

The Biology and Conservation of the Damara Tern in Namibia

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**For my parents,
Rod and Sigi Braby,
who have devoted so much to the Damara Tern**

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Abstract

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The globally Near-threatened Damara Tern *Sterna balaenarum* is little known and faces several conservation issues. The aim of this study was to provide a description of the ecology and numbers of the species and discuss conservation management plans that will effectively ensure its survival. Because 98% of the population breeds in Namibia, all data for the study pertaining to the species' breeding biology were collected here.

Overall breeding success (probability of fledging one chick per pair per season) in Namibia was 0.36, although breeding success fluctuated between seasons and colonies. Predation of eggs and chicks was found to be the main factor impacting the breeding success of Damara Terns. Chick growth rate was slower than that of chicks of similar species. Resources allocated to growth favoured initial development of legs, then wings, and lastly, bill.

Immature survival from fledging to breeding was estimated using mark-capture-recapture techniques and found to be 0.59 (95% confidence interval=0.48–0.68). This estimate includes an element of chick mortality. The survival estimate for chicks older than 23 days (fledging age) was 0.84. Age at first breeding was found to be three to four years. Annual adult survival was found to be 0.88 (95% CI=0.73–0.96). Annual dispersal between two adjacent breeding colonies was 0.06 (95% CI=0.03–0.12); these low

dispersal probabilities indicate that protection of breeding sites is an important management approach for the species.

Prey capture success of Damara Terns in relation to six environmental variables was investigated at two colonies in southern Namibia. Prey capture success was greatest at high tide, strong winds and in least turbid water. Overall prey capture success was 30.5%. (SD=3.1%).

Mining activities, in the form of discharging sediment into the sea where breeding Damara Terns fed, were not found to overall significantly impact the breeding success of Damara Terns at one colony in southern Namibia. The effectiveness of conservation measures on breeding Damara Terns was assessed at a colony vulnerable to extensive recreational off-road vehicle disturbances in central Namibia. The study found that Damara Terns benefited from reduced disturbance because the access restrictions prevented entry to the colony by off-road vehicles.

A review of all accessible information of breeding populations in Angola, Namibia and South Africa found that 70 breeding colonies exist globally. The breeding population of Damara Terns was estimated to range up to 5370 breeding individuals. The continued survival of the species requires an urgent updated survey of the breeding population to reassess the species' conservation status. Conservation measures should focus on the protection of important breeding colony sites in Namibia, and also at the extremities of the range in South Africa and Angola. On migration along the west coast of Africa, and during the non-breeding season in West Africa, legal and enforced protection of Damara Terns from human disturbance (such as off-road driving trampling nests, trapping and killing birds, indirect disturbances affecting breeding and feeding habitat) is required.

Layout and contributions

This thesis consists of eight main chapters, most of which are written as papers for submission to a journal. Tables and figures follow the text of each chapter; references for all chapters are combined at the end of the thesis.

I collected all field data in southern Namibia from January 2007 to March 2009, and at various colonies in central Namibia from December 2009 to February 2010, and have contributed to field data collection at most other Damara Tern colonies since 1995. I collated, computerized and validated monitoring data for Damara Terns collected by staff of the Ministry of Environment and Tourism for various breeding areas from 1982–1993 and by Rod and Sigi Braby who monitored the breeding sites called Caution Reef and Horses Graves from 1995–2010. Without their fieldwork various aspects of this thesis would not have been possible; their vital roles will be acknowledged in co-authorships of the forthcoming series of papers. I was responsible for the analysis and writing of each chapter. I discussed some of the fundamental ideas with my supervisors, Les Underhill, Rob Simmons and Jean-Paul Roux. Les Underhill (and to some extent, Jean-Paul Roux and Rob Simmons) advised on methods of data analysis. All three supervisors assisted with the wording of some methods sections and commented on chapter drafts. Jessica Kemper, Rod and Sigi Braby, Res Altwegg, David Wiggins, Teresa Catry, Nicole Braby, Rene Navarro, Mariette Wheeler and Katrin Ludynia commented on some of my chapter drafts. Res Altwegg assisted with the analysis and drafting of Chapter 4 and 5 and will be acknowledged in co-authorship for those papers. Katrin Ludynia conducted the bomb calimetry work for Chapter 6. Maps for all chapters except one were constructed by Holger Kolberg. The maps in Chapter 8 were constructed by Chris Bartholomeau. Photographs not taken by me were credited accordingly.

The planned co-authorships for the papers are outlined below.

Chapter 2: Braby J, Braby RJ, Braby SJ, Simmons RE, Underhill LG, Roux JP and Kolberg H. Clutch size and breeding success of Damara Terns in Namibia.

Chapter 3: Braby J and Underhill LG. Growth patterns, fledging period and feeding rate of Damara Tern chicks in Namibia.

Chapter 4: Braby J, Braby SJ, Braby RJ and Altwegg R. Immature survival and age at first breeding of Damara Terns: conservation from a non-breeding perspective.

