BREEDING PRODUCTION OF CAPE GANNETS *Morus capensis* AT MALGAS ISLAND, 2002/03

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Abstract

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This MSc thesis consists of an introduction to the study species and its context, and two scientific papers. These papers are a contribution to the project on top predators in the Benguela upwelling system of the Benguela Current Large Marine Ecosystem (BCLME) Programme.

The study was undertaken at Malgas Island (33°03'S, 17°55'E), South Africa during the 2002/03 breeding season. Malgas Island is situated at the northern entrance to Saldanha Bay in the Benguela upwelling system and is one of only six breeding localities for Cape Gannets. Large numbers of Cape Gannets have been banded at Malgas Island over several decades, including many fledged chicks, providing a large number of birds of known age. Prior to this study, from 1978 to 2002, the Marine and Coastal Management Branch of the Department of Environmental Affairs and Tourism banded 22 497 gannets at the island. In addition to this, between 1951 and 1955 Broekhuysen *et al.* (1961) banded 15 507 gannets there.

We investigated whether breeding success, as measured by fledged chicks, varied with the age of the adults, including an investigation of a number of factors such as determining whether age affects time of breeding and nest site selection. The influence of breeding success relative to the location of the nest site was also investigated, i.e. is it better to be within or on the edges of the colony? Replacement clutches were also recorded and their breeding success investigated.

We also investigated whether the growth rates of chicks were influenced by the age of the adults, and a set of other explanatory variables. A method to estimate the growth coefficient of chicks of Cape Gannets *Morus capensis* is described. At Malgas Island in 2002/03, growth was most rapid for chicks hatched early in the season and there was

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Chapter 1

Introduction

Introduction

The Pelecaniformes

The order Pelecaniformes, with suborders Phaethontes and Pelecani, probably originated in the late Cretaceous, more than 60 million years ago, one to which gannets and boobies (family Sulidae) belong (Del Hoyo *et al.* 1992). The suborder Phaethones is comprised of three species from the family Phaethontidae (tropicbirds), Red-billed tropicbird *Phaethon aethereus,* Red-tailed tropicbird *P. rubricauda* and White-tailed tropicbird *P. lepturus (*Del Hoyo *et al.* 1992*).*

Based on the taxonomy of Del Hoyo *et al.* (1992), the suborder Pelecani comprises of a number of species from the remaining five families in the order: Pelecanidae (pelicans), Sulidae (gannets and boobies), Phalacrocoracidae (cormorants and shags), Anhingidae (darters) and Fregatidae (frigatebirds). The Pelecanidae family includes seven species of pelicans, namely Great White Pelican *Pelecanus onocrotalus*, Pink-backed Pelican *P. rufescens*, Spot-billed Pelican *P. philippensis*, Dalmation Pelican *P. crispus*, Australian Pelican *P. conspicillatus*, American White Pelican *P. erythrorhynchos* and Brown Pelican *P. occidentalis.*

The Sulidae family comprises three species of gannet, North Atlantic Gannet *Morus bassana*, African or Cape Gannet *M. capensis* and Australasian Gannet *M. serrator* and seven species of boobies, White, Masked or Blue-faced Booby *Sula dactylatra*, Nazca Booby *S. granti*, Brown Booby *S. leucogaster*, Blue-footed Booby *S. nebouxii*, Peruvian Booby *S. variegata*, Red-footed Booby *S. sula* and Abbot's Booby *S. abbotti.* (Pitman and Jehl 1998). The Abbot's Booby is sometimes named separately as *Papasula abbotti*, on the grounds of being dissimilar to the rest of the boobies; Friesen and Anderson (1997) argued strongly that this species was closer to the gannets than the boobies and should be placed in its own genus.

The largest family of the order is the Phalacrocoracidae, comprising of 39 species of cormorants and shags (Del Hoyo *et al.* 1992): Double-crested Cormorant *Phalacrocorax auritus*, Neotropic Cormorant *P. olivaceus*, Little Black Cormorant *P. sulcirostris*, Great Cormorant *P. carbo*, Indian Cormorant *P. fuscicollis*, Cape Cormorant *P. capensis*, Socotra Cormorant *P. nigrogularis*, Bank Cormorant *P. neglectus*, Japanese Cormorant *P. capillatus*, Brandt's Cormorant *P. penicillatus*, European Shag *P. aristotelis*, Pelagic Cormorant *P. pelagicus*, Red-faced Cormorant *P. urile*, Rock Shag *P. magellanicus*, Guanay Cormorant *P. bougainvillii*, Pied Cormorant *P. varius*, Black-faced Cormorant *P. fuscescens*, Rough-faced Shag *P. carunculatus*, Stewart Shag *P. chalconotus*, Chatham Shag *P. onslowi*, Auckland Shag *P. colensoi*, Campbell Shag *P. campbelli*, Bounty Shag *P. ranfurlyi*, Imperial Shag *P. atriceps*, Antarctic Shag *P. bransfieldensis*, South Georgia Shag *P. georgianus*, Heard Shag *P nivalis*, Crozet Shag *P. melanogenis*, Kerguelen Shag *P. verrucosus*, Macquarie Shag *P. purpurascens*, Red-legged Cormorant *P. gaimardi*, Spotted Shag *P. punctatus*, Pitt Shag *P. featherstoni*, Little Pied Cormorant *P. melanoleucos*, Long-tailed Cormorant *P. africanus*, Crowned Cormorant *P. coronatus*, Little Cormorant *P. niger*, Pygmy Cormorant *P. pygmeus* and Flightless Cormorant *P. harrisi* (Del Hoyo *et al.* 1992).

The Anhingidae family is the smallest in the order, comprising of two species, Anhinga *Anhinga anhinga* and Darter *A. melanogaster*. The three subspecies of the Darter are frequently considered full species (Delany and Scott 2002). The final family in the order is the Fregatidae, comprising of five species, namely Ascension Frigatebird *Fregata aquila*, Christmas Frigatebird *F. andrewsi*, Magnificent Frigatebird *F. magnificens*, Great Frigatebird *F. minor* and Lesser Frigatebird *F. ariel* (Del Hoyo *et al.* 1992).

Table 1 shows the latitudinal breeding distribution of the all species in the six families within the Pelecaniformes, summarized from the distribution maps of Del Hoyo *et al.* (1992). Three families, the frigatebirds, the tropicbirds and the gannets and boobies, have distribution patterns concentrated in the tropics, fairly symmetrically both north and south of the equator. In contrast, the pelicans, cormorants and darters have a much wider distribution range and spread across into the north and south temperate zones, as well as into the sub-Arctic and sub-Antarctic zones. One species of cormorant, the Antarctic Shag breeds as far south as the continent of Antarctica, and three species of cormorant, the European Shag, Great Cormorant and Pelagic Cormorant breed as far north as the Arctic. The largest numbers of species of cormorants occur in the sub-Antarctic (17 species) and south temperate (16 species) zones (Table 1), indicating an overall concentration of this family in the southern hemisphere. In this thesis I focus mainly on the sulids; however, the variation of the growth rates of the order Pelicaniformes is considered in the final chapter.

The Sulidae

The various sulids resemble one another in several aspects of their behaviour, but have each evolved their distinctive 'sets' of behaviour patterns which relate to habitat and other factors such as breeding, feeding and migration. All are colonial, though hugely variable in this. The major 'categories' of colony, in terms of size and density, can be related to food, and in some cases, availability of nesting sites. They lay clutches of between one and four eggs, and clutch size can be related to food and foraging techniques. Similarly the timing of breeding can be related mainly to the seasonal (or non-seasonal) nature of food. The three gannets are treated as allospecies. They differ substantially in breeding strategies. The North Atlantic Gannet apparently has the richest and most seasonal food supply and the strongest tendency towards seasonal breeding. It is the heaviest, and the quickest growing and apparently the most site-competitive. It also takes longer to reach breeding age. The migrations of the young of the three gannets offer remarkable parallels, with the northward migration of the juvenile Cape Gannet, along the west coast of Africa, and the northward migration of the Australasian Gannet both moving towards the equator and the equivalent southward migration of the juvenile North Atlantic Gannet, also to equatorial waters off northern Africa (Nelson 1978). The Cape and Australasian Gannets both fly from their natal island to begin their migration, whereas the North Atlantic Gannet may swim for up to two weeks of its migration before taking flight (Nelson 1978). The boobies differ greatly in size and shape, and this may be related to food and foraging techniques. The breeding strategies of all the boobies, from the Brown Booby, which may breed every nine months, to Abbot's Booby which mostly lays only once every two years, may be determined by food (Nelson 1978).

The Cape Gannet

The Cape Gannet is endemic to southern Africa, breeding only at six islands off the coasts of Namibia and South Africa (Fig.1). Apart from the selected study site, Malgas Island, the other five islands are Mercury, Ichaboe and Possession Islands in Namibia, and Bird (Lamberts Bay) and Bird (Algoa Bay) Islands in South Africa.

Mercury Island (25° 43' S, 14° 50' E) is located in Spencer Bay, 100 km north of Luderitz. It is a small island (3 ha), 1.5 km offshore, and resembles an elongated, steep pyramid, with its highest point 35 m above sea level. The island is managed by the Ministry of Fisheries and Marine Resources, Namibia, and is permanently staffed. In 1995, the Cape Gannet population on Mercury island was approximately 2 100 pairs (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Ichaboe Isand (26° 17'S, 14° 56'E) is another small island (6.5 ha) about 1.5 km offshore, 48 km north of Lüderitz, opposite a restricted diamond area (Sperrgebiet). Guano scraping started here in 1843, with the peak during 1845, when no less than 450 boats lay off Ichaboe Island and an estimated 6 000 men scraped the island. The latest scrape took place during the winter of 2000 (J Kemper pers. comms), under the strict supervision of the island's chief technician, to ensure minimum disturbance to the birds. Ichaboe Island supports by far the largest number of Cape Gannets in Namibia (28 000 pairs in 1995) (Hockey *et al.* 2005; RJM Crawford *in litt.*), but numbers are declining at an alarming rate, thought to be due to lack of food, resulting in poor recruitment of new breeders to the colony (Crawford and Shelton 1978; Crawford and Shelton 1981; Crawford *et al.* 1983; Crawford 1999; Marine and Coastal Management unpublished data) and incidental mortality in longline fishing (Du Toit *et al.* 2002). Namibian colonies declined by almost 80 % between 1950 and 1995, with the most rapid decline occurring at Ichaboe Island (Du Toit *et al.* 2002)

Possession Island (27° 01' S, 15° 12' E) is the largest of the offshore islands in Namibia (90 ha). Together with the adjacent North Reef (27° 00' S, 15° 11' E), the two islands are situated 2.7 km offshore, opposite the restricted diamond area (Sperrgebiet), roughly 40 km south of Luderitz. Cape Gannets colonized Possession Island between 1828 and 1885, possibly as a result of displacement of birds from Ichaboe Island during the guano collection there from 1843 to 1845. Possession Island has a relatively small gannetry (800 pairs in 1995) (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Bird Island, Lamberts Bay (32° 05' S, 18° 18'E) is the northernmost of the main seabird islands on the west coast of South Africa. The island is small (about 2.2 ha) and is about 60 m offshore, connected to the mainland by a causeway built in 1959, which helps create the storm shelter for the small harbour at Lamberts Bay. Apart from Robben Island, Bird Island is the only island along the South African coastline that is permitted to receive tourists, and is the only accessible place for an "authentic" guano island experience. The tourist facilities include a hide, built in 1998, on the edge of the gannet colony, a small museum which portrays the history of the guano industry and a restaurant. The gannet colony at Lamberts Bay is believed to have formed in 1912, and the numbers have fluctuated over the years largely due to the impact of guano scraping. The Bird Island gannets were in decline between 1956 and 1967, but the population has recovered, and currently about 10 000 pairs breed annually (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Bird Island, Algoa Bay (33° 50' S, 26° 17' E), is situated 62 km east of Port Elizabeth and 8 km from the nearest mainland at Woody Cape. Bird Island, about 19 ha, is one of a cluster of four islands and has South Africa's most populous gannetry with about 68 000 pairs in 1994 (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Malgas Island (33°03'S, 17°55'E) is located at the northern entrance of Saldanha Bay (Fig. 2) in the Benguela upwelling system and is one of five Saldanha Bay islands, situated on the West Coast of South Africa, approximately 120 km north of Cape Town. "Malgas" is an Afrikaans word meaning "Gannet". Malgas Island is circular and flat, approximately 8.3 ha, with the highest point raising about 9 m above sea level. The other islands in this group are Jutten, Marcus, Schaapen and Meeuw. All fall within the West Coast National Park, which also includes Langebaan Lagoon and the Postberg Nature Reserve.

The five islands are diverse, and home to nearly 250 000 coastal seabirds. Large boulders are scattered across parts of Malgas Island, which is largely unvegetated. Malgas Island is one of only six localities in the world supporting breeding Cape Gannets. Breeding by Cape Gannets was first reported on Malgas Island on 23 October 1648 (Crawford *et al.* 1983). Based on areas of occupancy and densities of nests, the overall population in 2000 was of the order of 167 000 breeding pairs, of which 58 000 pairs are breeding at Malgas Island (Hockey *et al.* 2005; RJM Crawford *in litt.*) which amounts to 35 % of the global population. Together, the islands hold important numbers of African Penguin *Spheniscus demersus*, and for this species there is considerable cause for concern because the populations at Malgas, Marcus and Jutten islands have declined by 90 %, 83 % and 53 % respectively since 1970 (Barnes 2000). Nearly 10 % of the global Hartlaub's Gull *Larus hartlaubii* population, 7.3 % of the global Crowned Cormorant *Phalacrocorax coronatus* population. In addition, Bank Cormorant *P. neglectus,* Cape Cormorant *P. capensis,* White-breasted Cormorant *P.carbo*, Kelp Gull *Larus dominicanus* and Crested Tern *Sterna bergii* breed at the various islands. 12 % of the world's African Black Oystercatcher *Haematopus moquini* population is found scattered throughout the West Coast National Park, mostly on the islands (Barnes 2000). All the islands host some exotic plant species: Malgas, Marcus and Jutten Island have stands of *Porcellio scaber, Musca domestica, Dermestes maculates, Atriplex semibaccata, Chenopodium murale, Lavatera arborea, Malva parviflora* and *Senecio vulgaris* (Barnes 2000).

Since the completion of the Sishen–Saldanha railroad in the early 1970s and a deep-water harbour in Saldanha Bay, the area has been committed as a major port of iron ore export. Metal pollution from the iron-ore berth and pollution and oiling incidents from urbanization and shipping pose a threat to the future of the lagoon and the bay. A Corex steel smelter has been constructed near Saldanha Bay (Barnes 2000). The smelter could cause potential damage to at least two highly valuable systems: through water abstraction on the Lower Berg River and indirectly at Langebaan lagoon and the Saldanha Bay islands (Barnes 2000).

Gannets formerly bred on Hollamsbird Island, Namibia, which was their most northerly breeding station, from at least 1828 to 1938, as well as Halifax Island, Namibia, in the mid 19th century, possibly due to the displacement of birds from Ichaboe Island during guano collection from 1843 to 1845. In the Western Cape, gannets were reported breeding on Seal Island, False Bay, in the 17th century and Dyer Island in the 19th century. Records of earlier breeding at Marcus and Dassen Islands are unreliable and have not been accepted (Rand 1952; Crawford *et al.* 1983; Shaughnessy 1984; Berruti 1985).

General Biology and Behaviour

The Cape Gannet has a wing span of about 171–185 cm and an overall length of about 84–94 cm. Its body plumage is snow white, and the primaries, primary coverts and secondaries are black, giving a black trailing edge to the wing though the black stops several centimeters short of the body. The humerals are white. The tail is usually all black, although the shafts of the central tail feathers are often conspicuously bleached. Broekhuysen and Liversidge (1954) found that about 11% of birds which were more than a year old had varying amounts of white in the tail, the commonest variant being birds with two white outer feathers on each side. The head is a deep golden buff and the black gular stripe (unfeathered, bare skin) on the throat is 13–19 mm long. The gular stripe is longer in males than females (Jarvis 1971) and it probably helps regulate body temperature. Black facial skin appears in front of, beneath and behind the eye. The eyelids are bright blue but the irises are typically darker than the light grey-blue of the North Atlantic Gannet. The bill is light blue and the legs and feet blackish (sometimes greyer) with light greenish-yellow lines.

Adult plumage is attained during the fourth year. There is a lack of information on the full series of intermediate plumages from juvenile to immature to adult. Of 28 known two-year olds, many were adult-plumaged though some had black feathers on the wing coverts and rump. Of 12 of these, captured again a year later when three years old, all except two had adult plumage (Jarvis 1972). Adults moult in summer, extending into June–July, by which time all new feathers are fully-grown. Birds may replace feathers whilst incubating (Rand 1959).

Males are slightly larger than females, and females show greater variation in weight than males (Rand 1959). Males have slightly higher pitched voices than females. The repetitive 'urrah' call is delivered by incoming birds and also accompanies displays such as bowing, mutual fencing, menacing and fighting. The groaning 'oo-ah' call accompanies sky-pointing. Birds recognize the voice of their mate and chicks the voice of their parents (Nelson 1978).

Population

Counts of birds on aerial photographs of breeding colonies adjusted for absenteeism of some mates suggested that in 1956 there was an overall population of 149 000 – 176 000 pairs. The population fell to 119 000 pairs in 1967, 111 000 pairs in 1978 and 80 000 pairs in 1980, a decrease of 44 % or more (Rand 1963; Crawford *et al.* 1983). More recent assessments have been based on the area occupied by breeding birds at colonies and densities of nests (Batchelor and Ross 1984; Klages *et al.* 1992). In terms of area, the three Namibian colonies measured 5.64 ha in 1956, continuously decreasing over the years to 5.22 ha in 1967, 2.22 ha in 1978, 0.95 ha in 1995 and 0.38 ha in 2003. The decreases at the three Namibian colonies resulted from an inadequate supply of food after the collapse of the Namibian Sardine *Sardinops sagax* resource (Hockey *et al.* 2005; RJM Crawford *in litt.*). The three South African colonies measured 1.77 ha in 1956, and then increased to 2.20 ha in 1969, 2.82 ha in 1978, 4.39 ha in 1995 and 5.23 ha in 2001. The increase in the size of the gannet colonies in South Africa followed the collapse of the Sardine *Sardinops sagax* off South Africa but, whereas off Namibia there was no alternative prey, in South Africa gannets were able to switch from feeding on Sardine to Anchovy *Engraulis encrasicolus* (Crawford 1999). The overall area of occupancy was 7.41 ha in 1956 and 1967/69, then decreased to 5.01 ha in 1978, then 5.41 ha in 1995 and 5.67 ha in 2001 (Hockey *et al.* 2005; RJM Crawford *in litt.*). Figure 3 shows the population trends of South African and Namibian Cape Gannet colonies, as well as the total population from 1956 – 2000 (Hockey *et al.* 2005; RJM Crawford *in litt.*).

