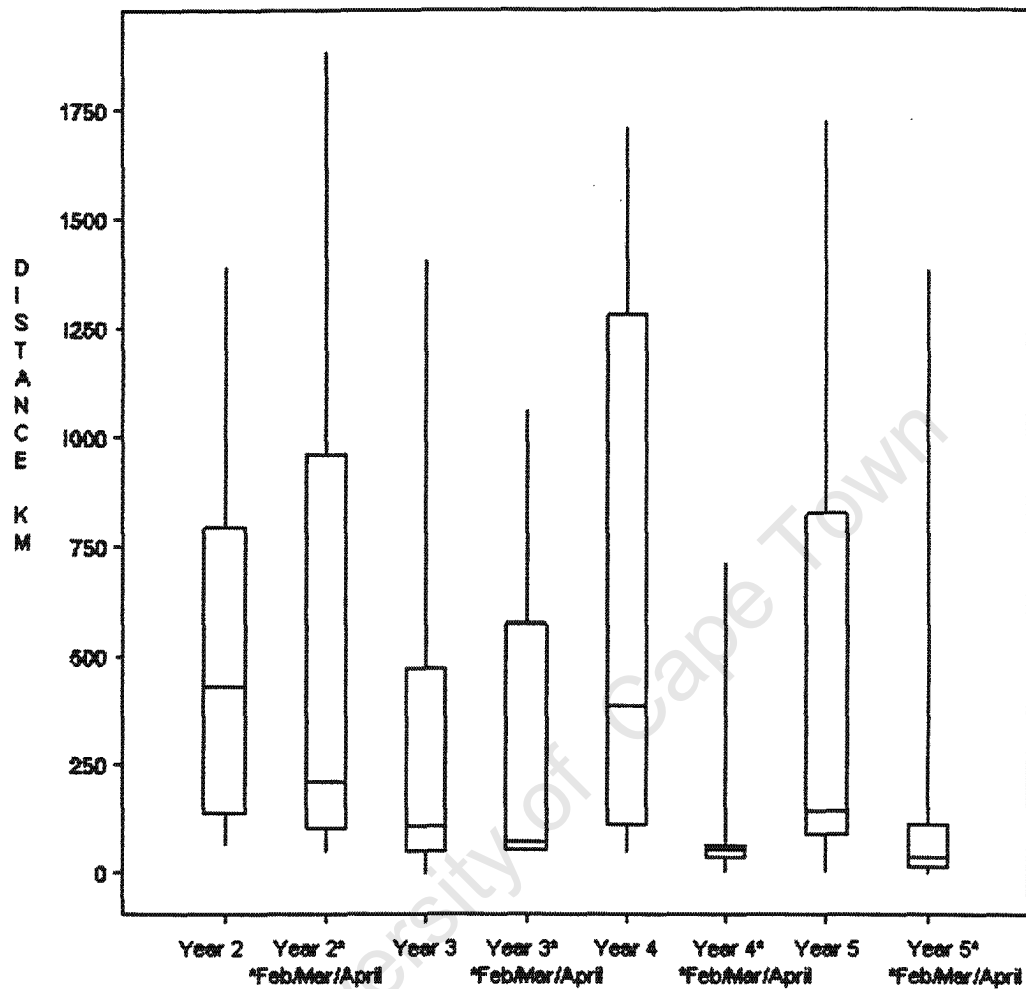
Figure 3: Monthly movements of Swift Terns aged two years and upwards represented as box-and-whisker plots; birds recovered during the breeding season (February, March and April) and during the non-breeding season (May to January) are separated. The movement was calculated as coastal distances (km) from the natal colony. The plot is restricted to birds which moved eastwards from the Western Cape. Data are tabulated in Table 5

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