Chapter 5: Braby J, Braby SJ, Braby RJ and Altwegg R. Annual survival and dispersal of a seabird adapted to a stable environment: implications for conservation. Submitted to Journal of Ornithology.

Chapter 6: Braby J, Underhill LG and Simmons RE. Prey capture success and chick diet of Damara Terns in southern Namibia..

Chapter 7: Braby J, Underhill LG, Simmons RE and Roux JP. The impacts of diamond mining activities on breeding Damara Terns in southern Namibia.

Chapter 8: Braby J, Braby RJ, Braby N and Simmons RE. 2009. Protecting Damara Terns from recreational disturbance in the Namib Desert increases breeding density and overall success. *Ostrich* 80: 71–75.

Chapter 9: Braby J, Braby RJ, Braby SJ, Simmons RE, Kolberg H, Braine S, Loutit R, Whittington P, Tree T, Underhill LG, Cooper J, Boorman M, Lonser J, Bartlett P, Kemper J and Roux JP. Population estimates, distribution and conservation of breeding Damara Terns.

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Chapter 1

Introduction



INTRODUCTION

Introduction

The study species of my thesis, the Damara Tern *Sterna balaenarum*, is a small desert-breeding seabird found off the coast of south-western Africa that faces several conservation issues. There are many gaps in our knowledge of the species that prevent efficient planning of the protection strategies that could ensure its continued survival. This thesis aims to fill these gaps.

This introductory chapter provides the overall background to the thesis. The Damara Tern is described and compared with the ecology of the six other small terns. Previous research and available literature on the species are summarized. The harsh desert environment of the study area, the Namibian coast, is introduced. Detailed descriptions are given for the study sites where most field work was done and the bulk of the data were collected. Finally, this chapter describes the general layout of each chapter and its aims.

The study species

The small terns

Closely related to gulls (Laridae), terns (Sternidae) are a cosmopolitan, highly homogenous group (Gochfeld and Burger 1996). Compared to gulls, terns are more specialized in terms of nesting habitat, diet and foraging methods, and morphology (Gochfeld and Burger 1996).

Forty-four species are recognized in the tern genera, of which a third are black-capped terns of the genus *Sterna*. The very small *Sterna* terns, once placed in a separate genus *Sternula*, have a mass of less than 70 g (Gochfeld

and Burger 1996, Table 1.1).¹ These are small versions of typical terns. With the exception of the Damara Tern, they have a yellow bill with or without a black tip (Gochfeld and Burger 1996). These seven small terns are the Damara, Fairy *S. nereis*, Little *S. albifrons*, Saunder's *S. saundersi*, Least *S. antillarum*, Yellow-billed *S. superciliaris* and Peruvian *S. lorata* Terns (Table 1.1).

Although all the seven small terns feed on small fish by plunge-diving and contact dipping and primarily rely on aquatic organisms, some, including the Little, Least, Saunder's and Yellow-billed Terns, also feed on insects (Table 1.1). Most of the small terns are of Least Concern within international conservation rankings (IUCN 2009). Those that are in need of protection due to their ranking (e.g., the Damara Tern is listed as Near-Threatened, the Peruvian Tern as Endangered) are placed in these categories because of small and declining populations coupled with poorly known status (Gochfeld and Burger 1996). Least and Little Terns have populations breeding on inland rivers and the Yellow-billed Tern is strictly a riverine species; the others breed along the coastlines of islands and the mainland. The Damara and Peruvian Terns predominantly breed on desert plains on the mainland (e.g., Simmons and Braine 1994 for Damara Tern, Zavalaga *et al.* 2008 for Peruvian Tern, Table 1.1), sometimes up to 11.5 km inland (Damara Tern; Braby *et al.* 2001). All have similar breeding and feeding ecologies (Table 1.1). The Peruvian and Damara Tern are nearly identical in most aspects (Table 1.1). Human disturbance and high predation rates are the most common causes of failure in the breeding success of all the small terns (Table 1.1).

¹ These seven terns are regarded by many as *Sternula* presently (Bridge *et al.* 2005).

The Damara Tern

Morphology of the Damara Tern

One of the smallest members of the family Sternidae, the Damara Tern has an average mass of 52 g (Simmons 2005a, Table 1.1). It is less than one twelfth the mass of the largest tern, the Caspian Tern *Hydroprogne caspia* (average mass 690g, Gochfeld and Burger 1996). Similar in size to the other small terns, it can be distinguished by its black, slightly curved bill and overall grey plumage with a white underside. When in breeding plumage it has a black cap that becomes mottled grey with a white forehead during non-breeding (Gochfeld and Burger 1996). It is a fast-flying tern with a shallowly forked tail and a wing length of 160–176 mm (Simmons 2005a).