At Malgas Island, breeding gannets occupied an area measuring 0.88 ha in 1956, which then increased to 1.08 ha in 1967. The breeding occupancy decreased to 0.99 ha in 1978 and gradually started to increase again to a high density of 1.87 ha in 1989, then decreasing again to 1.02 ha in 1990, and then slightly increasing again to 1.14 ha in 1993 and 1.76 ha in 1995, and then slightly decreasing again to 1.71 ha in 2001, when the breeding population was *ca* 58 000 pairs (Rand 1963; Jarvis 1971; Crawford and Shelton 1981; Crawford *et al.* 1983; Crawford 1987; Crawford 1999; Crawford and Dyer 1995; Marine and Coastal Management unpublished data).

Feeding

Cape Gannets feed at sea singly and in flocks ranging in size from a few birds to thousands (Rand 1959). Flapping flight is interspersed with gliding (Nelson 1978). Between 1951 and 1953 adults moved 100 km offshore, the maximum distance at which birds were sighted throughout every month of these years seldom dropped below 38 km and was usually between 52 and 90 km (Rand 1959). Thus even during the breeding season they moved far offshore. In fact, Rand (1959) characterizes them as essentially offshore feeders, seldom entering bays or moving close to land. Nevertheless, the numbers seen at sea drop off in October, when birds are incubating or with small chicks, and are highest between June and September.

Cape Gannets plunge dive from the air onto prey from heights of 5-20 m (Rand 1959). They can attain depths of 2-4 m from plunging, but are able to descend deeper by swimming. They forage during the day, leaving breeding colonies one hour after sunrise and returning 1-2 hours before sunset (Cooper 1978). Birds rarely return to colonies after dusk (Adams and Walter 1993), but are able to land in the dark. They generally do not forage in stormy weather or heavy mist, but return to islands, shelter in bays or float on the sea surface (Rand 1959).

Gannets do not follow any definite daily trend in feeding. If they encounter plentiful food early in the day they feed to repletion and either return to the islands or cease feeding. Otherwise they feed steadily and slowly over a long period, foraging all the time. Rand (1959) stated that at least 85 % of the stomach contents need to be digested before feeding is resumed. The rate of digestion varies with the amount of food and the rapidity with which it is taken. Rand (1959), in an experiment that would no longer be permitted, gave each of five captive gannets a meal of mullets and killed birds at hourly intervals; one had digested 35 % of its food in two hours but another, given twice as much, had digested 41 % in two hours (Rand 1959).

Movements

Within its normal range the Cape Gannet generally stays on the continental shelf. In the 1960s about 70 % of birds seen off the Western Cape were within 50 km of land and few were reported >100 km offshore (Crawford *et al.* 1983), although Cape Gannets have been recorded to occur up to 160 km from the mainland (Rand 1959; Cooper 1984).

Cape Gannets move more along the west coast of Africa than along the east coast, and also move farther north on the west coast (Hockey *et al.* 2005; RJM Crawford *in litt.*). Most young of the year leave the vicinity of their natal islands by May, many before April (Rand 1959). Of 10 145 birds banded as juveniles on Malgas Island between 1951 and 1957, 104 birds (1 %) were recovered at localities away from the island. By March 1960, 56 out of 4 000 chicks (1.4 %) banded on Bird Island, Algoa Bay, in 1954 had been recovered (Broekhuysen *et al.* 1961). The recoveries showed that juveniles from Malgas Island mainly migrate between 2 000 and 4 000 km north from the island, whilst 15 percent of recoveries were more than 4 000 km distant, up to 6 800 km. Numbers of juveniles may be heavily depressed due to human predation. Rand (1959) reported that, in the 1950s, large numbers of Cape Gannets were killed with canoe paddles and the rings were often kept; this practice has ceased to be a mortality factor. Surviving birds return to breeding colonies when about two years old (Rand 1959) usually to their natal colony (Broekhuysen *et al.* 1961). Adults may disperse from breeding islands for about 3 months during the non-breeding season (Duffy and La Cock 1985) but this dispersion is not always the case. They often follow shoals of Sardine migrating to Kwazulu-Natal in winter (Rand 1959; Cyrus and Robson 1980). Of 5 362 adults ringed on Malgas Island, only 99 (2 %) were recovered away from the island. The birds which were recovered were mainly (71 %) less than 540 km away from Malgas. However, many adults did travel further and 17 % were recovered more than 1 460 km away. The two greatest distances recorded were 2 700 km and 3 380 km (Broekhuysen *et al.* 1961). The few birds reaching Australia have journeyed even farther (Ross 1988).

There was little interchange of gannets between Bird Island and other breeding colonies during 1978-1994 (Klages 1994). In the Western Cape during 1978-1997, at least 59 birds bred at a non-natal island, and 27 other Cape Gannets probably also transferred colonies: 16 birds emigrated from Namibian colonies to the Western Cape; 41 moved from Lamberts Bay to Malgas Island; 29 moved from Malgas Island to Lambert's Bay. All movements were of birds banded as chicks (Crawford 1999).

In the 1950s and 1960s, recoveries of banded birds were regularly received from Angola, north to the Gulf of Guinea, and as far west as Nigeria. In recent years no recoveries of gannets have been forthcoming from these areas, although the number of birds banded since 1979 amounts to 75 % of the provisional total of gannets banded up to 1968 (Oatley 1988). Political changes in what were previously West African colonial states have almost certainly resulted in a diminished reporting rate of bird bands, but are unlikely to be entirely responsible for the recent lack of records from the north. The South African Bird Ringing Unit (SAFRING) still receives band recovery reports of other birds from independent African states, including some in West Africa. Moreover, four Cape Gannet recoveries have been reported from Mocambique (one from Maputo and three from

Beira) since 1982. These compare with 14 reported recoveries from Mocambique in the 1950s and 1960s.

The majority of recoveries of Cape Gannets are first-year birds, the mean elapsed time since banding of first-year birds recovered north of 17° S in the 1950s and 1960s was eight months, and ranged from one month to 12 months (Oatley 1988). Some adults of up to seven years of age were also recovered in the Gulf of Guinea, so the movement up the west coast in those years was unlikely to be solely a post-fledging dispersal of first-year birds.

One explanation for the recent lack of records from the north may be that Cape Gannets are now able to find sufficient food in the vicinity of the demersal fishing grounds in the Benguela upwelling region, but the previous northward movement seems to have been sufficiently well marked to entertain the possibility that the birds were following a migration of fish prey.

Breeding

The most important feature of the Cape Gannets breeding habitat is its restriction to relatively few highly crowded bird islands mainly in the vicinity of the Benguela Current and the generally hot, windy, dry and flat nature of islands at which it breeds (Jarvis 1971). Colonies possess runways, to which departing birds make their way for take-off (Nelson 1978). This feature sometimes precludes colonization of parts of the periphery of an island (Jarvis 1971). Cape Gannets are capable of breeding on sloping ground, as on Mercury Island (Rand 1963) though this habit is clearly exceptional. The more northerly islands, which formerly held most of the gannets, are barren and windswept, but suffer sea fog, high seas and excessive spray. Piled boulders, which Cape Gannets avoid, are conspicuously absent from northern islands (Jarvis 1971).

There is considerable variation in nesting density of Cape Gannets. They nest at variable densities even on the same island. Normal spacing on Malgas Island is said by Rand

(1963) to be 2.3 nests per square metre (nests mainly 56 – 58 cm apart) and 'occasionally' more congested than is allowed by lunging distance. Broekhuysen and Rudebeck (1951) earlier gave the average density in the main areas of Malgas Island as 2.5 nests/sq.m. Density may be related to the suitable habitat at islands. In 1957, man-levelled ground on Malgas Island was occupied almost immediately (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Cape Gannets nest mainly on flat ground, sand, bare rock, cement surfaces and platforms (Crawford *et al.* 1994). They make their nests entirely from guano and detritus such as feathers and nest material dropped by other species. Nests are shaped in a mound with a cup-shaped depression (Berruti 1987). The size of the nest depends on the amount of guano available (on Malgas Island the average nest weight was 1770 g) and if it is nearly all removed by man there may be so little remaining that birds lay on bare rock. This is of interest since, as Jarvis (1970) showed, the onset of laying is earlier and breeding success is probably higher (egg loss reduced) when ample nest material is present. The effect of availability of nesting material on laying date was checked, by providing one area out of four comparable ones with much guano. As a result, by 20 October 1967, this area held three times as many nests with eggs as the next most laid-in area. If the positive correlation between the amount of nest material and the onset of laying is valid, it is important, since early fledged chicks tend to be heavier than the later ones and therefore may be expected to survive better (Jarvis 1971). Abundant nest material could facilitate laying by intensifying interactions between birds with concomitant effects on the maturation of gonads (Jarvis 1971). The habit of using guano for the nest depends on a dry climate during the breeding season, otherwise the nest becomes wet and sticky and would coat the egg or chick. One advantage of using guano for nest material is that it eliminates the need for take-offs and landings entailed in fetching seaweed, which is scarce, and as a result saving both time and energy. It may have resulted from the Cape Gannet's habit of regulating its body temperature by excreting on its feet (Jarvis 1971). Another advantage of the guano nest is the continuous nest building and re-shaping of the cup, which takes place throughout the breeding season (Hockey *et al.* 2005; RJM Crawford *in litt.*), which may help to keep the egg or young chick from falling out the nest and also enables the re-building and repair of nests which are often damaged due to continuous gannet movement through the colony, as well as heavy rain falls, causing nests to completely collapse (pers. obs.)

The Cape Gannet congregates at islands when about to nest in late August (Rand 1959). Eggs are mainly laid from mid-October to mid-December, but some birds may lay as early as mid-June. The onset of breeding can be delayed due to insufficient nesting material (Crawford and Cochrane 1990) or extreme scarcity of food (Crawford and Dyer 1995), which could also lead to a high mortality of chicks from starvation (Crawford *et al.* 1983).

Juvenile Cape Gannets return to the breeding colony in their third year, and congregate on the fringes. First breeding attempts usually occur at four years of age. Cape Gannets are faithful to breeding sites and localities (Crawford *et al.* 1994; Klages 1994). At Malgas Island, 80 % of recoveries of birds banded as adults were from that part of the island where they were banded (Hockey *et al.* 2005; RJM Crawford *in litt.*). At Bird Island, Algoa Bay, 72 % of young adults took over vacant sites near to the site where they hatched; 8 % moved once and were then faithful to their new site. Birds settling at the edge of the colony did not later vacate their sites to move towards the centre of the colony (Klages 1994).

The breeding cycle begins with the males establishing a nesting territory, which is typically just big enough to accommodate the nest and a pair of birds. In the meantime prospecting females wander on the outskirts of the colony ready to respond to inviting males. The unpaired males have to impress females with much calling, head shaking and bowing. The female will then respond by approaching the male, usually with the head tilted upwards. Once the pair-bond has been consolidated, after much mutual bill fencing and bowing, the partners co-operate in nest construction, which continues throughout the breeding season, and in the constant guarding of the territory. During copulation the male bites the female's nape, treads the females back and waves his wings (Jarvis 1972;

Nelson 1978). Cape Gannets are monogamous, but long-term fidelity to mates has not been investigated.

Typically the clutch is a single bluish egg, which soon becomes soiled. Very rarely two eggs have been found in a nest, and parents have incubated and successfully reared the chicks to become fledglings. Two egg clutches could possibly be due to accidental inclusion of a stray egg, but on occasion two eggs are likely to be laid by the same female. Both parents are involved in the incubation process, which lasts for about 42 - 46 days until hatching. Gannets use the webs of their feet , which are richly irrigated with blood vessels, to incubate the egg. This use enables efficient heat transfer for both the egg and the thermal regulation of the bird. Birds losing clutches may relay 2 – 4 weeks later (Jarvis 1970). Replacement laying is common amongst birds nesting on the edge of the colony at Bird Island, Algoa Bay (Randall *et al.* 1981).

The chick becomes vocal before even breaking free from the shell. This signals the impending hatching process and precipitates a shift in parental behaviour. Parents shift from incubation to brooding. The hatchling is black, naked and blind, weighing about 70 grams, but within three weeks its body mass is one third of that of an adult. At approximately eight weeks the chick outweighs the adult and it remains heavier until it becomes a fledgling at 14 – 17 weeks (Jarvis 1971).

Once the chick has hatched, both parents continue to attend to the needs of the fast growing chick. Feeding takes place in a mouth-to-mouth fashion, where the chick inserts its beak deep into the adult's gape where the fish is regurgitated directly into the chick's throat. Within a few seconds the chick has swallowed the fish and is begging for more. It usually takes two or three feeding bouts to transfer the food that a parent brings back to the nest into the chick's hungry stomach. During the first few weeks of the chick's life it is fed primarily high-energy pelagic shoaling fish such as Anchovy, depending on food availability (Jarvis 1971). One of the parents constantly broods the chick at the nest. Larger chicks are usually fed whole fish, ideally Sardine, but this once again depends on food availability. It is not uncommon for the larger chicks to be left unattended for several hours while both parents are out foraging. In some cases one of the parents is so overwhelmed by the needs of an insatiable chick that it is driven to one of the bachelor's clubs on the fringes of the colony to roost in peace (Jarvis 1971).

Once the chicks have their full complement of brown feathers, they are ready to fledge. Now they often wander off to the fringes of the colony where they practice hop-flying, but return to their nests to be fed. This stage is a vulnerable one for the fledgling and the first steps towards independence are fraught with dangers. Most of the fledglings prefer to walk to the shore and swim rather than follow the adults into flight from one of the runways. But it is also the time when they can become prey for Cape Fur Seals *Arctocephalus pusillus* (David *et al.* 2003).

Gannets fledge with just enough fat reserves for them to be able to survive without food for up to ten days. It is during this short time that they have to learn the necessary skills of capturing sufficient food to ensure their survival. In fact, it is during this period that the mortality rate of the Cape Gannet is at its highest. The many carcasses of brown gannets washed ashore on the beaches near breeding colonies attest to this. Those young gannets that survive the fledging stage migrate, usually northwards to rich fishing grounds in tropical latitudes (Nelson 1978).

Threats

Gannets mainly eat commercially exploited pelagic shoaling fish such as Anchovy and Sardine (Rand 1959; Crawford and Shelton 1978; Klages *et al.* 1992) and are likely to be affected if overfishing takes place. Extreme scarcity of food may lead to fewer birds attempting to breed (Crawford and Dyer 1995) or to high mortality of chicks from starvation (Crawford *et al.* 1983).

Gannets face further threats through entanglement in fishing gear. Cape Gannets are sometimes caught in demersal trawls, and through incidental mortality from swallowing hooks or being caught by hooks from longline fishing activities (Du Toit *et al.* 2002).

Between 1956 and 1980 the global Cape Gannet population declined some 50 %. The collapse was attributed to the decline in Pilchard *Sardinops sagax* stocks, the gannets primary food source. Despite the global decline, which affected mainly Namibian colonies, the Malgas Island colony has been increasing since the late 1960's to early 1970's (Fig. 3), a phenomenon which correlates with the local recovery of Pilchard stocks in the Western Cape. The African Penguin and Cape Cormorant are also thought to have been affected by competition with commercial fisheries, especially purse-seining for surface-shoaling fish, such as Anchovy and Sardine (Hockey *et al.* 2005; RJM Crawford *in litt.*).

Cape Gannets are susceptible to human disturbance. Large mortalities of gannet chicks have occurred at Malgas Island because of guano-scraping, a practice that ceased when the islands were incorporated into the West Coast National Park. Cape Gannets were one of the most important producers of seabird guano in southern Africa, which was collected annually at gannet breeding localities until the mid 1980s or early 1990s (Crawford and Shelton 1978; Schwartzlose *et al.* 1999). Guano was collected in April or May, at the conclusion of the gannet breeding season, but at Malgas Island in 1977, commencement of collecting at too early a date caused the deaths of 800 chicks after they had been displaced from nests. About the same time unrecorded numbers of chicks at Ichaboe and Possession Islands suffered a similar fate (Crawford *et al.* 1983). As a result of guano collecting, gannets had little material at the islands with which to construct nests, they bred later and sometimes were forced to nest on flat ground (Jarvis 1974), and eggs were probably lost from nests constructed from too little guano (Jarvis 1970). Parts of some colonies became basin-shaped as a result of guano-scraping, allowing rain water to accumulate, to flood nests and to decrease breeding success (Randall and Ross 1979). After four years of not collecting guano at Malgas Island, the mean height of nests in September 1989 was 106 mm compared with a mean of 31 mm at Lambert's Bay, where guano was still being harvested (Crawford and Cochrane 1990).