World population estimates and migration patterns

Damara Terns breed in widely dispersed colonies in the largely inaccessible Namib Desert. Consequently, attempts at estimating the world population have been particularly difficult (Simmons *et al.* 1998a). Most of these estimates have been based on breeding populations. In 1978, the global population was estimated to consist of 4000 individuals, 2000 of which were found in Namibia (Clinning 1978). In 1991 the world population estimate increased to 7000 individuals when a single flock of *c.* 5000 birds was found in northern Namibia at the end of the breeding season (Braby *et al.* 1992). Random sampling techniques were devised in 1992 to more accurately assess the population of Damara Terns (Simmons 1993), and in 1998 the population was estimated to be 13500 individuals (Simmons *et al.* 1998a). This was a much greater number than previously estimated (Simmons *et al.* 1998a). The increase is more likely to be attributable to an improvement of knowledge, rather than to genuine increases in the population size.

Because most of the breeding terns are found in Namibia, the Damara Tern is often considered an endemic breeder to the Namibian coast (Crawford and Simmons 1997). However, small breeding populations have been found along the western coast of South Africa (McLachlan and Liversidge 1978) and southern Angola (Simmons 2010). A small breeding population was found in Cape Town in 1928 (Vincent 1946) and in 1978 breeding populations were found as far east as the Sundays River estuary in Algoa Bay in the Eastern Cape (Every 1979, Underhill *et al.* 1980). Breeding populations occur in Angola as far north as Baia dos Tigres (Simmons *et al.* 2006, Simmons 2010). Apart from sporadic and short-term breeding surveys, Angolan populations are poorly known (Brooke 1984, Simmons *et al.* 2006, Simmons 2010).

All but a small fraction leave southern Africa for non-breeding grounds on the west African coast (Simmons 2005a). Birds leave their respective breeding grounds at the end of summer, usually around March, and move northwards along the Namibian coast where they coalesce with other post-breeding birds into larger flocks before migration (Simmons 2005a). Groups then migrate northward to overwinter in countries such as coastal Congo, Benin, Gabon and even as far as Nigeria (Bourdillon 1944, Elgood *et al.* 1973, Wallace 1973), Liberia (Borrow and Demey 2001) and Senegal (Brown 1979).

Breeding adaptation

Damara Terns return to the southern and western coast of southern Africa every year to breed. Breeding usually starts in October and ends latest in June (Simmons 2005a). The majority of Damara Terns nest along sections of the Namibian coastline, on habitats ranging from salt pans, gravel plains, rocky outcrops and dune fields (Simmons *et al.* 1998a). The small breeding populations in Angola and South Africa breed predominantly in gravel and sand slacks between dunes (Randall and McLachlan 1982, Watson *et al.* 1997, Vincent 1946).

Damara Terns typically breed in loose aggregations 3–5 km inland (Simmons 2005a), even up to 8 km (Simmons and Braine 1994) and 11.5 km in extreme cases (Braby *et al.* 2001). Breeding between dunes leaves incubating and brooding terns vulnerable to wind and sand exposure. Shifting sand can pose a problem to incubating terns and there is a record of an egg being covered by 10 cm of sand in one night at a breeding site at Elizabeth Bay (Johnson 1979). Nesting habitat availability is not a limiting factor to breeding population numbers (Randall and McLachlan 1982, Simmons *et al.* 1998a).

Individuals pair up after courtship feeding and locate a suitable nest site (Simmons 2005a). Unlike most other terns, the clutch size of the Damara Tern is predominantly a single egg; less than 1% of all monitored nests have contained two eggs (de Villiers and Simmons 1997). Frost and Shaughnessy (1976) suggested that the small clutch size is largely the consequence of selection for maximum growth rate of young, as a result of the exposed nest site and the risk of predation. Eggs are buff-coloured with a variable patterning of brown spots underlain with lighter brown spots (Randall and McLachlan 1982). The single egg is laid in a nest scrape on the ground (Plate 1). Nest scrapes are sometimes decorated with small shells and pebbles when eggs are laid in gravel, and on hard ground when eggs are laid in salt pans (Simmons and Braine 1994). Both sexes share incubation duties (Clinning 1978). Incubation time varies between 18 and 22 days (Simmons 2005a) and is typical of small terns (Table 1.1). Hatching of the single egg takes place over a period of several hours (Clinning 1978), and chicks move away from the nest site within two to three days of hatching (Simmons and Braine 1994). This is probably an evolutionary strategy to avoid predation (Frost and Shaughnessy 1976). During the first 3–4 days chicks are brooded more or less continuously by a parent (Clinning 1978, Simmons and Braine 1994). Newly hatched chicks are pale fawn coloured, with few dark brown and black spots dorsally, and white below (Frost and Shaughnessy 1976,

Clinning 1978). Feet and legs appear yellow, while their bill is black with a prominent egg tooth (Clinning 1978). Once chicks are mobile they can move quite far (up to 2 km within two days, Simmons and Braine 1994). The distance chicks move has been found to be dependent on the level of disturbance (Simmons and Braine 1994). Feathers first emerge on the scapulars and mantle of chicks during the end of the first week (Clinning 1978). The earliest recorded age at which chicks fledge is 20 days (Clinning 1978) and fledged chicks are still considerably smaller at this age than adults, averaging 6 g lighter (Clinning 1978). Chicks are fed until at least two and a half months after fledging (Clinning 1978, Williams and Meyer 1986).