References

Adams NJ and Walter CB 1993. Maximum diving depths of Cape Gannets. Condor 95: 734-736

Barnes KN (ed) 2000. The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg

Batchelor AL and Ross GJB 1984. The diet implications of dietary change of Cape Gannets on Bird Island, Algoa Bay. Ostrich 55: 45-63

Berruti A 1985. Cape Gannets *Sula capensis* ashore at Dyer and Robben Islands, southwestern Cape, South Africa. Cormorant 13: 71-72

Berruti A 1987. The use of Cape Gannets in management of the purse-seine fishery of the western Cape. PhD Thesis, University of Natal, Pietermaritzburg

Broekhuysen GJ and Liversidge R 1954. Colour variation in the tailfeathers of the South African Gannet (*Morus capensis*). Ostrich 25: 19-22

Broekhuysen GJ, Liversidge R and Rand RW 1961. The South African Gannet *Morus capensis*. 1. Distribution and movements. Ostrich 32: 1-19

Broekhuysen GJ and Rudebeck G 1951. Some notes on the Cape Gannet. Ostrich 22: 132-138

Cooper J 1978. Energetic requirements for growth and maintenance of the Cape Gannet (Aves; Sulidae). Zoologica Africana 13: 305-317

Cooper J 1984. Changes in resource division among four breeding seabirds in the Benguela upwelling system. In: Ledger JA (ed) Proceedings V Pan-African Ornithological Congress: South African Ornithological Society, Johannesburg. Pp 217-230

Crawford RJM 1987. Food and population variability in five regions supporting large stocks of Anchovy, Sardine and Horse Mackerel. South African Journal of Marine Science 5: 735-757

Crawford RJM 1999. Seabird responses to long-term changes of prey resources off southern Africa. In: Adams NJ and Slotow RH (eds) Proceedings 22nd International Ornithological Congress, Durban: Birdlife South Africa, Johannesburg. Pp 688-705

Crawford RJM and Cochrane KL 1990. Onset of breeding by Cape Gannets *Morus capensis* influenced by the availability of nesting material. Ostrich 61: 147-149

Crawford RJM and Dyer BM 1995. Responses by four seabirds to a fluctuating availability of Cape Anchovy *Engraulis capensis*. Ibis 137: 329-339

Crawford RJM, Dyer BM and Brooke RK 1994. Breeding nomadism in Southern African seabirds – constraints, causes and conservation. Ostrich 65: 231-246

Crawford RJM and Shelton PA 1978. Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. Biological Conservation 14: 85-109

Crawford RJM and Shelton PA 1981. Population trends for some southern African seabirds related to fish availability. In: Cooper J (ed) Proceedings of the Symposium on Birds of the Sea and Shore: African Seabird Group, Cape Town. Pp 15-41

Crawford RJM, Shelton PA, Cooper J and Brooke RK 1983. Distribution, population size and conservation of the Cape Gannet *Morus capensis*. South African Journal of Marine Science 1: 153-174

Cyrus D and Robson N 1980. Bird Atlas of Natal. University of Natal Press, Pietermaritzburg

David JHM, Cury P, Crawford RJM, Randall RM, Underhill LG and Meyer MA 2003. Assessing conservation priorities in the Benguela ecosystem: analysing predation by seals on threatened seabirds. Biological Conservation 114: 289-292

Del Hoyo J, Elliott A and Sargatal J (eds) 1992. Order Pelecaniformes. In: Handbook of the Birds of the World. Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona. Pp 279-374

Delany S and Scott D (eds) 2002. Waterbird Population Estimates Third Edition. Wetlands International Global Series 12: 38

Duffy DC and La Cock GD 1985. Partitioning of nesting space among seabirds of the Benguela upwelling region. Ostrich 56: 186-201

Du Toit M, Boere GC, Cooper J, de Villiers MS, Kemper J, Lenten B, Petersen SL, Simmons RE, Underhill LG, Whittington PA and Byers OP 2002. Conservation Assessment and Management Plan for Southern African Coastal Seabirds. Workshop Report. Cape Town, South Africa

Friesen VL and Anderson DJ 1997. Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. Molecular Phylogenetics and Evolution 7: 252-260

Hockey PAR, Dean WRJ and Ryan PG (eds) 2005. Roberts Birds of Southern Africa VII Edition. Published by the Trustees of the John Voelcker Bird Book Fund, Cape Town

Jarvis MJF 1970. Interactions between man and the South African Gannet, *Sula capensis*. Ostrich Supplement 8: 497-514

Jarvis MJF 1971. Ethology and ecology of the South African Gannet, *Sula capensis*. PhD Thesis, University of Cape Town

Jarvis MJF 1972. The systematic position of the South African Gannet. Ostrich 43: 211-215

Jarvis MJF 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis* (Lichtenstein)). Journal of Animal Ecology 43: 1-17

Klages NTW 1994. Dispersal and site fidelity of Cape Gannets *Morus capensis*. Ostrich 65: 218-224

Klages NTW, Willis AB and Ross GJB 1992. Variability in the diet of the Cape Gannet at Bird Island, Algoa Bay, South Africa. South African Journal of Marine Science 12: 761-771

Nelson JB 1978. The Sulidae: Gannets and Boobies. Oxford University Press

Oatley TB 1988. Change in Winter Movements of Cape Gannets. South African National Scientific Programmes Report No 157: 40–42

Pitman R and Jehl JR 1998. Geographic variation and reassessment of species limits in "Masked" Boobies of the eastern Pacific Ocean. Wilson Bulletin 110: 155-170

Rand RW 1952. The birds of Hollamsbird Island, South West Africa. Ibis 94: 452-457

Rand RW 1959. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape Gannet, *Morus capensis*, off the south-western coast of the Cape Province. Investigative Report Sea Fisheries Research Institute, South Africa. 39: 1-36

Rand RW 1963. The biology of guano-producing seabirds. 4. Composition of colonies on the Cape islands. Investigative Report Sea Fisheries Research Institute, South Africa. 43: 1-32

Randall RM and Ross GJB 1979. Increasing population of Cape Gannets on Bird Island, Algoa Bay, and observations on breeding success. Ostrich 50: 168-175

Randall RM, Randall BM, Batchelor AL and Ross GJB 1981. The status of seabirds associated with islands in Algoa Bay, South Africa, 1973-1981. Cormorant 9: 85-104

Ross GJB 1988. Capture of a ringed gannet *Sula capensis* off Australia. Cormorant 16: 54

Schwartzlose RH, Alheit J, Bakun A, Baumgartner TR, Cloete R, Crawford RJM, Fletcher WJ, Green-Ruiz Y, Hagen E, Kawasaki T, Lluch-Belda D, Lluch-Coasta SE, MacCall AD, Matsuura Y, Nevârez-Martînez MO, Parrish RH, Roy C, Serra R, Shust KV, Ward MN and Zuzunaga JZ 1999. Worldwide large-scale fluctuations of Sardine and Anchovy populations. South African Journal of Marine Science 21: 349-366

Shaughnessy PD 1984. Historical population levels of seals and seabirds on islands off southern Africa, with special reference to Seal Island, False Bay. Investigative Report Sea Fisheries Research Institute, South Africa 127: 1-61

Table 1: Latitudinal distribution of breeding Pelecaniformes. Each entry provides the number of species of the family with a substantial fraction of the breeding range in the latidudinal zone. The analysis is based on the distribution maps of Del Hoyo *et al.* (1992).

	Phaetontidae (Tropicbirds)	**Pelecanidae** (Pelicans)	**Sulidae** (Gannets and boobies)	**Phalacro-coracidae** (Cormorants)	**Fregatidae** (Frigatebirds)	**Anhingidae** (Darters)	**Total**
Arctic				3			3
Sub-Arctic (45°N-67°N)		2		6			8
North Temperate Zone (23°N-45°N)		4	1	11		2	18
North Tropics (0°-23°N)	3	5	5	8	4	2	27
South Tropics (0°-23°S)	3	5	7	12	5	2	34
South Temperate Zone (23°S-45°S)		3	3	16		2	24
Sub-Antarctic (45°S-67°S)		1		17		1	19
Antarctic				1			1

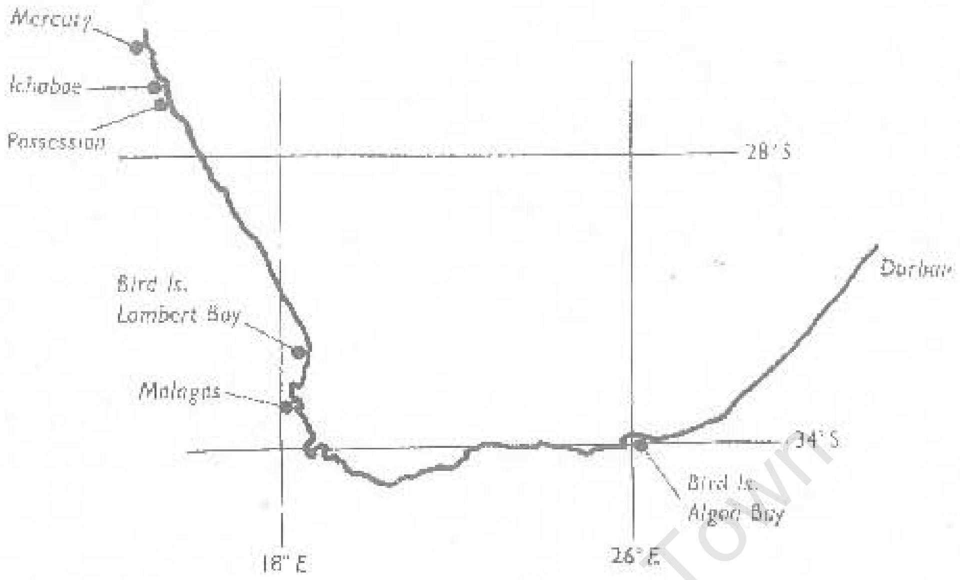

Figure 1: The breeding distribution of the Cape Gannet

Figure 2: The entrance to Saldanha Bay, showing the positions of three of the five Saldanha Bay Islands

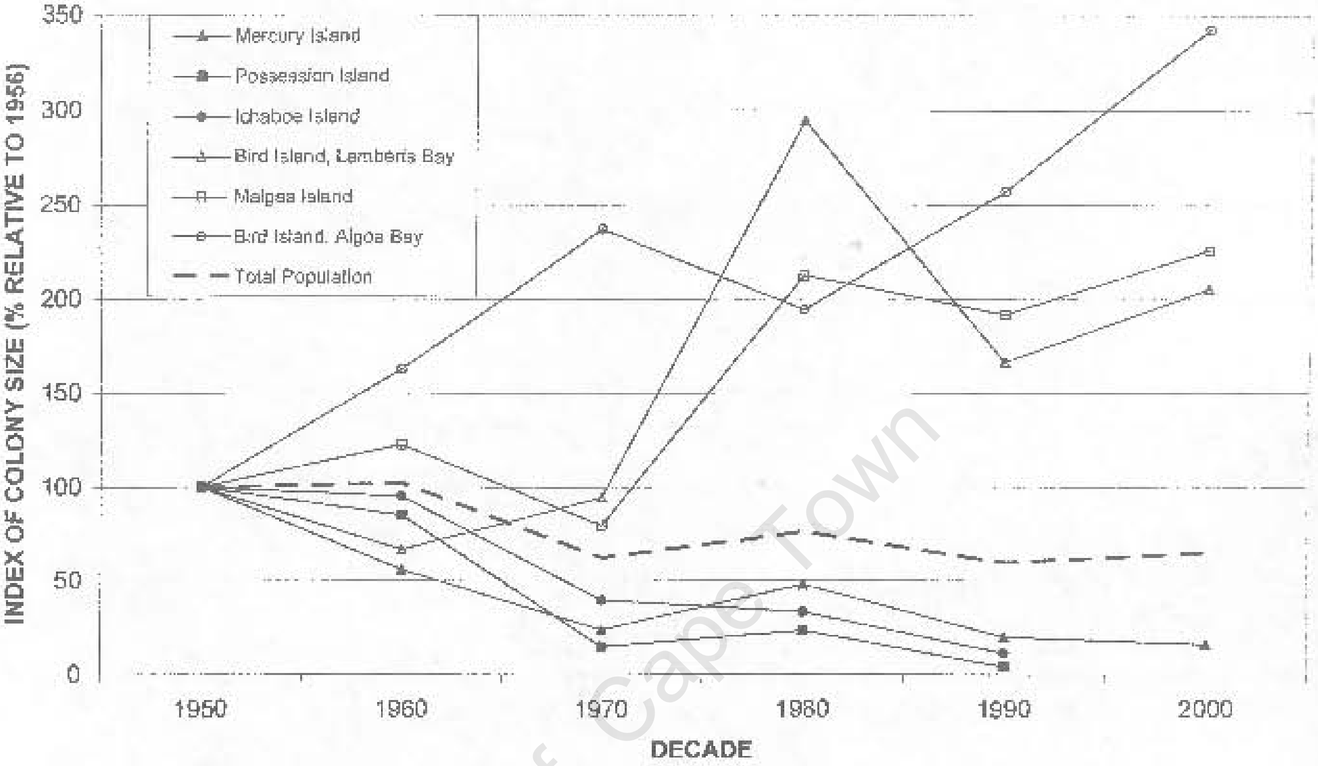

Figure 3: Relative population trends of South African (open symbols) and Namibian (solid symbols) Cape Gannet colonies by decades since the 1950s (RJM Crawford, Marine and Coastal Management, unpublished data). The trend for the total population is depicted by the broken line.

Chapter 2

Factors influencing the breeding success of Cape Gannets *Morus capensis* at Malgas Island, 2002/03

Factors influencing the breeding success of Cape Gannets *Morus capensis* at Malgas Island, 2002/03

Abstract

In the 2002/03 breeding season at Malgas Island, South Africa, breeding success at 125 nests of Cape Gannets *Morus capensis*, of which at least one partner was of known age, was monitored. The age of birds at these nests ranged from 5–22 years. At five nests, the ages of both partners were known; ages were similar for birds younger than 10 years but dissimilar for older birds, suggesting Cape Gannets initially choose partners of a similar age but may replace lost partners with younger birds. First clutches, all consisting of one egg, were estimated to be laid between 15 August and 1 November, mostly in late September. Of first clutches, 61 % failed. Relaying took place at 11 % of failed nests. Overall, pairs successfully fledged single chicks at 43 % of nests; no pair fledged two chicks. Breeding success was positively related to the distance of the nest from the edge of the colony but tended to decrease as age increased. Height of nest and date of laying did not influence breeding success. Older birds bred earlier and further from the edge of the colony than did younger birds.

Key words: Age, breeding success, edge effect, Cape Gannet, laying date, *Morus capensis*, nest height

Introduction

Cape Gannets are regarded as "Vulnerable" in South Africa and internationally (Crawford 2000; Du Toit *et al.* 2003; BirdLife International 2004). An additional factor of concern is that the species has only six breeding colonies world-wide (Crawford *et al.* 1983). Gannets are constrained to laying eggs regularly in the same season each year, whereas many other seabird species may adapt their laying dates to food availability (Del Hoyo *et al.* 1992). Like most other seabirds, gannets and boobies are long-lived, with a mean life expectancy of between 10 and 20 years with some individuals living to be well over 40, as well as having a very low adult mortality rate. These two factors help explain their relatively low chick production (usually one chick per breeding season) in comparison with other birds, as well as their deferred maturity, with breeding commencing between the ages of four to six years (Del Hoyo *et al.* 1992).

In some long-lived birds breeding success increases with age (Coulson 1966; Brooke 1978; Ollason and Dunnet 1978; Nisbet *et al.* 2002), but it is unclear whether this results from greater breeding effort or greater breeding efficiency (Nur 1984). There is little evidence that age *per se* has any effect except during the first few years of a bird's reproductive career (Wooller *et al.* 1989). Later, improved breeding success may be attributed to increased experience with a particular mate (Wooller *et al.* 1989; Bradley *et al.* 1995).

The influence of age on the breeding success of Cape Gannets *Morus capensis* is unknown but may affect the population dynamics of the species, along with other factors including the timing of breeding and nest site selection.

For the Australasian Gannet (*Morus serrator)* at Pope's Eye, Port Phillip Bay, age influences the date of arrival of birds at the colony, nest location, laying date, chick mass and fledging success (Gibbs *et al.* 1999). In this single-season (1994/95) study, age was not known, but birds were grouped into age classes that were inferred from the habitat distributions of known-age birds. Chick growth at Pope's Eye and fledging success increased with parental age, then remained more or less constant for older birds before, in some cases, decreasing for the oldest age group. Gibbs *et al.* (1999) suggested that offspring of older gannets have a higher survival rate than those of younger parents since their body mass at fledging is greater, due to the enhanced breeding experience and foraging success of older parents. Conversely chicks of younger parents are relatively lighter at fledging. A severe storm at Pope's Eye in November 1994 destroyed most nests, which resulted in extensive re-laying. Younger birds replaced fewer lost eggs, whereas older birds replaced more than the average, suggesting a reduced reproductive effort by younger birds (Gibbs *et al.* 1999).

This study explored the relationship between breeding success and known age, based on birds banded as fledglings, in Cape Gannets at Malgas Island in one breeding season. It also attempted to ascertain whether breeding success was influenced by the timing of laying, location of nest sites, height of nests and the extent of replacement of failed clutches.

Methods

The study was undertaken at Malgas Island (33°03'S, 17°55'E), South Africa during the 2002/03 breeding season. Malgas Island is situated at the northern entrance to Saldanha Bay in the Benguela upwelling system (Barnes 1998). A total of 31 782 Cape Gannet fledglings were banded at Malgas Island between 1951 and the 2001/02 breeding season, which immediately preceded this study. Between 1951 and 1955, Broekhuysen *et al.* (1961) banded 10 145 fledglings and a further 21 637 have been banded since 1979, providing a large number of birds of known age within the study colony (Table 1).

During September and October 2002, gannets at Malgas Island that appeared to be incubating were gently lifted by placing a crook attached to a pole under their chests or tails, to ascertain whether they were banded. All metal-banded birds that were incubating eggs were caught and the band numbers read. Using records of SAFRING (South African Bird Ringing Unit) their age was determined, if they had been banded as chicks. As the breeding season progressed, fewer birds were incubating eggs and more were brooding naked or downy chicks. Banded adults at these nests were also caught. If at least one of the adults at a particular nest was known age, the nest was marked.

Known-age adults at selected nests were banded with an engraved plastic band, fitted on the leg not already banded with a metal band. These engraved plastic bands were made from a hard plastic ("Darvic") and each had a unique letter and colour combination. On completion of banding, the adult bird was placed in a plastic crate to reduce handling and stress, while the nest was marked and the egg or chick was measured. Thereafter, the adult was returned to the nest.

If the breeding partner of a known-age bird was already banded with a metal band, the band details were recorded and it was determined whether the partner was also of a known age. The partner was then banded with an engraved plastic band on its unbanded leg. If the breeding partner was not banded, a metal band (16 mm stainless steel bands, SAFRING) was placed on one leg and an engraved plastic band on the other. The ages of these birds were unknown. The presence, if any, of black secondary coverts on either wing was noted. Birds of about two years returning to breeding colonies retain traces of dark juvenile plumage on their head, back, wing coverts and rump (Rand 1959). Adult plumage is attained at an age of 3 - 4 years (Jarvis 1972).