Predation

The chief natural predator of Damara Tern eggs and chicks is the Black-backed Jackal *Canis mesomelas* (Clinning 1978). The Black-backed Jackals found along the coast are generally scavengers, feeding on dead seals and other carcasses along the coastline. This is why the greatest densities of jackals are found near seal colonies. However, they do hunt opportunistically. Other predators include the Pied Crow *Corvus albus* and Kelp Gull *Larus dominicanus* (Simmons and Braine 1994, Braby *et al.* 2001). Because the highest densities of predators occur along the shoreline, inland breeding is hypothesized to be an evolutionary adaptation to avoid predation (Clinning 1978, Simmons and Braine 1994). By nesting in loose aggregations, with considerable distances between nests, breeding terns are expected to be less conspicuous and thus less vulnerable to predation (Clinning 1978). However, they still benefit from the communal “warning system” that breeding colonially affords, because nests are close enough to each other that an incubating bird is aware of the mobbing activities of “neighbours” and flies off to participate in them. Thus when a predator approaches or enters a breeding colony, it is actively mobbed by many of the terns breeding in the colony to

deter or distract them from nests in the area (Randall and McLachlan 1982, pers. obs).

Feeding and diet

Damara Terns feed mainly by plunge-diving for food (Frost and Shaughnessy 1976, Williams and Myer 1986, Simmons and Braine 1994), but they occasionally also float on the sea surface beyond the breakers and pick up minute prey (Braby *et al.* 1992) or swoop and pick up prey on mud-flats (Williams and Meyer 1986). Like most of the small tern species, Damara Terns are essentially inshore feeders and usually frequent sheltered bays, estuaries and lagoons (McLachlan and Liversidge 1970). Their diet consists mainly of small fish and crustaceans (Clinning 1978, Simmons and Braine 1994). Food items collected from adults provisioning their chicks and chick regurgitations included needlefish (Belonidae), mullet sp. (Mugilidae) tiny squid (Loliginidae), and Cape Anchovy *Engraulis encrasicolus* (Simmons and Braine 1994), as well as larval blennies (Blennidae) (Clinning 1978). Lengths of fish delivered to chicks vary in length from 1.5–12.5 cm and vary in mass from 2–30² g, depending on the size of the chick (Clinning 1978). Prey capture success is poorly known, but the few studies that have been conducted (Simmons and Braine 1994, Simmons 2005b) have looked at prey capture success in relation to water turbidity. At a breeding colony in Elizabeth Bay, Simmons (2005b) considered that prey capture success was found to be negatively affected by mining-induced sediment discharge into feeding areas.

Conservation issues

The conservation of Damara Terns poses considerable problems, mainly due to their vulnerability to disturbance during the breeding season (Frost and Shaughnessy 1976, Braby *et al.* 2001, Williams *et al.* 2004). In Namibia and

² 30 g is exceptional, and this prey specimen was fed to a 18-day old chick. No average is given for the mass of fish fed to chicks in Clinning's (1978) study.

South Africa the highest density of breeding terns coincides with the highest density of people in both time and space. This poses serious considerations regarding their protection. The most adverse influences on breeding numbers have been the disruption and displacement of breeding sites through public recreation and coastal development (Frost and Shaughnessy 1976, Braby *et al.* 2001, Williams *et al.* 2004). In some breeding areas, Damara Terns may be threatened by diamond mining (Brooke 1984, Simmons 2005b). In their migratory countries, Damara Terns are trapped and eaten or sold for food (Braby 2010, Annex 1).

Recreational disturbance mainly refers to off-road driving in breeding areas. Off-road vehicles have been considered a threat to breeding waders since 1977 (Summers and Cooper 1977), and Damara Terns have been directly impacted by traffic along their breeding grounds (Plate 2). Off-road driving can directly cause egg and chick losses by trampling, or could cause disturbance and stress to breeding birds and their chicks. The South African Minister of Environmental Affairs and Tourism banned the use of ORVs from South Africa's beaches with effect from 21 December 2001 (Williams *et al.* 2004). In the first year after the ban all 11 pairs at a colony of breeding Damara Terns at Struisbay, Western Cape, South Africa, raised a chick to fledging before the end of January, allowing juveniles more time to prepare for northward migration to the non-breeding grounds in West Africa. This was in contrast to before the ban when most nests failed and adults had to relay, prolonging the breeding season to March (Williams *et al.* 2004).

Since banning of vehicles on the beaches of South Africa has been enacted, off-road vehicle driving along the central Namibian coast has increased (R.J. Braby pers. comm.). The Damara Tern breeding grounds, in the past, have been adversely affected by recreational off-road driving, but after conservation measures were taken in the form of fences restricting off-road

vehicles from one breeding ground, breeding productivity and breeding numbers increased (Braby *et al.* 2001). More recently however, these conservation measures are under pressure as enforcement along the central Namibian coast is lacking and off-road vehicle drivers have been cutting fences and traversing breeding grounds anyway, despite the restrictions (R.J. Braby pers. comm.).

Coastal development has caused the extinctions of various colonies, both in South Africa (Vincent 1946), and in Namibia (Frost and Shaugnessy 1976, Clinning 1978, R.J. Braby unpubl. data), and continues to threaten important breeding colonies between the two main coastal towns of Namibia, Swakopmund and Walvis Bay (R.J. Braby pers. comm.).

Diamond mining occurs mainly on the southern coastline of Namibia and the north-western coastline of South Africa, although small-scale mining and prospecting occurs along the coastline of northern Namibia as well. Profitable mineral deposits here could result in large-scale mining (Clinning 1978). Although these areas are protected and largely isolated through public access restrictions, breeding terns have been negatively affected by diamond mining in the past, mainly by sediment discharge into their feeding grounds (Simmons 2005b). Diamond mining could of course directly negatively affect breeding grounds if mining (excavations, dune-stripping, developments etc) were to be conducted on breeding grounds.

The Damara Tern is currently listed as Near-Threatened owing to its moderately small population (which is currently estimated at 13500 individuals, Simmons *et al.* 1998a, IUCN 2009). If the population is found to be undergoing a decline, the species may qualify for uplisting to a higher threat category. In most migratory countries protection laws for the Damara Tern either do not exist, or are weakly enforced. Very little is known of the

breeding population in Angola. Angola is signatory to the Convention on Migratory Species (CMS entered into force in Bonn in 1983), which legally binds Angola to create laws protecting species like the Damara Tern. However, these national laws currently do not exist. In the Iona National Park, where breeding terns are found, enforcement that should secure their protection, is weak to non-existent (Simmons 2010, R.E. Simmons pers. comm.). In Namibia, the Damara Tern is Near-Threatened (Simmons and Brown 2008) and is considered a “Specially Protected” species under the draft Protected Areas and Wildlife Management Bill. In South Africa it is Endangered because of low and decreasing numbers (Barnes 2000).

The study area

The Benguela Upwelling System

The Benguela Current is the eastern boundary current of the South Atlantic (Shannon 1989, Peterson and Stramma 1991, Wedepohl *et al.* 2000). It begins as a northward flow off the Cape of Good Hope and moves equator-ward along the south-west African coast until around 24–30°S (Gyory *et al.* 2009). The southern part of the Benguela system is bounded to the south by the warm retroflection zone of the Agulhas Current and is different meteorologically from most other current systems (Shannon 1989). However, the oceanography of the northern Benguela has much in common with its equivalent in the South Pacific, the Humboldt Current (Shannon 1989). Crawford *et al.* (2006) compared and contrasted the seabird assemblages between these two upwelling systems.

The typical sea surface temperature (SST) of the Benguela is 13–15°C, but this varies both seasonally and spatially (Shannon 1989). Off the coast of Namibia there is a definite seasonal temperature cycle (Shannon 1989). Just as there are seasonal changes so are there changes from year to year

(Shannon 1989). A noteworthy phenomenon that can be encountered in the Benguela system is the Benguela Niño (Gyory *et al.* 2009). Benguela Niños can be caused by anomalous atmospheric conditions in the western tropical Atlantic (Boyer *et al.* 2000). Every year there is a south-ward intrusion of warm Angolan water into the northern Benguela, but during a Benguela Niño the Angola-Benguela front is displaced south, causing the movement of warm, highly saline water as far as 25°S (Shannon *et al.* 1986, Boyer *et al.* 2000). During Benguela Niños heavy rains may fall over adjacent desert or escarpment regions (Shannon 1989).

Phytoplankton, the basis of the marine food chain, needs light to grow. This is why, in the sea, most biological productivity takes place in the upper layers (Shannon 1989). The important physical process on the shelf of the Benguela is coastal, wind-induced upwelling. This upwelling brings deep, cold, nutrient-rich water to the surface where there is abundant light. Once oxygenated at the surface, this in turn creates the conditions for the growth of phytoplankton. Because the prevailing wind along the western seaboard of southern Africa is southerly or alongshore, conditions are favourable for upwelling along the entire coast as far as southern Angola (Shannon 1989). However, the upwelling rate is not uniform along the entire coast as the upwelling-favourable winds are stronger in some areas (Shannon 1989). Other factors that influence the rate of upwelling are the effects of topography on wind direction, and the depth and width of the continental shelf (Shannon 1989). The biggest upwelling cell occurs near Lüderitz where the region is windier, colder and more turbulent than elsewhere in the Benguela (Shannon 1989). Preferred habitats for a number of species tend to exist downstream of this upwelling cell. Called “delayed blooming”, the plants “bloom”, consume nutrients, die and release nutrients (Shannon 1989, Simmons and Cordes 2000). This process is speeded up in warm, oxygenated water and occurs rapidly in semi-closed regions such as near Walvis Bay

(Shannon 1989). The high productivity results in large populations of fish and other marine life which creates the ideal conditions for breeding seabirds like the Damara Tern.