Once a selected nest was marked, its height and the circumference of the top of the cup-shaped mould were measured. These measurements were recorded twice during the study period. Once at nest selection and again at the end of the breeding season once the breeding adults and chick (if present) had left the nest. The height was measured, to the nearest 0.5 cm using a 150 cm plastic tape measure run perpendicularly from the top of the nest to where the nest joined the ground surface. The height of nests was not always uniform around the circumference of the nest, so the highest part of the nest was always recorded for consistency. The distance of each study nest from the nearest edge of the colony was also measured. This measurement was done to the nearest centimetre with a 3 m metal measuring tape, an end of which was placed against the side of the nest facing the edge of the colony.

After the nest of an incubating bird had been marked, its egg was carefully removed and weighed, using a Tanita digital scale (model 1212) with an accuracy of 0.1 g up to 150 g. An earlier study reported that 86 eggs had a mean mass of 97.8 g (SD=0.8 g) (Navarro 1991). For each egg, one measurement of length and two of breadth, at right angles to each other at the widest part of the egg, were taken using a pair of callipers, with an accuracy of 0.1 g. Using these size and mass measurements, a reference table of mass of eggs of different sizes at laying (R.A Navarro *in litt.*) and the known incubation period for Cape Gannets of 43–44 days (Jarvis 1970), the period since laying of the egg and the expected date at hatching of the chick were determined. The underlying method makes use of the fact that the eggs of most bird species lose about 16 % of their initial mass during incubation and that, until the eggs are pipped, the rate of mass loss is linear, i.e. the eggs lose the same amount of mass each day (Hlatshwayo 2001). The cause of the decrease in the mass of eggs is loss of water, which evaporates out of tiny pores in the egg shell during incubation. Larger eggs have a greater surface area and lose mass more rapidly than do smaller ones but the loss is in the same proportion to surface area (Randall 1983; Hlatshwayo 2001). Nests were also selected at the brood stage; these nests were selected early in the hatching period, and were from first breeding attempts. The age of the chick was estimated by weighing it and using information on mass of chicks at age in Jarvis (1972). The mass of chicks increases approximately linearly until they are aged about 60 days (Cooper 1978). There may be a number of factors that cause chicks of similar ages to have varying mass, such as varying delivery rates by parents. This was taken into consideration when using this method to determine approximate laying dates.

Nests were monitored on a daily basis every alternate week between 18 September 2002, soon after commencement of the breeding season, and 15 April 2003, when breeding was complete at all the study nests. Monitoring was continued at nests that failed in order to record any replacement laying.

Chicks at study nests were banded with metal and coloured (yellow and green) plastic bands at about five weeks of age, when body mass was about half that at fledging (Jarvis 1974), so that their development to fledging could be followed. Once the chicks were almost completely feathered and started to move away from the nest, a strip on their backs was marked pink with Rhodamine B, so that the birds remained clearly visible amongst other feathered chicks moving around the colony. In total, 74 chicks were banded.

After chicks had been banded, twice-monthly checks were carried out in the nesting areas and around the edge of the island for dead birds. A fully-grown juvenile that left a study nest and moved to the outskirts of the colony was assumed to have fledged successfully in the absence of its carcass being found.

At the end of the breeding season, a nest was recorded as "closed" (when the cup shaped mound had been filled and was almost flat), as "open" or as destroyed.

The influence on breeding success of age of parent, distance of nest from the edge of the colony, height of nest and date of laying was investigated using a generalized linear model with the logit link function:

$$Y_i = \text{logit}(p) = \alpha + \beta_1 X_{1i} + \beta_2 X_{2i} + \ldots\ldots \beta_m X_{mi},$$

where Y_i is the outcome of breeding at nest i (1 if successful, 0 if failed), α is the regression coefficient for the intercept and the β values are the regression coefficients (for explanatory variables X_1 through X_m) computed from the data (McCullagh and Nelder 1983). The logit link function is defined as

$$Y = \text{logit}(p) = \log \frac{p}{1-p},$$

with back transformation:

$$p = \frac{e^Y}{1+e^Y}.$$

Using this model, the effects of four explanatory variables on breeding success were evaluated: age of one of the partners (years), distance into the colony (cm), nest height (cm) and week of nest initiation (week 0 is 4–10 August 2002). The value of including simple transformations of these explanatory variables (squares, logarithms) as explanatory variables were also explored. Models were fitted using Genstat Release 7.1 (Payne 2000).

Results

In total 125 nests of known-age birds were selected and monitored at various parts of the colony and at various distances into the colony. Of the 125 monitored nests, 96 were selected during the incubation period, 28 were selected during the brooding period, and in one instance a nest was marked prior to egg laying when two birds were observed mating.

Known-age gannets breeding at Malgas Island in 2002/03, ranged from 5–22 years old (Fig. 1). The lack of birds of ages 16 to 18 years corresponds to years in which little or no banding was undertaken (Table 1). The ages of both members of a breeding pair were known at five of the 125 monitored nests. For these five nests the age differences were 8 years (20 vs 12 years), four years (14 vs 10 years), one year (8 vs 7 years) and in two instances, when both partners were either nine years old or five years old, zero.

The mean height of the monitored nests was 18 ± 9 cm (range 0–38 cm, n = 125).

Of the 125 monitored nests, it was not possible to estimate the date of laying for four nests. One of these nests was selected due to the breeding pair having been observed mating, but they never produced an egg. The other three nests were all selected at the brood stage and the chicks died before they were weighed.

At monitored nests, the earliest egg was estimated to have been laid on 15 August 2002 and the last on 1 November 2002. Most eggs (24.8 %) were laid during week seven, between 22 and 28 September 2002 (Fig. 2).

In one instance no egg was known to have been laid. At 75 nests the first clutch failed. In 28 cases (37 %) the egg was lost; in 47 cases (63 %) the chick was lost. Gannets relayed at 11 (14 %) of these nests. All relays followed egg loss; none occurred after loss of the chick. In five of the relays (45 %) the adult birds successfully fledged young. Of the six nests that failed during the second clutch, the egg was lost in five of the nests (83 %) and the chick was lost in one nest (17 %). Of aged birds at study nests where relaying occurred, one was six years, three seven years, one eight years, one 10 years, two 12 years, one 13 years, one 19 years and one 20 years. Those that were successful included two birds aged seven years, one of eight years, one of 10 years and one of 20 years.

Overall, breeding pairs successfully fledged a single chick at 54 (43 %) of the 125 nests. No pair fledged two chicks. The youngest breeder of known age that successfully reared a chick was five years old and the oldest was 22 years old, spanning the full age range recorded.

Of the successful nests, 74.1 % were "closed" at the end of the breeding season, 12.9 % were left "open" and 12.9 % were "destroyed". Of the unsuccessful nests, 9.9 % were "closed", 54.9 % were left "open" and 35.2 % were "destroyed". Nests were significantly more likely to be "closed" if they were successful (chisquare = 54.2, df = 2, $P < 0.001$).

Of the broad range of generalized linear models considered to model the probability of breeding success, p, in relation to the four available explanatory variables, the following model with two variables was the best:

$$\text{logit}(p) = 0.43 + 0.01145 \text{ distance} - 0.837 \log_e(\text{age}).$$

This relationship explained 11 % of the deviance (SE $\beta_1 = 0.00303$, $P < 0.001$, SE $\beta_2 = 0.492$, $P = 0.045$, one sided test). Figure 3 shows the estimated probability of birds fledging chicks as a function of age and various distances into the colony. Inclusion of height of nest and date of laying did not significantly increase the proportion of deviance explained by the model and neither parameter could therefore be considered to influence breeding success. There was a clear trend for breeding success to improve with increasing distance of the nest from the edge of the colony. However, breeding success tended to decrease as birds aged (Fig. 3).

Older birds were found to breed earlier than younger individuals:

$$Z_i = 8.991 - 0.1937.\text{age},$$

where Z_i = date of laying in weeks (where week 0 = 4–10 August 2002). Hence, for every five years that age increased, a bird bred about one week earlier.

Distance of nest from the edge of the colony increased with age:

$$Z_i = 75.20 + 3.24.\text{age},$$

where Z_i = distance in cm. Therefore, for every five–year increase in a bird's life, its nest was located about 16 cm deeper in the colony.

Nest height also increased with age with:

$$Z_i = 11.32 + 0.59.\text{age},$$

where Z_i = height of nest in cms. This represents a small increase in nest height with increasing age (a modelled average increase of 0.59 cm per year, or a total of 9 cm between a five-year old bird and a 22-year old bird).

Discussion

The absence at Malgas Island in 2002/03 of Cape Gannets that were aged 16 - 18 and 21 years and the few that were aged 14 and 15 years corresponds with the few (sometimes none, always < 250) birds that were banded as chicks in 1982 and 1985-1988 (Table 1). The absence of birds younger than five years suggests that many of these birds were not yet breeding, although reduced numbers of chicks were banded after 1997. The mean age of Cape Gannets at first breeding is four years (Crawford 1999).

Previous studies of breeding success of gannets in relation to age are limited. For the North Atlantic Gannet *Morus bassana*, Nelson (1978) recorded the success of first, second and subsequent attempts at breeding, therefore considering experience rather than age. For the Australasian Gannet *Morus serrator* at Port Phillip Bay, Australia, age was found to influence nest location, date of arrival of birds at the colony, laying date, rate of growth and mass at fledging of chicks and fledging success (Gibbs *et al.* 1999). However, in that study the actual ages of most birds were not accurately known but were assumed from the location of nests relative to those of a few birds of known age. It was suggested that offspring of older Australasian Gannets have a higher survival rate than those of younger parents because their body mass at fledging is greater. Conversely chicks of younger parents are relatively lighter at fledging (Gibbs *et al.* 1999). A severe storm in Port Phillip Bay, Australia, in November 1994 destroyed most nests of breeding Australasian Gannets, which resulted in extensive re-laying. Younger birds replaced fewer lost eggs, whereas older birds replaced more than the average (Gibbs *et al.* 1999).

Unlike in the study of Gibbs *et al.* (1999) on Australasian Gannets, the age of Cape Gannets at Malgas Island did not exert a major impact on breeding success. In fact results indicate a decreasing rather than increasing breeding success with age (Fig. 3). It should be borne in mind that, in order to minimise disturbance, nests in our study were only monitored within a few metres of the edge of the colony. As breeding success increased with increased distance of a nest from the edge of the colony (Fig. 3), the average success of older birds may have been greater than that measured, if most old birds nested away from the edge of the colony. However, at Bird Island in Algoa Bay, Cape Gannets nesting on the edge of the colony did not, in subsequent years, vacate their nest sites to move towards the centre of the colony (Klages 1994). In Californian Gulls *Larus californicus*, older gulls bred more centrally in the colony and had a higher success than younger birds (Pugesek 1981).

Breeding success in Short-tailed Shearwaters *Puffinus tenuirostris* is related both to age and the length of time birds have bred together. The latter factor appears to exert the stronger effect (Wooller *et al.* 1989; Bradley *et al.* 1990; Bradley *et al.* 1995). Parental experience may lead to improved growth of chicks in Thick-billed Murres *Uria lomvia* (Hipfner and Gaston 2002) and Short-tailed Shearwaters (Wooller *et al.* 1989; Bradley *et al.* 1990; Bradley *et al.* 1995). For Short-tailed Shearwaters, in the first year of a pair-bond, female breeding age is more important than that of the male in determining the probability of reproductive success (Bradley *et al.* 1995). Studies of other seabirds have also shown that breeding experience with the same mate is a significant determinant of successful reproduction (e.g. Mills 1973; Coulson and Thomas 1983; Ollason and Dunnet 1988). In the study at Malgas Island there was no way of determining how long each pair of breeding gannets had been together.

In this study the ages of both birds in five pairs of breeding partners were known. On all three occasions when both birds were younger than 10 years, the difference in age of partners was one year or less. In the two instances when one of the pair was older, there was a larger discrepancy in ages. Unfortunately, this is a small sample size of both breeding pairs being of a known age, but this contrast suggests that birds initially breed with partners of similar age. Older birds may have lost partners and replaced them with birds of different ages. Mating between individuals of similar age has been noted for several seabirds (Mills 1973; Coulson and Thomas 1983; Shaw 1985; Reid 1988; Crawford *et al.* 2001). Coulsen and Horobin (1976) showed that in 29 pairs of Arctic Terns *Sterna paradisaea*, whose ages ranged from 3 - 18 years, 83 % of mated pairs differed in age by no more than two years.

Improved breeding success may arise from early breeding (Gibbs *et al.* 1999). For a number of seabirds, experienced breeders have returned to their colonies earlier in the breeding season than inexperienced birds (Serventy 1967; Ainley *et al.* 1983). For the Califonian Gull *Larus californius* timing of breeding had more influence on breeding success than did age (Pugesek 1981). However, in our study the date of laying did not influence breeding success, even though older birds did tend to lay earlier in the breeding season than younger birds.

That a higher proportion of successful as opposed to unsuccessful Cape Gannets "closed" their nests could reflect the fact that successful birds and their chicks remain at their nest sites longer than failed breeders, with resultant guano production and trampling leading to a filling of the cup-like depressions. Cape Gannets have been shown to exhibit strong fidelity to nest sites (Klages 1994) and at the onset of the following breeding season nests are reshaped (pers. obs.). Although in this study the height of the nest increased with the bird's age, it had little influence on breeding success. However, the effect of nest height might be larger in wetter years when flooding of nests decreases breeding success (Randall and Ross 1979).

Several factors might result in distance from the edge of the colony influencing breeding success. Nests at the edge of a colony may be more susceptible to predation, flooding and disturbance by humans, including tourism. Although tourists often visit Malgas Island they are not allowed to walk freely around the island, but are confined to the same areas on each visit, which are close to the houses on the island. These areas are within a few meters of many of the study nests. In addition to scientists and tourists, Malgas Island also had a permanent Nature Conservation Officer patrolling the island every day. A Cape Fur Seal *Arctocephalus pusillus* killed an adult gannet on the edge of the colony at Malgas Island (Crawford and Cooper 1996), where Kelp Gulls *Larus dominicanus* regularly hunt for eggs (pers. obs). In Port Phillip Bay, a severe storm in November 1994 destroyed most nests of Australasian Gannets (Gibbs *et al.* 1999), with the nests on the edges of the colony receiving the most damage.

In Port Phillip Bay, 84 % of Australasian Gannets relaid after a storm destroyed most nests there, compared with 38 % following losses at other times (Gibbs *et al.* 1999). Relaying by Cape Gannets, which occurred at 14 % of the nests at Malgas Island in 2002 /03, was lower than both the values for Australasian Gannets and does not appear to have been influenced by age.

This study was limited by the fact that all nests studied were within 4 m of the perimeter. It would be preferable to include nests farther into the colony. Another limitation was the fact that at most nests the age of only one partner was known. The effort required to band sufficient fledglings to obtain a large sample in which both adults are of a known age is probably not achievable. During the period for which ringing was undertaken prior to this study, 5–10% of the chicks produced each year were ringed (2000–3000 chicks). This results in the proportion of pairs that have both adults banded being less than 1%. In order to increase the proportion of pairs with both birds banded to 10% would require one third of the chicks to be banded (ca 9000 chicks), which is an unattainable goal in terms of both resources and levels of disturbance generated. However, it is desirable that the sex of the known age birds is determined. This determination could be achieved from observations of behaviour or taking of blood samples. An extensive study to determine nest site and mate fidelity and how this impacts breeding success in the long term is feasible. It would also be useful to do a blood analysis to determine the sexes of the breeding partners (behavioural observations are not feasible due to the number of nests, as well as their wide distribution over the island), which could also be used to determine the parental care of the male and the female Cape Gannets with respect to the egg and chick brooding stages, as well as the feeding efforts of each parent and different ages.

It may also be useful to try and create access routes to the core of the colony prior to the start of the breeding season, to create pathways which will allow safe access to nests that are more distant to the edge of the colony than was attainable in this study.

References

Ainley DG, LeResche RE and Sladen WJ 1983. Breeding biology of the Adelie Penguin. University of California Press, Berkley, USA

Barnes KN (ed) 1998. Important bird areas of the western Cape. In: The Important Bird Areas of Southern Africa. BirdLife South Africa, Johannesburg. Pp 219-267

BirdLife International 2004. Threatened Birds of the World 2004. CD-ROM. BirdLife International, Cambridge

Bradley JS, Wooller RD, Skira IJ and Serventy DL 1990. The influence of mate retention and divorce upon reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. Journal of Animal Ecology 59: 487-496

Bradley JS, Wooller RD and Skira IJ 1995. The relationship of pair-bond formation and duration to reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. Journal of Animal Ecology 64: 31-38

Broekhuysen GJ, Liversidge R and Rand RW 1961. The South African Gannet *Morus capensis*. I. Distribution and movements. Ostrich 32: 1-19

Brooke ML 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater, *Puffinus puffinus*. Journal of Animal Ecology 47: 477-495

Cooper J 1978. Energetic requirements for growth and maintenance of the Cape Gannet (Aves; Sulidae). Zoologica Africana 13: 305-317

Coulsen JC 1966. The influence of the pair bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. Journal of Animal Ecology 35: 269-279

Coulson JC and Horobin J 1976. The influence of age on the breeding biology and survival of the Arctic Tern, *Sterna paradisea*. Journal of Zoology 178: 247-260

Coulson JC and Thomas CS 1983. Mate choice in the Kittiwake Gull. In: Bateson P (ed) Mate Choice. Cambridge University Press, Cambridge. Pp 361-376

Crawford RJM 1999. Seabird responses to long-term changes of prey resources off southern Africa. In: Adams NJ and Slowtow RH (eds) Proceedings 22nd International Ornithological Congress, Durban. Birdlife South Africa, Johannesburg. Pp 688-705

Crawford RJM 2000. Cape Gannet. In: Barnes KN (ed) The Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg. Pp 63-64

Crawford RJM and Cooper J 1996. Cape Fur Seal *Arctocephalus pusillus* catches Cape Gannet *Morus capensis* ashore at Malgas Island. Marine Ornithology 24: 53-54

Crawford RJM, Dyer BM, Upfold L and Ward VL 2001. Age at first breeding of Bank, *Phalacrocorax neglectus*, and Cape Cormorants, *P. capensis*. Ostrich 72: 145-148

Crawford RJM, Shelton PA, Cooper J and Brooke RK 1983. Distribution, population size and conservation of the Cape Gannet *Morus capensis*. South African Journal of Marine Science 1: 153–174

Del Hoyo J, Elliott A and Sargatal J (eds) 1992. Order PELECANIFORMES. In: Handbook of the Birds of the World. Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona. Pp 279-374

Du Toit M, Boere GC, Cooper J, De Villiers MS, Kemper J, Lenton B, Petersen SL, Simmons RE, Underhill LG, Whittington PA and Byers OP (eds) 2003. Conservation Assessment and Management Plan for Southern African Seabirds. Avian Demography Unit, Cape Town and Conservation Breeding Specialist Group, Apple Valley, Minnesota

Gibbs HM, Norman FI and Ward SJ 1999. Reproductive parameters, chick growth and adult 'age' in Australasian Gannets *Morus serrator* breeding in Port Phillip Bay, Victoria, in 1994–95. Emu 100: 175–185

Hipfner JM and Gaston AJ 2002. Growth of nestling Thick-billed Murres (*Uria lomvia*) in relation to parental experience and hatching date. Auk 119: 827-832

Hlatshwayo F 2001. Estimating the incubation stage of penguin eggs. B.Com. (Hons), Department of Statistical Science, University of Cape Town

Jarvis MJF 1970. Interactions between man and the South African Gannet, *Sula capensis*. Ostrich 8: 497-514

Jarvis MJF 1972. The systematic position of the South African Gannet. Ostrich 43: 211-216

Jarvis MJF 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis* (Lichtenstein)). Journal of Animal Ecology 43: 1-17

Klages NTW 1994. Dispersal and site fidelity of Cape Gannets *Morus capensis*. Ostrich 65: 218–224

McCullagh P and Nelder JA 1983. Generalized linear models. Chapman and Hall, New York

Mills JA 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus*. Journal of Animal Ecology 42: 147-163

Navarro RA 1991. Food addition and twinning experiments in the Cape Gannet: effects on breeding success and chick growth and behaviour. Colonial Waterbirds 14: 92-102

Nelson JB 1978. African or Cape Gannets. In: The Sulidae Gannets and Boobies. Oxford University Press, Oxford. Pp 231-255

Nisbet ICT, Apanius V and Friar MS 2002. Breeding performance of very old Common Terns. Journal of Field Ornithology 73: 117-124

Nur N 1984. Increased reproductive success with age in the Californian Gull: due to increased effort or improvement of skill? Oikos 43: 407-408

Ollasen JC and Dunnet GM 1978. Age, experience, and other factors affecting the breeding success of the Fulmar, *Fulmarus glacialis*, in Orkney. Journal of Animal Ecology 47: 961-976

Ollasen JC and Dunnet GM 1988. Variation in breeding success in fulmars. In: Clutton-Brock TH (ed) Reproductive Success. University of Chicago Press, Chicago. pp 268-278

Payne RW (ed) 2000. The Guide to Genstats Part 2: Statistics. VSN International, Oxford

Pugesek BH 1981. Increased reproductive effort with age in the Californian Gull *Larus californicus*. Science 212: 822-824

Rand RW 1959. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape Gannet, *Morus capensis*, off the south-western coast of the Cape Province. Investigational Report Sea Fisheries Research Institute, South Africa 39: 1-36

Randall RM 1983. Biology of the Jackass Penguin at St. Croix Island, South Africa. PhD Thesis, University of Port Elizabeth

Randall RM and Ross GJB 1979. Increasing population of Cape Gannets on Bird Island, Algoa Bay, and observations on breeding success. Ostrich 50: 168-175

Reid WV 1988. Age correlations within pairs of breeding birds. Auk, 105: 278-285

Serventy DL 1967. Aspects of the population ecology of the Short-tailed Shearwater *Puffinus tenuirostris*. Proceedings of the XIV International Ornithological Congress. Alden Press, Oxford. Pp 165-190

Shaw P 1985. Age-differences within breeding pairs of Blue-eyed Shags *Phalacrocorax atriceps*. Ibis 127: 537-543

Wooller RD, Bradley JS, Skira IJ and Serventy DL 1989. Short-tailed Shearwater. In: Newton I. (ed) Lifetime Reproduction in Birds. Academic Press, London. Pp 405–417

Table 1: Numbers of fledgling Cape Gannets banded at Malgas Island between 1951 and 2002 (Broekhuysen *et al.* 1961, H.D. Oschadleus, SAFRING, *in litt.*).

Year	Age in 2002/03 breeding season (years)	Number of fledglings banded
1951	52	53
1952	51	143
1953	50	582
1954	49	4980
1955	48	4387
1956 - 1978	0	0
1979	24	2
1980	23	950
1981	22	1010
1982	21	235
1983	20	3399
1984	19	1138
1985	18	0
1986	17	0
1987	16	218
1988	15	33
1989	14	601
1990	13	1205
1991	12	1200
1992	11	1493
1993	10	1300
1994	9	1209
1995	8	1277
1996	7	1224
1997	6	1314
1998	5	790
1999	4	754
2000	3	913
2001	2	654
2002	1	718

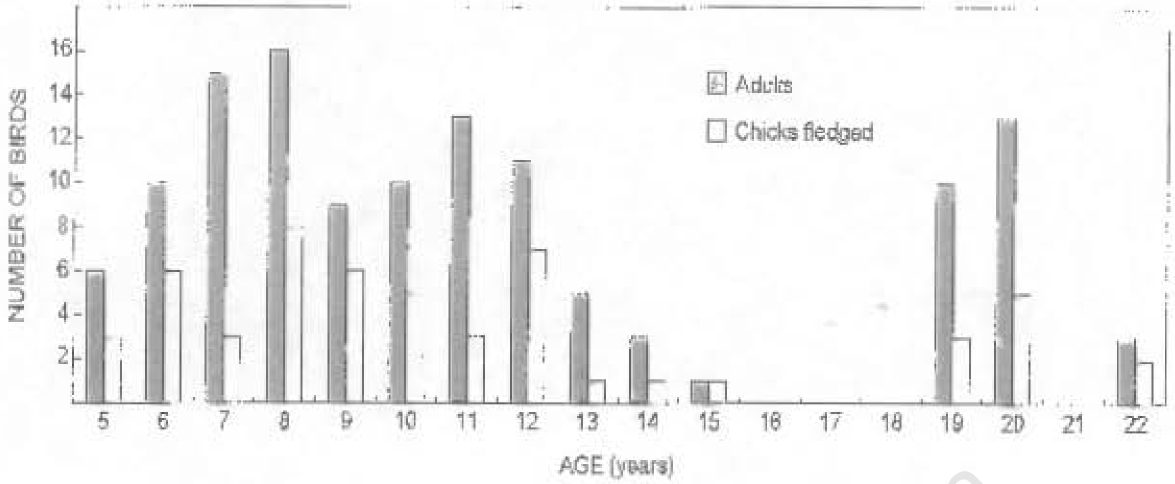

Figure 1: The frequency of occurrence and breeding success of Cape Gannets (n=125) of different ages, monitored on Malgas Island in 2002/03.

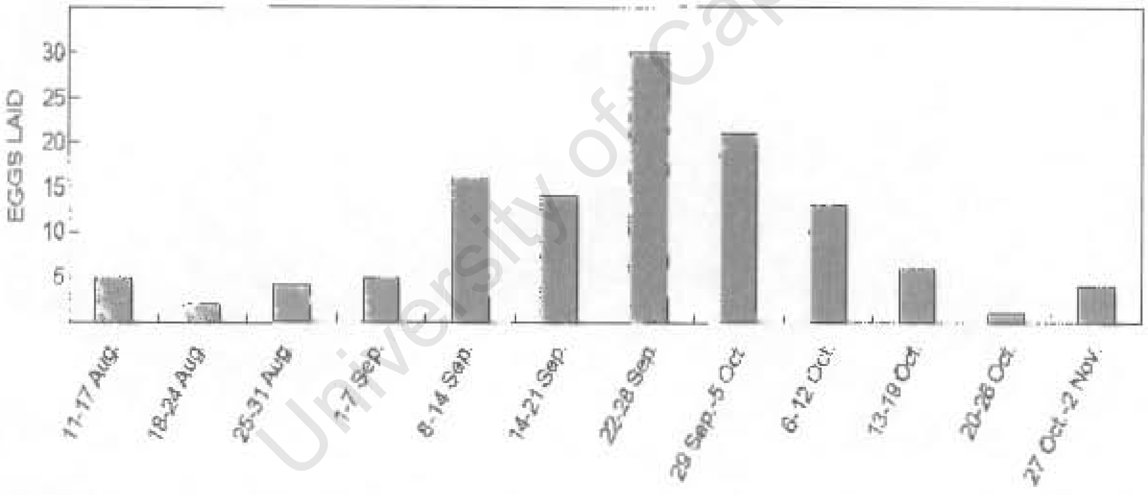

Figure 2: The estimated number of eggs laid each week (first breeding attempts) on Malgas Island, where week 1 was 11–17 August 2002 (n=124).

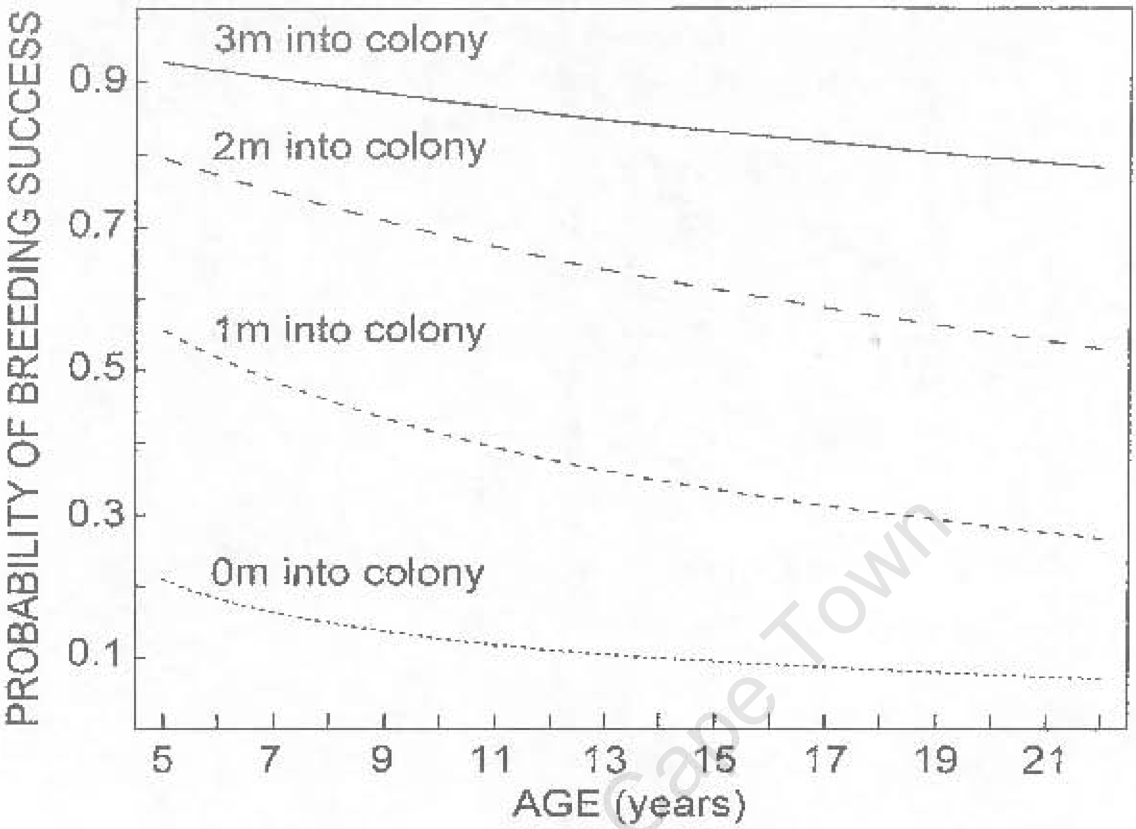

Figure 3: Breeding success probability for Cape Gannets of different ages as a function of nest distances from the edge of the colony, at Malgas Island in 2002/03.

Chapter 3

Factors influencing the growth of Cape Gannet *Morus capensis* chicks, and growth in the Pelecaniformes

Factors influencing the growth of Cape Gannet *Morus capensis* chicks, and growth in the Pelecaniformes

Abstract

A method to estimate the growth coefficient of chicks of Cape Gannets *Morus capensis* is described. At Malgas Island in 2002/03, growth was most rapid for chicks hatched early in the season and there was higher pre-fledging survival of faster-growing chicks. Age of parents and distance of nest from the edge of the colony had no apparent influence on survival. A comparison of growth rates obtained from the literature for seabirds in the order Pelecaniformes showed no significant relationship between growth rate and mass of adults, but growth rate was significantly related to latitude. However, within five families in the order there was no obvious relationship between growth rate and latitude. The statistically significant relationship obtained for the order as a whole is attributable to the presence of frigatebirds and the absence of cormorants (for which growth rates were available) at low latitudes. Members of these families generally have lower and higher, respectively, growth rates than members of other families within the order.

Introduction

The order Pelecaniformes, an ancient and diverse one to which gannets and boobies (family Sulidae) belongs, includes also five other families: pelicans (seven species, Pelecanidae), cormorants and shags (39 species, Phalacrocoracidae), darters or snake birds (two species, Anhingidae), frigatebirds (five species, Fregatidae) and tropicbirds or bosunbirds (three species, Phaethontidae). They are all web-footed fish eaters, partly or wholly marine and between them employ a wide range of fishing methods (Nelson 2002). Ecological and morphological adaptations of the Cape Gannet *Morus capensis* can be seen by comparing this species to other members of the family Sulidae. The differences between the species have come about because each species has each moved into its own feeding and nesting "niche" to which it has become intimately suited physically, ecologically and behaviourally.

Friesen and Anderson (1997) used molecular phylogeny to test competing models of speciation in the Sulidae. They demonstrated that the Abbott's Booby is more closely related to the three gannet species than the other six booby species and placed it in a monospecific genus *Papasula*. Their finding for Abbott's Booby contrasts with some earlier ecological and morphological studies, which considered that there were affinities between the six species of boobies, such as a tropical distribution and similarities in several osteological characters (Warheit 1990), but agrees with several ecological, ethological and morphological similarities between the Abbott's Booby and the gannets, such as the absence of a "wing flicking" display (Nelson 1970) and a relatively long humerous (Warheit 1990). We adopt the conservative approach and retain Abbot's Booby in the genus *Sula*.

Relationships between chick growth rates and parental age had been little examined in seabirds (Ricklefs 1967), but more recent studies relating fledgling mass or feeding efficiency to age, or comparing growth curves between species are more common (Ainley *et al.* 1983; Gales 1984). The decline in the breeding success and chick growth of Australasian Gannets *Morus serrator* in Port Phillip Bay during the 1998/99 breeding period was associated with a massive and sudden reduction in the availability of a major prey (Bunce and Norman 2000; Bunce 2001). When food was not limited, both young and experienced breeders were equally capable of rearing chicks and had similar levels of breeding success (Bunce *et al.* 2005). Older breeders may be able to adjust foraging effort to maintain constant levels of parental care and hence may act to buffer the effect of reduced food supply from reproductive or chick growth parameters (Weimerskirch 1990; Catry and Furness 1998, Ratcliffe *et al.* 1998; Daunt *et al.* 2001). Lequette and Weimerskirch (1990) found early (but not later) chick growth was slower in inexperienced pairs of Wandering Albatrosses *Diomedea exulans*, suggesting a lesser feeding efficiency early in the guard stage. They considered that efficiency was not enhanced with later attempts at breeding.

All gannet pairs, regardless of age, presumably have similar foraging opportunities, with respect to food availability while breeding, so increased efficiency with age could allow earlier egg formation and laying in older females (date of laying may be influenced by foraging before breeding). Food availability may influence the reproductive state of breeding birds in some gannet species (Adams and Walter 1991). Starvation of chicks may be high during rough weather (Waghorn 1982; Navarro 1991), either directly from lack of food returns or from increased thermoregulatory demands

Starck and Ricklefs (1998a, b) reviewed growth rates in birds and assembled a database of 1117 estimates of the growth rates of 557 avian species. They confirmed a general overall trend for an inverse relationship between adult body mass A (g) and growth rate of chicks. For logistic growth rates, their allometric relationship was $k_L = 0.962\ A^{-0.316}$; the exponent of body mass was negative so that larger species grow more slowly than smaller species. They also performed analyses within orders and found a similar relationship for all except one order, the Pelecaniformes. For this order, for the 17 species for which they had growth rate data available, there was a positive relationship between mass and growth rate; in their analysis the fitted exponent of body mass was +0.21, so that the chicks of heavier species grew faster than those of lighter species. This relationship was significantly different to that for all avian species, but the fitted exponent was not significantly different from zero. They commented that this unexpected result required further investigation.

There are substantial differences in chick growth rates within the Sulidae family, which could be related to varying clutch sizes as well as post fledging feeding. The three gannet species all have a clutch size of one egg, but chicks of the North Atlantic Gannet *M. bassana* have extremely fast growth rates when compared to those of the Cape Gannet and the Australasian Gannet *M. serrator* (Nelson 2002). The North Atlantic Gannet also has a much higher maximum weight than the other two species, and takes a shorter time to reach it (Nelson 2002). Adult North Atlantic Gannets attend and feed their chicks until the day or even hour of departure, compared to the behaviour of chicks of Cape and Australasian Gannets, which hang around the edge of the colony for a few days after leaving the nest. Some chicks may still be fed by the parents if they return to the nest, but generally they are not. This contrast could be an adaptation to both their climate as well as their breeding habitats. North Atlantic Gannets breed in colder climates, so may need the extra fat reserves for warmth. They also breed on cliffs, so that the initial flight off the cliff is much easier to undertake at high mass. Cape and Australasian Gannets tend to breed on low, flat islands, in warmer climates, so therefore do not need the extra fat reserves. Some also walk into the sea and take their initial flight from the water, and thereafter from runways on the island. Excess mass may make the use of runways more difficult.

It is also suggested that the North Atlantic Gannet is heavier at fledging because it completes its growth after fledging, during the swimming phase of its southward migration, lasting about two weeks. In comparison, the Cape and Australasian Gannets fly from their natal island (there is no swimming phase to their migration), so it is more advantageous for them to spend their last few days completing the growth of their flight feathers, instead of gaining weight.