The Namibian coast

The coast of Namibia extends 1570 km from the Cunene River (17°14'S, 11°45'E, Angolan border) in the north to the Orange River (28°36'S, 16°27'E, South African border) in the south (Figure 1.1). The Cunene and Orange Rivers, which form the northern and southern boundaries of Namibia, are the only perennial rivers along the coast.

The coast is relatively straight and lacks indentation apart from two large bays, Walvis Bay and Lüderitz Bay, and a number of smaller inlets (Molloy 2003). The coastline falls within the ancient Namib Desert, which pre-dates the two-million-year-old Benguela Current by tens of millions of years. It is thought to be one of the oldest deserts in the world (65–70 million, Molloy 2003). Rainfall is very low at 15–20 mm per year and only during periods of good inland rains do ephemeral rivers reach the sea (Molloy 2003). Fog is a common occurrence on the coast. The fog belt can extend 20–50 km inland and is essential to the survival of plants and animals along the coastal belt (Molloy 2003).

The five coastal towns, Hentiesbay (4 000 inhabitants), Swakopmund (28 000), Walvis Bay (45 000), Lüderitz (16 000) and Oranjemund (10 000), account for the entire human coastal population. Together, these towns form a small proportion (*c* 5%) of the total national population of Namibia of 2.1 million people (Molloy 2003, World Bank 2009). Because most of the coastline is a desert, and falls into one or other of the restricted conservation or mining areas, there is virtually no rural way of life on the coast (Molloy 2003).

The area extending from the Cunene River to the Ugab River is the Skeleton Coast Park (Figure 1.1). The area between the Ugab River and south of Walvis Bay is the recently proclaimed Dorob National Park, which is heavily used during holiday periods (Figure 1.1). From south of Walvis Bay to north of Hottentots Bay is the Namib-Naukluft Park (Figure 1.1). Finally, from north of Hottentots Bay to the Orange River is the restricted diamond area, under the control of Namdeb; the area was proclaimed the Sperrgebiet National Park in 2009 (Figure 1.1). The coastal waters of Namibia and its islands were given protection in 2010 by the declaration of the Namibian Islands Marine Protected Area (NIMPA) (Ludynia and Kemper 2010). The provisionally-named Namib-Skeleton Coast National Park is a mega-park which includes all parks (Skeleton Coast, Dorob National Park, Namib-Naukluft Park, Sperrgebiet National Park and the NIMPA) (Tarr 2009). It will be the eighth largest protected area in the world. It will form transfrontier parks with Iona National Park in southern Angola and the Ai-Ais/Richtersveld Transfrontier Conservation Area (Tarr 2009).

The Skeleton Coast Park (SCP, northern Namibia)

The coastline of the Skeleton Coast Park is approximately 495 km long, extending from the Cunene River (17°14S, 11°45E) on the Angolan border to the Ugab River (21°11S, 13°37E) in the south (Figures 1.1 and 1.2). Breeding habitat consists of gravel and rocky plains of various colours (e.g. white, pink, purple and black), salt pans and dunes. Annual rainfall averages less than 20 mm and fog is common (van der Merwe 1983). Vegetation is scarce but *Salsola* sp. hummocks occur as well as scattered plants of *Arthrerea leubnitziae* and *Zygophyllum stapfii*. There are various small and large colonies of breeding terns in the Skeleton Coast Park, but only a few records and limited data were collected here from a variety of colonies and single

pairs along the coastline. However, three colonies were of significance, namely Möwe Bay Airstrip (S19°22 E12°43), Huab (S20°50 E13°26) and Ogden Rocks (S24°22 E24°42, Figure 1.2). All of these areas consist of gravel plains.

The Dorob National Park (DNP, central Namibia)

Ugab River to Swakopmund

The coastal area extending south of the Ugab River to Swakopmund forms part of the Dorob National Park and consists of gravel plains sloping upwards from a narrow belt of 1–2 m high *Salsola* sp. hummocks immediately inland of the beach. The only permanent vegetation on these plains is scattered plants of *Arthroerua leubnitziae* and *Zygophyllum stapfii* (Giess 1968). In some areas there is considerable growth of lichens of two species, whilst in other areas barren dry salt pans occur. Data were sporadically collected from various Damara Tern breeding colonies in this area. However, two colonies were of significance, namely Durissa Bay Pans (S21°15 E13°41), which consists mainly of salt pans, and White Stones (S21°39 E13°58), which consists of sparsely vegetated gravel plains (Figure 1.3).

Swakopmund to Walvis Bay

Two important tern colonies are described for this area (Figure 1.3, Plate 3).