The boobies differ in their breeding ecology to the gannets. Five of the seven booby species have more than one egg in a clutch and there are varying degrees of post fledging feeding. The breeding strategies between the boobies differ substantially, and could be related to food availability and foraging techniques (Nelson 2002). Boobies are also slightly smaller and lighter than gannets, and are therefore adapted to flat, relatively windless nesting sites. Chick growth rates tend to be slower than the gannets. The Red-footed Booby *Sula sula* and the Abbott's Booby *S. abbotti* both have a clutch size of one egg, whereas the Masked *S. dactylatra*, Brown *S. leucogaster* and Nazca Boobies *S. granti* have clutch sizes of 1 – 2 eggs (usually 2), the Blue-footed Booby *S. nebouxii* has a clutch size of 1 – 3 eggs (usually 2) and the Peruvian Booby *S. variegata* has a clutch size of 1 – 4 eggs (usually 3) (Nelson 1978; Nelson 2002; Snow and Nelson 1984). The Masked Booby tends to feed its chicks for approximately eight weeks post fledging, the Brown Booby for 4 – 8 weeks, but up to 36 weeks post fledging, the Blue-footed Booby for 4 – 6 weeks, the Peruvian Booby for 4 – 8 weeks, the Red-footed Booby for 4 – 13 weeks, and the Abbott's Booby for 20 – 40 weeks, but in some cases up to one year post fledging (Nelson 2002).

The aim of the current study was to determine the growth rates of Cape Gannet chicks in relation to explanatory variables such as the age of parent and distance from the edge of the colony. We also followed the suggestion made by Starck and Ricklefs (1998a) and investigated the growth rates within the order Pelecaniformes. We therefore assembled a set of growth rates for species in the order from the literature and followed the approach pioneered by Klaassen *et al.* (1989) to analyse them.

Methods

Fieldwork

Malgas Island (33°03'S, 17°55'E), circular and flat, is situated in Saldanha Bay on the West Coast of South Africa. The first reported breeding of Cape Gannets on Malgas Island was in 1648. Now most of the central areas of Malgas Island are occupied by nesting Cape Gannets, with other nesting seabirds mostly confined to the periphery of the island. Malgas Island was one of the guano scraping islands but due to large mortalities of chicks as a result of the scraping, this activity was ceased in 1995, when Langebaan Lagoon and islands in Saldanha Bay were proclaimed a national park. During the months of September to December 2002, gannet nests at Malgas Island were selected for studies on breeding success related to age, as well as chick growth in relation to mass.

Once hatched, monitored chicks were weighed approximately every second week (a range of 11 – 21 days between weighs, with the longer periods being towards the end of the breeding season when chicks were not always present at the nests). Mass was measured by gently placing the chick inside a bag, and both chick and bag weighed using precision spring balances (Pesola 100 g, 200 g, 300 g and 500 g and Salter 1 kg and 5 g). The measurement precision was 1 g up to 100 g, 2 g between 100 g and 300 g, 5 g between 300 g and 2 kg, and 25 g above 2 kg. The bags used were soft material bags, in a variety of sizes and weights, turned inside out so the seams did not injure the birds. Draw-string sewn into the top of the bags was used to hang the bag from the scale.

Naked chicks and small downy chicks were lifted from the nest without removing the brooding adult, to reduce stress and disturbance. For nests at the edge of the colony, a wooden shield was used to lift the adult slightly off the nest. The chick was then gently removed from underneath the adult by hand. Once weighed and measured, the chick was returned to the nest in the same manner. For nests away from the edge of the colony, chicks were lifted out of the nest using a flat ladle-like spoon fitted to the end of a pole. The adult's chest and body was first lifted up using a pole with a crook, and the spoon was then inserted underneath the chick and then lifted out of the nest. Once weighed and measured the chick was returned to the nest in the same manner. Once the chicks were larger, they were often left alone at the nest and were caught with the aid of the crook pole. At times the chicks, especially the larger ones, tended to regurgitate once in the bag, and the regurgitated mass was included in the mass measurements.

Chicks at study nests were banded with metal and coloured (yellow and green) plastic bands at about five weeks of age, when body mass was about half that at fledging (Jarvis 1974), so that their development to fledging could be followed. The plastic rings were used to distinguish the monitored chicks from chicks ringed at the island in a separate study, as well as to monitor their movements, if any, to other areas of the island not in the vicinity of their nests. On the southern and south western side of the island, chicks were banded with yellow plastic rings, and on the north and north western sides, chicks were banded with green plastic rings. Chicks on the eastern side of the island were banded with both yellow and green plastic rings. To ensure the plastic ring did not open once on the bird's leg, a small amount of super glue was applied to the ring to keep it closed. This prevented the ring from opening and slipping down over the foot of the bird, which may cause deformation or even loss of the foot (BM Dyer pers. comm.).

Once the study chicks were almost completely feathered and had started to move away from the nest, a strip on their backs was marked pink with Rhodamine B, so that they remained clearly visible among other feathered chicks moving around the colony. In total 74 chicks were banded.

Nests were monitored on a daily basis in alternate weeks from 18 September 2002, soon after commencement of the breeding season, until 15 April 2003, when breeding was complete at all the study nests. Monitoring was continued at nests that failed in order to record and monitor any replacement laying.

After chicks had been banded, twice-monthly checks were carried out in the nesting areas and around the edge of the island for dead birds. A juvenile that left a study nest and moved to the outskirts of the colony was assumed to have fledged successfully in the absence of its carcass being found.

Statistical analysis

We used the Gompertz model to describe the growth of the Cape Gannet chicks. This growth curve has been widely used to model gannet growth (e.g. Navarro 1991; Bunce *et al.* 2005). We assume that the primary goal is to estimate the growth coefficient k, and that we have good estimates of both the hatchling mass H (g), and the asymptotic mass A (g). We used the parameterization $M=A\exp(-b\exp(-kt))$ for the Gompertz curve, where A, b and k coefficients, t is age in days, and M is the mass (g) at age t. The asymptote A is known, and we will show below that b can be estimated from H, so that k is the only parameter that needs to be estimated.

The growth curve can be written as $M/A = \exp(-b\exp(-kt))$. Take natural logarithms twice, obtaining $\log(-\log(M/A)) = \log(b) - kt = B - kt$. Suppose that mass (or some other measurement) has value M_1 on calendar date t_1, and M_2 and on date t_2. Then, $\log(-\log(M_1/A)) = B - kt_1$ and $\log(-\log(M_2/A)) = B - kt_2$. Subtracting the second of these equations from the first yields $\log(-\log(M_1/A)) - \log(-\log(M_2/A)) = k(t_2 - t_1)$, and therefore an immediate estimate of k is

$$k = \frac{\log(-\log(M_1/A) - \log(-\log(M_2/A)}{t_2 - t_1} \qquad (1)$$

This equation solves the problem of estimating the growth coefficient k in the situation where we have two observations on a chick of unknown age. If we have m observations on a chick, we can find $p=m(m-1)/2$ values for k by considering all pairs of observations. We now apply the concept underpinning Theil's robust regression (Theil 1950a, b, c) and reduce the impact of any outlying observations by taking the median of the p values as the estimate of k for this bird.

For q chicks of a species, we obtain q independent estimates of the growth coefficient k. We choose their median as a representative growth coefficient for the species. Suppose now that we have a value for k derived from the Gompertz model (equation (1)). We assumed a value for the asymptote A, but still require a value for b. This estimate can readily be determined by arranging the growth curve in such a way that the mass at time $t=0$ is given by the initial value H at hatching. For the Gompertz equation, $M=A \exp(-b \exp(-kt))$, putting $t=0$ yields $b=-\log(H/A)$. This approach ensures that the growth curve starts at the appropriate value at time $t=0$.

The advantage of using Theil's (1950a, b, c) robust regression over the least squares approaches and approaches based on Ricklefs' (1967) graphical method, which is based on a transformation to least squares linear regression, is that sensitivity to the choice of asymptote is substantially reduced.

The growth rate k of each chick was used as the dependent variable in a multiple regression. We used four explanatory variables: the known age (years) of one of the adults; the distance of its nest (cm) from the edge of the colony; the outcome (successfully fledged or not) as a categorical variable; and the mid-date of the period over which the growth rate was estimated, measured in days since 15 August 2002. We anticipated that growth rate k would either decrease through the breeding season or increase to a peak and then decrease; we therefore included the mid-date variable in several ways: linear, quadratic, and as a categorical variable with four levels, the cutpoints being determined by the median and quartiles. One-sided tests were used where the alternative hypothesis made this appropriate.

To undertake the study of growth for species within the Pelecaniformes, as defined by Del Hoyo *et al*. (1992), Gompertz growth rates were collated from the literature, using mainly Starck and Ricklefs (1998b) as a source of 39, and returning to their original papers 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). In addition, Gompertz growth rates were estimated for an additional five species of southern African cormorants, using data sources which had been overlooked by Starck and Ricklefs (1998b). These papers reported average masses of chicks of various ages. These growth parameters were estimated using the FITCURVE directive of GenStat (Payne 2005), using the method of least squares, the same procedure as had been used by Starck and Ricklefs (1998b) to estimate growth parameters from similar published datasets. Multiple linear regression of logarithmically transformed variables was used to model growth rates in relation to asymptotic mass and latitude (and also latitude north and south considered separately).

Results

Growth of Cape Gannet chicks

In total, 125 nests with at least one known-aged adult were selected and monitored at various parts of the colony and at various distances into the colony ranging from 0 – 385 cm. Of these, 96 were selected during the incubation period, 28 were selected during the brooding period, and in one instance a nest was marked prior to egg-laying when two birds were observed mating. Except for the solitary nest where birds were observed mating, each nest had a single egg or chick.

The known age of the adults at study nests ranged between five and 22 years. The mean distance into the colony of the nest for the 84 chicks was 127 cm. Nine of the study chicks were in nests which were on the edge of the colony and the overall range of distance was from 0 cm to 385 cm.

At monitored nests, the earliest egg was estimated to have been laid on 15 August 2002 and the last on 1 November 2002, a period of 78 days. The peak egg-lay period was the week 22–28 September, during which 24.8 % of eggs in monitored nests were laid. The earliest mid-date of the measured growth period was day 99 (22 November 2002); the latest mid-date was day 230 (2 April 2003). The mean was date 171 (2 February 2003).

Of the 125 study nests, no egg was laid in one. At 28 nests, the egg was lost, probably due to predation by Kelp Gulls *Larus dominicanus*. At 11 of these, eggs were relayed, of which five were lost. There were 102 hatchlings, of which 54 fledged. Growth rates were obtained for 84 of the chicks for which at least two mass measurements were obtained, ranging from a minimum of two to a maximum of eight, where most averaged between five and seven mass measurements for each chick.. For the remaining 18 chicks, only one mass measurement was obtained because the chick died within 10 days. Growth rates were obtained for all 54 chicks that fledged and 30 chicks that failed to fledge.

In the multiple regression, two explanatory variables were significant: mid-date (days since 15 August 2002) of the measured growth period and successful fledging. Successful chicks grew significantly faster than unsuccessful chicks. The best fitting model was

$$k = 0.04967 - 0.0000879 * \text{mid-date} + 0.00436 \text{ (if successful)}$$

The standard errors of the mid-date coefficient were 0.0000509 (P=0.044) and 0.00242 (P=0.038), respectively. The age of parents was not significant (P=0.43) in influencing the growth rate of chicks nor was distance from the edge of the (P=0.14). At the median value for mid-date, the estimated growth rate coefficient (k) for a successful gannet chick was 0.0390 compared to an estimated growth rate of 0.0346 for unsuccessful chicks (Fig. 1). For successful chicks, the estimated growth rate coefficients at the lower quartile, median, and upper quartiles values for mid-date were 0.0453, 0.0390 and 0.338, respectively (Fig. 2).

Growth rates in the Pelecaniformes

Our data set for the Gompertz growth rates of Pelecaniformes contained 44 values for 24 species (Table 1). As with the smaller sample analysed by Starck and Ricklefs (1998a), we found a positive but not statistically significant relationship between growth rate and mass, or strictly, the logarithm of growth rate and the logarithm of mass ($r = 0.086$, $P = 0.66$, Fig. 3). There was a significant positive relationship between growth rate and latitude (log $K_G = -3.093 + 0.01241$ (latitude) (SE of slope coefficient = 0.00325, $t_{40} = 3.82$, $P < 0.001$), a relationship which explained 24.9 % of the variance. We investigated the possibility that there were different slope coefficients in the northern and southern hemispheres, but found no significant difference. This absence of contrast suggests that growth rates increase symmetrically from the equator towards the poles (Fig. 4).

Modelling growth rate with family as a categorical variable accounted for 74.1 % of the variance; the growth rates of the Phaetontidae (tropicbirds) and Pelecanidae (pelicans) were not distinguishable, and the most parsimonious model, accounting for 74.2 % of the variance, had four parameters (Table 2). Based on the Akaike Information Criterion, this four parameter model was better than the five parameter model with five categorical variables. Adding latitude and mass, and interactions between these variables and family did not improve the model further. This outcome means, that we were unable to detect a significant relationship between growth rate and mass within any of the families, and that there was also no relationship between growth rate and latitude within any family.

Discussion

Cape Gannet chicks fledge (leave the nest area) at 90 – 105 days (mean 97 days; Jarvis 1970) and then usually spend a few days (up to six) on the edge of the colony before leaving the island, where they undertake extensive wing flapping in preparation for flight and lose weight at an average rate of around 50 g per day (Jarvis 1974). In the Cape Gannet, the most dangerous phase of the life history is presumed to be soon after birds fledge (leave the nesting area). These birds must learn to fly, fish, and avoid predators, apparently without aid from adults. At Malgas Island, large numbers are killed by Cape Fur Seals soon after fledging (David *et al.* 2003). It is probable that the body mass of chicks when they fledge has some relationship to their chances of post-fledging survival. This is supported by the observation that Cape Gannet fledglings with low mass have a greater than average mortality in the post-fledging period (Jarvis 1974).

Since only single egg clutches (rarely two egg clutches; Nelson 2002) are laid in these strongly philopatric species, long-term survival depends on successfully raising the chick to fledgling and beyond, rather than adjusting numbers of chicks fledged from a larger clutch (Norman and Menkhorst 1995). Here the relative improvement in long-term survival is important, and is perhaps maximised in gannets by marginal increases in (age-related) efficiency needed to increase chick mass, rather than the more substantial effort needed to produce larger clutches of smaller chicks. Fledging mass is thought to influence post-fledging survival in Cape Gannets. Chicks weighing < 2.25 kg at fledging were less active than heaver chicks or died (Jarvis 1974). In artificially-twinned broods of Cape Gannets at Lambert's Bay in 1966/68, the heavier twin had a growth rate similar to that of a single chick but the lighter twin was considerably under weight (Jarvis 1974). However, at Malgas Island during 1986/88 growth rates and fledging mass of artificially-twinned chicks did not differ from those of singleton broods (Navarro 1991).

In Port Phillip Bay, Australia, 14 (41 %) recoveries of Australasian Gannets banded as fledglings occurred within six months of banding, four within 17 – 24 months, two within 26 months, six within 34 – 39 months after banding and the remainder later. It was inferred that mortality is highest immediately after fledging, that young are absent from the area for at least one breeding period, and that they return to colonies two or three years after fledgling (Gibbs *et al.* 1999). The high post-fledging mortality supports the concept that condition at fledging is an important determinant of post-fledging survival.

It has been found that Australasian Gannet chicks with experienced parents have a faster growth rate than those with inexperienced parents (Gibbs *et al.* 1999). In Port Phillip Bay for the 1994/95 breeding season, chicks of younger adults had a lower mass and their mass increased at a lower rate than average for the first 40 days post-hatching, suggesting that their parents were less efficient providers of food than older, more experienced birds in this period. There was also a tendency for older birds to arrive earlier in the breeding period than younger birds. However, the oldest birds were not those with the heaviest chicks (Gibbs *et al.* 1999). Similarly, for Short-tailed Shearwaters *Puffinus tenuirostris* adults with the most experience had a lower breeding success than those of intermediate age Wooller *et al.* (1990). In the present study, although parental age did not influence the growth rate of Cape Gannet chicks, chicks that hatched earlier in the season grew faster than those raised later. In addition, chicks which fledged successfully had a faster growth rate than those which failed to fledge.

In another study of Australasian Gannets breeding in Port Phillips Bay during 1998/99, Bunce *et al.* (2005) found that age-specific differences in breeding performance and chick growth were only evident in the absence of a major prey species. This suggests that younger or less experienced breeders are not as efficient at rearing young, or that older birds may invest more energy into reproduction when food is limited. Younger parents may be less efficient at capturing prey. Conversely, older parents are presumably better able to adjust foraging effort to maintain constant levels of parental care and hence to buffer the effect of reduced food supply from reproductive or chick growth parameters (Orians 1969; Wunderle 1991).

Fledgling success in the Australasian Gannet is apparently related to site and season, being highly variable and often related to human disturbance (Wingham 1984). To an extent, weather conditions (e.g. wind speed) influence chick growth in Port Phillip Bay, perhaps affecting foraging efficiency by altering distribution, visibility or availability of prey. Ratcliffe *et al.* (1998) suggest that age-specific variations in the timing of breeding are related to differences in breeding experience between younger and experienced parents, whereas changes in breeding success or performance are the result of differences in foraging efficiency.

For the order Pelecaniformes as a whole, it appeared that birds breeding farther away from the tropics, in cooler climates had a more rapid growth rate (Fig. 4); this pattern has been observed within several other orders and families, for example, the Laridae and Sternidae (e.g. Klaassen *et al.* (1989), Drent and Klaassen (1989)). Near the equator the availability of food and the time available to forage in a day are considered to be less dependent on season than at higher latitudes, providing opportunity to extend the breeding period. Our larger sample confirmed the same unexpected positive (but not statistically significant) relationship between growth rate and adult body mass in the Pelecaniformes which was found by Ricklefs and Starck (1998a) (Fig. 3). In addition, we were unable to find a significant relationship between growth rate and mass within any of the five families of the Pelecaniformes for which we had data. The most parsimonious model we found had a growth rate parameter per family, with a common growth rate for the tropicbirds and pelicans, two families for which the ranges of adult body masses do not overlap. The cormorants are the family with the most rapid growth rate, but their distributions occur mostly at high latitutes; in contrast, the frigatebirds have the slowest growth rate and are distributed mostly in the tropics (Chapter 1, Table 2, Fig. 4). Therefore, the relationship between growth rate and latitude for the order Pelecaniformes appears to largely an artefact due to the fact that the species of cormorants for which growth rates were available are absent from the tropics and the frigatebirds are present there. The unusual pattern of growth rates within the order Pelicaniformes is a topic worthy of further investigation.

References

Adams NJ and Walter CB 1991. The occurrence of second clutches after successful breeding by Cape Gannets (*Morus capensis*). Colonial Waterbirds 14: 173-175

Ainley DG, LeResche RE and Sladen WJ 1983. Breeding biology of the Adelie Penguin. University of California Press, Berkley, USA

Barrett RT 1989. The effect of egg harvesting on the growth and breeding success of the Shag *Phalacrocorax aristotelis* and the Kittiwake *Rissa tridactyla* on Bleiksoy, North Norway. Ornis Fennica 66: 115-122

Belopol'skii LO 1957. Ecology of sea colony birds of the Barents Sea. Translated from Russian by the Israel Program for Scientific Translations. Jerusalem, 1961

Berry HH 1976. Physiological and behavioural ecology of the Cape Cormorant *Phalacrocorax capensis*. Madoqua 9: 5-55

Bunce A 2001. Prey consumption of Australian Gannets breeding in Port Phillip Bay, south-east Australia and competition with commercial fisheries. ICES Journal of Marine Science 58: 904-915

Bunce A and Norman FI 2000. Changes in the diet of the Australasian Gannet (*Morus serrator*) in response to the 1998 mortality of pilchards (*Sardinops sagax*). Marine and Freshwater Research 51: 349-353

Bunce A, Ward SJ and Norman FI 2005. Are age-related variations in breeding performance greatest when food availability is limited? Journal of Zoology 266: 163-169

Catry P and Furness RW 1998. The influence of adult age on territory attendance by breeding Great Skuas *Catharacta skua*: an experimental study. Journal of Avian Biology 30: 399-406

Daunt F, Monaghan P, Wanless S, Harris MP and Griffiths R 2001. Sons and daughters: age-specific differences in parental rearing capacities. Functional Ecology 15: 211-216

David JHM, Cury P, Crawford RJM, Randall RM, Underhill LG and Meyer MA 2003. Assessing conservation priorities in the Benguela ecosystem: analysing predation by seals on threatened seabirds. Biological Conservation 114: 289-292

Del Hoyo J, Elliot A and Sargatal J (eds) 1992. Order Pelecaniformes. In: Handbook of the Birds of the World. Volume 1: Ostrich to Ducks. Lynx Edicions, Barcelona. Pp 279-374

DeLaRonde II GG and Greichus YA 1972. Care and behavior of penned Double-crested Cormorants. Auk 89: 644-650

Diamond AW 1973. Notes on the breeding biology and behavior of the Magnificent Frigatebird. Condor 75: 200-209

Diamond AW 1975. Biology and behaviour of frigatebirds, *Fregata* spp. on Aldabra Atoll. Ibis 117: 302-323

Din NA and Eltringham SK 1974. Breeding in the Pink-backed Pelican, *Pelicanus rufescens* in Rwenzori National Park, Uganda, with notes on a colony of Marabu Storks, *Leptoptilus crumeniferus*. Ibis 116: 477-493

Dorward DF 1962. Comparative biology of the White Booby and the Brown Booby *Sula* spp. At Ascension. Ibis 103: 174-220

Drent R and Klassen M 1989. Energetics of avian growth: the causal link with BMR and metabolic scope. In: Bech C and Reinertson RE (eds) Physiology of cold adaptations in birds. New York, Plenum Press. Pp 349-359

Dunn EH 1975. The timing of endothermy in the development of altricial birds. Condor 77: 288-293

Fleet RR 1974. The Red-tailed Tropicbird at Kure Atoll. Ornithological Monographs 16: 1-64

Friesen VL and Anderson DJ 1997. Phylogeny and evolution of the Sulidae (Aves: Pelecaniformes): a test of alternative modes of speciation. Molecular Phylogenetics and Evolution 7: 252-260

Gales R 1984. Comparative breeding ecology of seabirds on the Otago coast. MSc Thesis. University of Otago, Dunedin

Gibbs HM, Norman FI and Ward SJ 1999. Reproductive parameters, chick growth and adult 'age' in Australasian Gannets *Morus serrator* breeding in Port Phillip Bay, Victoria, in 1994–95. Emu 100: 175–185

Jarvis MJF 1970. Interactions between man and the South African Gannet, *Sula capensis*. Ostrich 8: 497-514

Jarvis MJF 1971. Ethology and ecology of the South African Gannet, *Sula capensis*. PhD Thesis, University of Cape Town

Jarvis MJF 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis* (Lichtenstein)). Journal of Animal Ecolology 43: 1-17

Klaassen M, Bech C, Masman D and Slagsvold G 1989. Energy partitioning in Arctic Tern chicks (*Sterna paradisaea*) and possible metabolic adaptations in high latitude chicks. In: Bech C and Reinertson RE (eds) Physiology of cold adaptations in birds. New York, Plenum Press. Pp 339-347

Lequette B and Weimerskirch H 1990. Influence of parental experience on the growth of Wandering Albatross chicks. Condor 92: 726-731

Montevecchi WA, Ricklefs RE, Kirkham IR and Gabaldon D 1984. Growth energetics of nestling Gannets, *Sula bassanus*. Auk 101: 334-341

Navarro RA 1991. Food addition and twinning experiments in the Cape Gannet: effects on breeding success and chick growth and behaviour. Colonial Waterbirds 14: 92-102

Nelson JB 1964. Factors influencing clutch-size and chick growth in the North Atlantic Gannet *Sula bassana*. Ibis 106: 63-77

Nelson JB 1969. The breeding ecology of the Red-footed Booby in the Galapagos. Journal of Animal Ecology 38: 181-198

Nelson JB 1970. The relationship between behaviour and ecology in the Sulidae with reference to other sea birds. Oceanography and Marine Biology: An Annual Review 8: 501-574

Nelson JB 1971. The biology of Abbott's Booby *Sula abbotti*. Ibis 113: 429-467

Nelson JB 1978. African or Cape Gannets. In: The Sulidae Gannets and Boobies. Oxford University Press, Oxford. Pp 231-255

Nelson JB 2002. The gannet family and the order. In: The Atlantic Gannet, 2nd. Fenix Books Ltd, Norfolk. Pp 307-351

Norman FI and Menkhorst PW 1995. Aspects of the breeding and feeding ecology of the Australasian Gannet *Morus serrator* in Port Phillip Bay, Victoria, 1988-92. Emu 95: 23-40

Olver MD 1984. Breeding biology of the Reed Cormorant. Ostrich 55: 133-140

Olver MD and Kuyper MA 1976. Breeding Biology of the White-breasted Cormorant in Natal. Ostrich 49: 25-30

Orians GH 1969. Age and hunting success in the Brown Pelican *Pelecanus occidentalis*. Animal Behaviour 17: 316-319

Payne RW (ed) 2005. The Guide to GenStat Release 8. Part 2: Statistics. VSN International, Oxford, UK

Palmer RS (ed) 1962. Handbook of North American Birds. Vol. 1. Loons through Flamingos. New Haven: Yale University Press

Pearson TH 1968. The feeding biology of sea-birds breeding on the Farne Islands, Northumberland. Journal of Animal Ecology 37: 521-552

Phillips NJ 1987. The breeding biology of White-tailed Tropicbirds, *Phaeton lepturus*, at Cousin Island, Seychelles. Ibis 129: 10-24

Ratcliffe N, Furness RW and Hamer KC 1998. The interactive effects of age and food supply on the breeding ecology of Great Skuas. Journal of Animal Ecology 67: 853-862

Ricklefs RE 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978-983

Ricklefs RE 1968. Patterns of growth in birds. Ibis 110: 419-451

Ricklefs RE 1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115: 177-201

Ricklefs RE 1984. The optimization of growth rate in altricial birds. Ecology 65: 1602-1616

Schreiber RW 1976. Growth and development of nestling Brown Pelicans. Bird-Banding 47: 19-39

Snow BK 1960. The breeding biology of the Shag *Phalacrocorax aristotelis* on the island of Lundy, Bristol Channel. Ibis 102: 554-575

Snow DW and Nelson JB 1984. Evolution and adaptations of Galapagos sea-birds. Biological Journal of the Linnean Society 21: 137-155

Starck JM and Ricklefs R 1998a. Variation, constraint, and phylogeny: comparative analysis of variation in growth. In: Starck JM and Ricklefs R (eds) Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. Oxford: Oxford University Press. Pp 247-265

Starck JM and Ricklefs R 1998b. Avian growth rate data set. In: Starck JM and Ricklefs R (eds) Avian Growth and Development: Evolution within the Altricial-Precocial Spectrum. Oxford: Oxford University Press. Pp 381-423

Stonehouse B 1962. The tropicbirds (genus *Phaethon*) of Ascension Island. Ibis 103: 124-161

Stonehouse B and Stonehouse S 1963. The Frigatebird *Fregata aquila* of Ascension Island. Ibis 103: 409-422

Theil H. 1950a. A rank-invariant method of linear and polynomial regression analysis. I. Proceedings van de Koninklijke Nederlandse Akademie voor Wetenschappen A 53: 386-392

Theil H. 1950b. A rank-invariant method of linear and polynomial regression analysis II. Proceedings van de Koninklijke Nederlandse Akademie voor Wetenschappen A 53: 521-525

Theil H. 1950c. A rank-invariant method of linear and polynomial regression analysis III. Proceedings van de Koninklijke Nederlandse Akademie voor Wetenschappen A 53: 1397-1412

Waghorn EJ 1982. Studies on the Australasian Gannet *Sula bassana serrator* (Gray). Ph.D. Thesis, Victoria University, Wellington, New Zealand

Warheit KI 1990. The Phylogeny of the Sulidae (Aves: Pelecaniformes) and the morphometry of flight-related structures in seabirds: A study of adaptation. Unpubl. Ph.D. Thesis, University of California, Berkeley

Weimerskirch H 1990. The influence of age and experience on breeding performance of the Antarctic Fulmar, *Fulmarus glacialoides*. Journal of Animal Ecology 59: 867-875

Williams AJ and Cooper J 1983. The Crowned Cormorant breeding biology, diet and offspring-reduction strategy. Ostrich 54: 213-219

Wingham EJ 1984. Breeding biology of the Australasian Gannet *Morus serrator* (Gray) at Motu Karamarama, Hauraki Gulf, New Zealand. II. Breeding success and chick growth. Emu 84: 211-224

Wooller RS, Bradley JS, Skira IJ and Serventy DL 1990. The reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology 59: 161-170

Wunderle JM 1991. Age-specific foraging proficiency in birds. In: Power DM (ed) Current Ornithology 8. New York, Plenum Press. Pp 273-325

Table 1: Gompertz growth rates of 24 species of Pelecaniformes.

	Body Mass	K	Locality	Lat		Long		Reference
Phaetontidae (Tropicbirds)								
Red billed tropicbird *Phaeton aethereus*	800.0	0.06	Ascension Island	7.57	S	14.22	W	Stonehouse 1962 (in Ricklefs 1968; 1973)
White-tailed tropicbird *Phaeton lepturus*	392.2	0.074	Cousin Island, Seychelles	4.20	S	55.40	E	Phillips 1987
White-tailed tropicbird *Phaeton lepturus*	400.0	0.065	Ascension Island	7.57	S	14.22	W	Stonehouse 1962 (in Ricklefs 1968; 1973)
Red-tailed tropicbird *Phaeton rubicauda*	800.0	0.062	Kure Atoll, Hawaii	28.25	N	178.10	W	Fleet 1974
Red-tailed tropicbird *Phaeton rubicauda*	900.0	0.065	Christmas Island	1.52	N	157.20	W	Schreiber, unpublished data (in Ricklefs 1973)
Pelecanidae (Pelicans)								
Brown Pelican *Pelecanus occidentalis*	3500.0	0.081	Tarpon Key, Florida	28.09	N	82.45	W	Schreiber 1976
Brown Pelican *Pelecanus occidentalis*	4000.0	0.071	Tampa Bay. Fla	27.45	N	82.35	W	Schreiber, unpublished data (in Ricklefs 1973)
Pink-backed Pelican *Pelecanus rufescens*	5875.0	0.077	Rwenzori National Park, Uganda	0.07	N	30.05	E	Din and Eltringham 1974
Sulidae (Gannets and Boobies)								
North Atlantic Gannet *Morus bassana*	3700.0	0.070	Baccalieu Island, New Foundland	48.07	N	52.47	W	Montevecchi et al. 1984
North Atlantic Gannet *Morus bassana*	3800.0	0.073	**No Locality or position**					Ricklefs et al. 1984

Table 1: Cont.

North Atlantic Gannet *Morus bassana*	4080.0	0.063	England	52.30	N	1.30	W	Nelson 1964 (in Ricklefs 1968, 1973); Ricklefs 1984
North Atlantic Gannet *Morus bassana*	3236.4	0.073	Baccalieu Island, New Foundland	48.07	N	30.05	E	Montevecchi et al. 1984
Abbotts Booby *Papasula abbotti*	1840.0	0.035	Christmas Island, Indian Ocean	10.25	S	105.42	E	Nelson 1971
Masked Booby *Sula dactylatra*	1700.0	0.065	Ascension Island	7.57	S	14.22	W	Dorward 1962 (in Ricklefs 1968, 1973)
Nazca Booby *Sula granti*	2270.0	0.046	Kure Island	28.25	N	178.25	W	Kepler, unpublished data (in Ricklefs 1973)
Brown Booby *Sula leucogaster*	1242.1	0.073	Christmas Island, Indian Ocean	10.25	S	105.42	E	Nelson 1971
Brown Booby *Sula leucogaster*	1400.0	0.06	Ascension Island	7.57	S	14.22	W	Dorward 1962 (in Ricklefs 1968, 1973)
Brown Booby *Sula leucogaster*	1500.0	0.094	Kure Island	28.25	N	178.25	W	Fleet, unpublished data (in Ricklefs 1973)
Australasian Gannet *Morus serrator*	3101.0	0.055	Motu Karamarama, New Zealand	36.33	S	175.05	E	Wingham 1984
Red-footed Booby *Sula sula*	800.0	0.056	Gulf of California	28.00	N	112.00	W	Palmer 1962 (in Ricklefs 1968, 1973)
Red-footed Booby *Sula sula*	900.0	0.039	Galapogos Island	0.30	S	90.30	W	Nelson 1969 (in Ricklefs 1973)
Red-footed Booby *Sula sula*	950.0	0.035	Christmas Island	1.52	N	157.20	W	Schreiber, unpublished data (in Ricklefs 1973)
Cape Gannet *Morus capensis*	3300.0	0.039	Malgas Island	33.03	S	17.55	E	Staverees and Underhill unpublished data for M.Sc Thesis
Cape Gannet *Morus capensis*	3313.0	0.0555	Malgas Island	33.03	S	17.55	E	Navarro 1991

Table 1: Cont.

Cape Gannet *Morus capensis*	3378.0	0.05	Malgas Island	33.03	S	17.55	E	Jarvis 1971
Phalacrocoracidae (Cormorants)								
European Shag *Phalacrocorax aristotelis*	1600.0	0.120	English Channel	50.20	N	1.00	W	Snow 1960 (in Ricklefs 1968, 1973)
European Shag *Phalacrocorax aristotelis*	1650.0	0.129	England	52.30	N	1.30	W	Pearson 1968 (in Ricklefs 1973)
European Shag *Phalacrocorax aristotelis*	1724.2	0.100	Bleiksloy, North Norway	69.17	N	15.53	E	Barrett 1989
Double-crested Cormorant *Phalacrocorax auritus*	1900.0	0.133	Maine	45.15	N	69.15	W	Palmer 1962 (in Ricklefs 1968, 1973)
Double-crested Cormorant *Phalacrocorax auritus*	1900.0	0.141	**No Locality or position**					Dunn 1975
Double-crested Cormorant *Phalacrocorax auritus* (f)	1613.0	0.078	South Dakota State University	44.15	N	100.00	W	DeLaRonde and Greichus 1972
Double-crested Cormorant *Phalacrocorax auritus* (m)	1761.0	0.068	South Dakota State University	44.15	N	100.00	W	DeLaRonde and Greichus 1972
White-breasted Cormorant *Phalacrocorax carbo*	2500.0	0.078	Barents Sea	74.00	N	36.00	E	Belopolskii 1957 (in Recklefs 1973)
White-breasted Cormorant *Phalacrocorax carbo*	2232.6	0.1287	Cedara Agricultural College Dam	29.32	S	30.17	E	Olver and Kuyper 1976
Reed Cormorant *Phalacrocorax africanus*	490.5	0.1434	Cedara Agricultural College Dam	29.32	S	30.17	E	Olver 1984
Crowned Cormorant *Phalacrocorax coronatus*	816.3	0.09821	Dassen Island & Marcus Island	33.14	S	17.33	E	Williams and Cooper 1983
Bank Cormorant *Phalacrocorax neglectus*	1788.0	0.1087	Lamberts Bay	32.09	S	18.31	E	Cooper J unpublished
Cape Cormorant *Phalacrocorax capensis*	1461.9	0.082272	Namibia	22.37	S	14.30	E	Berry 1976

Table 1: Cont.

Fregatidae (Frigatebirds)

Ascension Frigatebird *Fregata aquila*	1250.0	0.027	Ascension Island	7.57	S	14.22	W	Stonehouse and Stonehouse 1963 (in Ricklefs 1968, 1973)
Lesser Frigatebird *Fregata ariel*	854.0	0.027	Aldabra Atoll	9.24	S	46.20	E	Diamond 1975
Magnificent frigatebird *Fregata magnificens* (f)	1455.0	0.029	Barbuda	17.35	N	61.45	W	Diamond 1973
Magnificent frigatebird *Fregata magnificens* (m)	1267.0	0.028	Barbuda	17.35	N	61.45	W	Diamond 1973
Great Frigatebird *Fregata minor*	1300.0	0.035	Christmas Island	1.52	N	157.20	W	Schreiber, unpublished data (in Ricklefs 1973)
Great Frigatebird *Fregata minor*	1447.0	0.0342	Aldabra Atoll	9.24	S	46.20	E	Diamond 1975 (b)

Table 2: Parameters of the most parsimonious model for growth rates of the Pelecaniformes. The regression model is $\log_{10}(k)$= effect for each Family (or group of Families). The estimated values of k in arithmetic space are given in the final column.