(a) *Horses Graves*

The Horses Graves colony covers 2.5 km² and occurs in the hyper-arid Namib Desert with a rainfall of less than 15 mm per year (Günster 1995, Mendelsohn *et al.* 2003). It is located 4 km south of Swakopmund (S22°42 E14°33, Figure 4.1 in Chapter 4, Plate 3). The study area is 3.7 km NNE of

the Caution Reef colony and comprises a series of barchan, linear, and crescent dunes separated by gravel plains in which the terns breed (Braby *et al.* 2001). Gravel plains are comprised of approximately 3 mm diameter, grey-coloured substrate, with little wind-blown material. By contrast the dunes have a much smaller sand particle diameter and sand transport during prevailing south-westerly winds could be high. The area is situated just south of a disused railway line, 3 km east of the sea, and runs parallel to the coast. The areas used by the breeding terns are devoid of vegetation.

(b) *Caution Reef*

Caution Reef, more commonly known as Patrysberg, is situated 8 km from Swakopmund (22°44S, 14°32E, Figure 4.1 in Chapter 4, Plate 3). The main road to Walvis Bay cuts across the breeding area. The area west of the road extends 2 km north to south and 1 km east of the sea. The area east of the road extends up to 600 m towards the high dunes (Braby *et al.* 2001). The habitat at Caution Reef consists mainly of open and sparsely vegetated sandy plains with a raised gravel ridge through the centre (Braby *et al.* 2001).

The Namib-Naukluft Park

This area consists mainly of vast expanses of dunes and dune fields. The area is protected and virtually inaccessible, although tourism concessions are given to tour operators. Few data were collected at colonies in this area, of which the main colony is Meob Bay (S24°22 E24°42, Figure 1.4). Meob Bay consists of extensive gravel plains backed by vast expanses of sand dunes.

The Sperrgebiet National Park (SNP)

The “Sperrgebiet”, directly translated from German as “restricted area”, is owned by Namdeb Diamond Corporation (Pty) Ltd and was proclaimed the

Sperrgebiet National Park in 2009 (Tarr 2009). It extends from the southern border of Namibia to north of Hottentots Bay (26°00'S, 15°58'E, Figures 1.1 and 1.5). Along this coastline, four main colonies exist: Hottentots Bay (26°14'S, 14°59'E), Grosse Bucht (26°43'S, 15°40'E), Elizabeth Bay (26°55'S, 15°14'E) and Marmora Pan (27°45'S, 15°34'E). Data were collected from these four colonies.

(a) *Hottentots Bay*

The breeding colony at Hottentots Bay is found on Anigab Pan (26°14'S, 14°59'E, Figure 7.1 in Chapter 7) which extends 20 km north to south and up to 5 km at its widest part. It is enveloped by rocky outcrops and mountains on the west side, dunes on the east side, vegetated dunes on the south side, and Hottentots Bay on the north side. The pan comprises pure salt, brown salt crusts and extinct lagoon molluscan fauna. The large areas of molluscan shells that are found on the salt flats today may date from the mid-Holocene marine transgression and the development of a short-lived tidal marsh (Kinahan and Kinahan 2002); subsequent lowering of the mean sea level has placed the lagoon beyond the reach of the normal tidal range and thus the entire pan is dry for most of the year. During spring tide some areas may become flooded; these areas are linked to the sea through channels between the western mountains and rocky outcrops (Figure 7.1 in Chapter 7).

(b) *Grosse Bucht*

Grosse Bucht is a bay found within the recreational area along the Lüderitz Peninsula and is about 2.5 km wide (Figure 7.1 in Chapter 7). The Lüderitz Peninsula is accessible to the public. This bay is surrounded by rocky outcrops on either side and is hugged by *Salsola* sp. hummocks. A salt pan can be found directly north and parallel to the bay at a distance of 800 m from the sea. Breeding Damara Terns are found within this salt pan (26°43'S, 15°05'E). The salt pan comprises pure salt, brown salt crusts and areas of

loose gravel and sparse vegetation and is approximately 500 m wide and 500 m long.

(c) *Elizabeth Bay*

Elizabeth Bay is about 4 km wide, with a rocky promontory known as Elizabeth Point forming the western arm, and rocky shores backed by sand dunes of the southern Namibian desert forming the eastern shoreline (Figure 7.1 in Chapter 7, Pulfrich *et al.* 2003). Possession Island, 8.5 km to the south of Elizabeth Point, offers the bay limited protection from the prevailing westerly to south-westerly Atlantic swells. Directly to the north-east of Elizabeth Bay is a channel comprised of salt pans and gravel plains, most of which have been heavily disturbed by diamond mining operations. To the south-east of Elizabeth Bay is an extensive area of sand dunes which reach the shoreline on the eastern side of the bay.

(d) *Marmora Pan*

Marmora Pan is situated 140 km south of Lüderitz (Figure 7.1 in Chapter 7). It is 10 km north of a mining site that has stopped production and was rehabilitated in 2007. The pan is 7 km long and 5 km wide and is partly covered in sand dunes. The pan is made up of soft brown salt crusts and sand dunes in the south, hard brown salt crusts in the north. There is no pure salt on the pan and prevailing southerly winds regularly blow dune sand over the surface.