Family	Parameter estimate	Standard error	t_{38}	P	k
Phaethontidae (Tropicbirds) and Pelecanidae (Pelicans)	−1.1610	0.0359	−32.34	<0.001	0.0690
Phalacrocoraridae (Cormorants)	+0.1727 [1]	0.0464	3.73	<0.001	0.1027
Frigatebirds	−0.3639 [1]	0.0548	−6.64	<0.001	0.0299
Sulidae (Gannets and boobies)	−0.1015 [1]	0.0440	−2.31	0.027	0.0546

[1] These parameter estimates are offsets in relation to the estimate for the tropicbirds and pelicans, used as the baseline. These offset effects are significantly different from the baseline, and from each other (P<0.05).

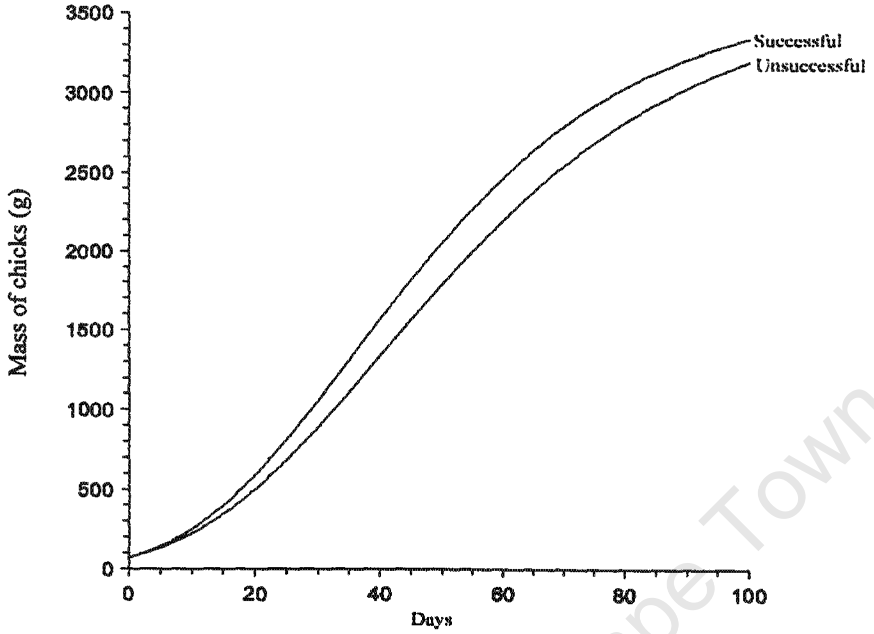

Figure 1: Estimated Gompertz growth rates for successful and unsuccessful Cape Gannet chicks.

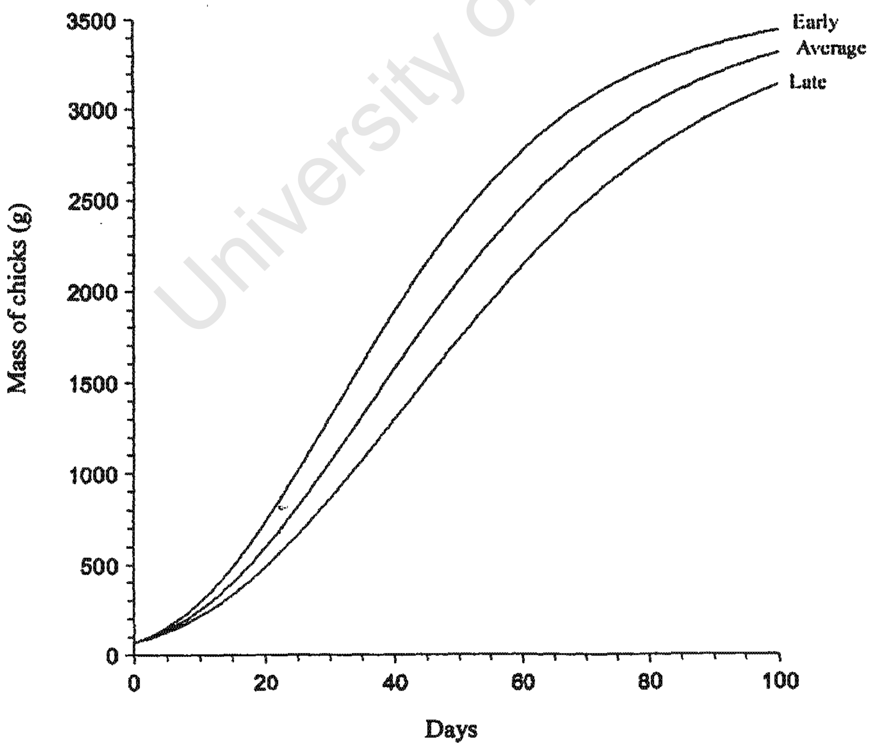

Figure 2: Estimated Gompertz growth rates for successful chicks with different mid-dates.

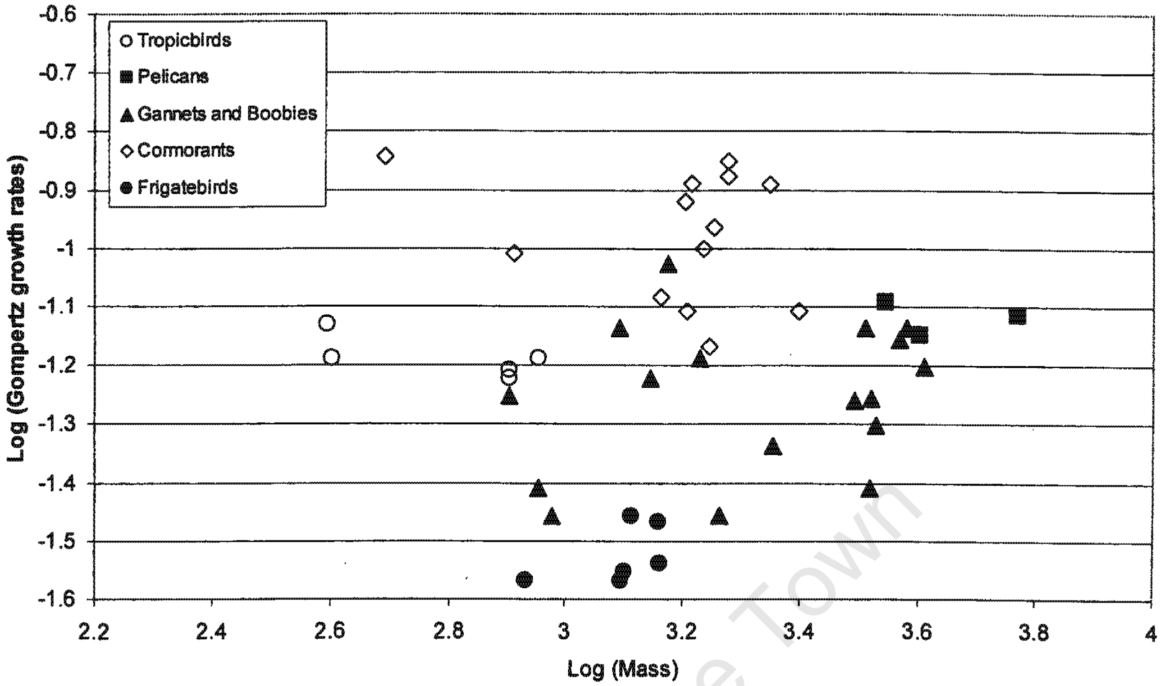

Figure 3: Gompertz growth rates for five of the six families in the order Pelecaniformes in relation to mass.

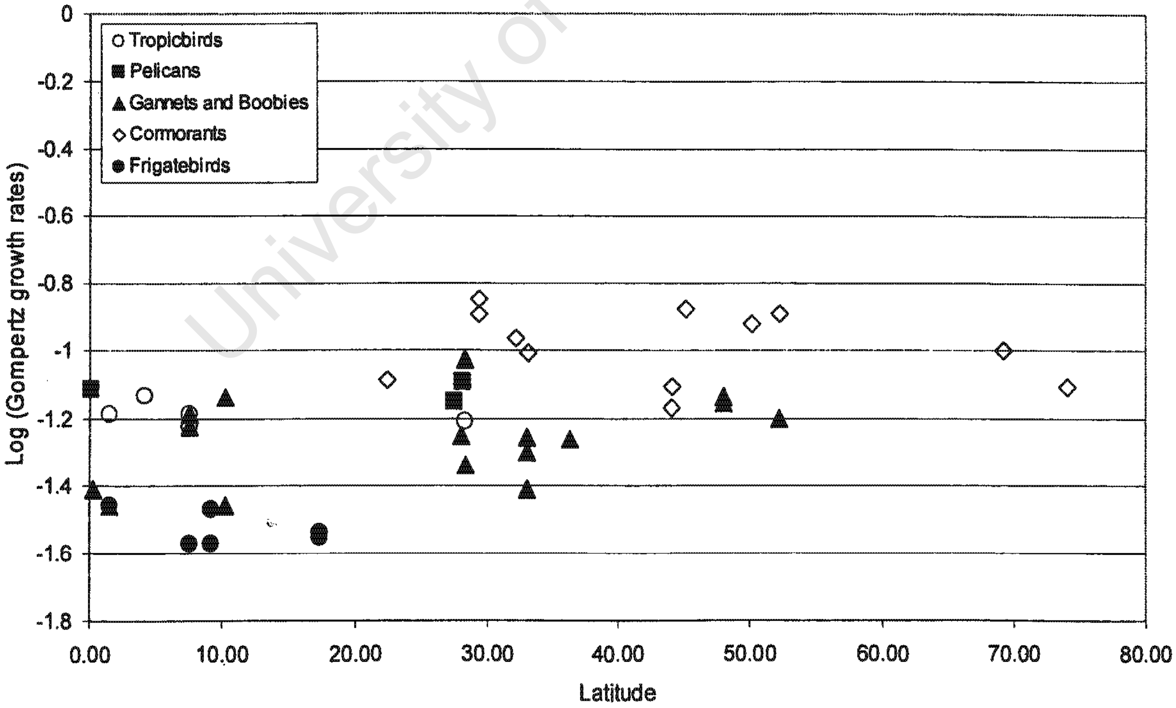

Figure 4: Gompertz growth rates for five of the six families in the order Pelecaniformes in relation to latitude, without regard for north or south.

Appendix 1

Data set for the analysis of breeding success of Cape Gannets *Morus capensis* at Malgas Island, 2002/03

Appendix 1

Data set for the analysis of breeding success of 125 Cape Gannet pairs at Malgas Island in 2002/03

Nest No.	Status	Age	Week	Distance	Height
1	0	12	5	0	10
2	1	22	3	143	19.5
3	1	12	3	150	22
4	1	11	4	141	20.5
5	1	9	5	223	35.5
6	1	12	3	169	30
7	1	6	4	205	23
8	0	13	5	116	28.5
9	0	19	5	255	37.5
10	0	10	5	272	10
11	1	20	5	222	29.5
12	1	15	5	243	11.5
13	1	9	4	263	28
14	0	12	1	114	14
15	0	20	5	132	26
16	1	8	7	101	16
17	0	12	1	216	26
18	1	8	7	152	4
19	0	12	6	41	17
20	0	11	7	173	10
21	0	20	7	90	20
22	0	7	7	116	16
23	0	7	7	120	21
24	0	8	7	0	7
25	0	7	7	118	18
26	0	22	1	84	27
27	0	19	6	87	27
28	0	13	6	71	20
29	0	14	6	68	16
30	0	19	7	0	22
31	1	7	7	0	0
32	1	7	7	101	0
33	0	7	7	169	16
34	0	11	6	109	19
35	1	6	7	110	9
36	0	20	7	86	24
37	0	20	5	117	24
38	0	10	7	43	28
39	0	6	7	122	14
40	1	20	8	300	15
41	0	5	*	220	20
42	1	12	8	130	26
43	1	8	8	385	27

Appendix 1: Data set for Cape Gannet breeding success

44	1	10	8	73	29
45	1	10	1	136	21
46	1	8	6	75	19
47	1	20	4	230	8
48	0	11	6	160	33
49	0	11	8	110	13
50	1	12	7	310	22
51	0	13	5	180	13
52	1	20	5	170	21
53	1	11	7	165	22
54	0	8	8	0	22
55	1	19	1	233	25
56	1	5	8	103	28
57	0	11	7	0	20
58	0	8	8	140	30
59	0	13	8	175	13
60	0	11	8	95	27
61	0	11	8	0	19
62	0	7	9	120	2
63	0	6	9	40	0
64	0	7	8	83	15
65	1	19	2	146	20
66	0	10	9	40	19
67	0	7	7	45	16
68	1	8	9	130	18
69	0	11	4	135	29
70	0	11	9	141	31
71	0	9	9	101	12
72	1	14	9	180	29
73	1	10	8	175	16
74	1	19	8	128	23
75	0	20	7	145	18
76	0	19	6	169	23
77	0	19	9	119	25
78	0	7	8	0	13
79	0	10	9	142	28
80	0	19	7	56	10
81	0	20	7	50	15
82	1	9	8	60	18
83	0	7	6	68	30
85	0	10	9	0	2
86	0	7	8	40	3
87	0	6	7	51	3
88	0	7	8	42	3
89	1	11	2	0	28
90	0	8	12	70	22
91	0	7	10	0	27
92	1	6	9	0	26
93	1	8	9	89	25
94	1	9	11	99	23

95	1	8	5	102	20
96	0	19	6	144	25
97	0	9	12	0	12
98	1	12	6	53	20
99	0	11	10	43	17
100	1	12	5	0	28
101	1	10	5	55	16
102	1	12	10	0	20
103	1	6	10	150	24
104	1	22	3	145	33
105	1	13	5	208	14
106	1	6	12	130	13
107	0	5	12	0	3
108	0	5	10	53	0
109	0	6	8	0	2
110	0	8	*	0	22
111	1	8	7	143	13
112	1	10	7	127	21
113	0	14	8	29	21
114	1	6	8	260	14
115	1	9	9	134	14
116	1	5	7	126	9
117	1	20	6	149	12
118	0	9	5	119	9
119	0	8	7	212	11
120	1	9	10	206	3
121	0	20	6	75	21
122	1	5	6	138	4
123	1	7	7	72	6
124	0	8	*	0	11
125	0	8	*	0	14
126	0	20	7	124	14

Appendix 2

Data set for Cape Gannet *Morus capensis* chick growth at Malgas Island, 2002/03

Appendix 2

Data set for the 84 chicks for which growth rates were obtained

Nest No.	Number of days for which chick was under observation	Gompertz growth rates	Age of parent (years)	Success (1=Fail. 2= Success)	Distance from edge of colony (cm)
2	83.00	0.0428	22	2	143
3	89.00	0.0319	12	2	150
4	70.00	0.0316	11	2	141
5	89.00	0.0441	9	2	223
6	87.00	0.0401	12	2	169
7	89.00	0.0417	6	2	205
9	26.00	0.025	19	1	255
10	26.00	0.0473	10	1	272
11	84.00	0.0347	20	2	222
12	75.00	0.0333	15	2	243
13	92.00	0.0286	9	2	263
15	56.00	0.0467	20	1	132
16	92.00	0.0321	8	2	101
17	12.00	0.0199	12	1	216
18	101.00	0.0223	8	2	152
20	29.00	0.0416	11	1	173
21	56.00	0.0358	20	1	90
22	12.00	0.0386	7	1	116
23	14.00	0.0437	7	1	120
31	84.00	0.0334	7	2	0
32	57.00	0.0445	7	2	101
35	80.00	0.0399	6	2	110
38	27.00	0.0302	10	1	43
40	92.00	0.0477	20	2	300
42	92.00	0.0387	12	2	130
43	38.00	0.0405	8	2	385
44	73.00	0.038	10	2	73
45	71.00	0.0335	10	2	136
46	74.00	0.0364	8	2	75
47	89.00	0.0307	20	2	230
48	27.00	0.0379	11	1	160
49	27.00	0.0345	11	1	110
50	75.00	0.0278	12	2	310
51	54.00	0.0387	13	1	180
52	89.00	0.0493	20	2	170
53	92.00	0.0285	11	2	165
54	62.00	0.031	8	1	0
55	87.00	0.0293	19	2	233
56	92.00	0.0317	5	2	103
58	40.00	0.0296	8	1	140

Appendix 2: Data set for Cape Gannet chick growth rates

61	40.00	0.0285	11	1	0
63	44.00	0.024	6	1	40
65	84.00	0.0355	19	2	146
66	63.00	0.0179	10	1	40
67	28.00	0.0267	7	1	45
68	80.00	0.0318	8	2	130
70	28.00	0.0289	11	1	141
72	92.00	0.03	14	2	180
73	92.00	0.026	10	2	175
74	92.00	0.0329	19	2	128
77	17.00	0.0434	19	1	119
78	28.00	0.0321	7	1	0
80	12.00	0.0503	19	1	56
82	75.00	0.0414	9	2	60
83	12.00	0.031	7	1	68
87	29.00	0.02	6	1	51
89	92.00	0.0346	11	2	0
90	11.00	0.0475	8	1	70
91	28.00	0.0366	7	1	0
92	80.00	0.0268	6	2	0
93	80.00	0.0387	8	2	89
94	63.00	0.0295	9	2	99
95	92.00	0.0309	8	2	102
98	75.00	0.0402	12	2	53
100	92.00	0.0309	12	2	0
101	75.00	0.0369	10	2	55
102	101.00	0.0292	12	2	0
103	80.00	0.04	6	2	150
104	75.00	0.0244	22	2	145
105	80.00	0.0173	13	2	208
106	84.00	0.0294	6	2	130
108	27.00	0.0363	5	1	53
111	63.00	0.0277	8	2	143
112	63.00	0.0429	10	2	127
113	11.00	0.0117	14	1	29
114	84.00	0.0171	6	2	260
115	84.00	0.0478	9	2	134
116	63.00	0.0374	5	2	126
117	63.00	0.0286	20	2	149
118	27.00	0.0398	9	1	119
120	63.00	0.0389	9	2	206
122	63.00	0.0398	5	2	138
123	63.00	0.0334	7	2	72
126	11.00	*0.0010	20	1	124