The structure and overview of this thesis

Because the Damara Tern has a restricted distribution and faces several anthropogenic threats, an increased and updated knowledge base of the species is critical to helping us construct necessary conservation strategies. This thesis presents information on the ecology and numbers of the Damara

Tern, most of which was previously unknown. It also outlines the conservation implications of these findings, and suggests ways forward. It comprises four sections and 10 chapters. **Chapter 1** reviews current knowledge of the species, and provides an overview and introduction to the thesis.

Section I investigates and discusses the breeding biology of the Damara Tern and consists of two chapters:

Chapter 2 updates previous information regarding clutch size, egg measurements, incubation periods using larger sample sizes, describes the breeding success, and the causes of nest losses of breeding Damara Terns in Namibia.

Chapter 3 discusses growth, fledging and feeding rate of Damara Tern chicks in Namibia.

Section II of this thesis investigates the life-history parameters of the Damara Tern at two colonies in Namibia and puts this within a conservation perspective; it consists of two chapters:

Chapter 4 investigates age at first breeding and immature survival of Damara Terns by using multi-state capture-mark-recapture models. It uses data of ringed nestling and adult individuals at two breeding colonies in central Namibia, and discusses the implications of these from a conservation perspective.

Chapter 5 discusses the dispersal and adult survival probabilities of Damara Terns breeding at two colonies in central Namibia. Multi-state capture-mark-recapture models were used to estimate annual adult survival at the two colonies, and the annual movement probabilities between them, while

accounting for the recapture probabilities at both colonies. The findings of the study are put in a conservation context.

Section III investigates the feeding ecology and chick diet of the Damara Tern and consists of one chapter:

Chapter 6 investigates the prey capture success and the composition of chick diet of the Damara Tern in southern Namibia and addresses the following research question:

- Does prey capture success in the Damara Tern differ according to environmental condition and habitat?

It aims to address this question by measuring the prey capture success of the Damara Tern under the following environmental conditions: tidal phase, wind strength, water clarity, cloud cover, water depth and location.

Section IV of this thesis investigates anthropogenic disturbances and conservation of the Damara Tern using two case studies and then discusses the population and overall conservation of the species; it consists of three chapters:

Chapter 7 investigates the impacts of diamond mining on the prey capture success and breeding productivity of the Damara Tern in southern Namibia.

It specifically aims to address the following question:

- Does increasing sediment into a bay where Damara Terns feed affect Damara Tern prey capture and breeding success?

This chapter addresses this question by comparing the prey capture success, chick condition, breeding success and colony size of Damara Terns at the mined colony with the nearest un-mined colonies.

Chapter 8 investigates the protection of a Damara Tern breeding colony from off-road vehicles and addresses the following question:

- Does restricting access for off-road vehicles from Damara Tern breeding areas increase breeding productivity of Damara Terns?

This chapter addresses this question by investigating the breeding productivity of the Damara Tern before and after restrictions to the breeding areas.

Chapter 9 collates published and unpublished data on breeding colonies of Damara Terns in their breeding range, estimates the global breeding population, discusses the threats and conservation and recommends additional survey and conservation measures for the future.

Chapter 10 concludes the thesis by providing an overview and synthesis of findings, and makes recommendations for future research and conservation interventions.

Table 1.1: A comparison of the ecology of the seven small terns of the genus *Sterna*.

	Damara Tern <i>S. balaenarum</i>	Peruvian Tern <i>S. lorata</i>	Little Tern <i>S. albifrons</i>	Least Tern <i>S. antillarum</i>	Saunders Tern <i>S. saundersi</i>	Fairy Tern <i>S. nereis</i>	Yellow-billed Tern <i>S. superciliaris</i>
Food and Feeding	Small Fish (e.g. mullet, anchovy), plunge-diving ^{1, 2}	Small fish (e.g. anchovy), krill, plunge-diving ¹	Small fish, crustaceans, annelids and mollusks, plunge-diving ¹	Small fish, shrimps, marine worms, flying ants, plunge-diving ¹	Small fish, crustaceans, mollusks, insects ¹	Small fish, gastropods, crustaceans ¹	Small fish, shrimps, insects ¹
Conservation Status	Near- Threatened ³	Endangered ³	Least Concern ³	Least Concern ³	Least Concern ³	Vulnerable ³	Least Concern ³
Breeding Range	Southern Africa, near-endemic to Namibia ^{1, 2}	Ecuador to Chile ¹	West Africa, Europe, India, Sri Lanka ¹	Florida, Texas, West Indies, California, Carriibbean ¹	Karachis and Sri Lanka, Red Sea, Gulf of Guinea, East African coast, India, Seychelles, Maldives, Madagascar ¹	South Australia, New Zealand, Tazmania ¹	Brazil, Argentina, Uruguay, Peru, Surinam ¹
Non-breeding Range	North west coast of Africa e.g. Gabon, Cameroon, Nigeria ^{1, 2}	Unknown ¹	East Africa, West Africa ¹	West-Mexico, Central America, Carriibbean, South America, Brazil ¹	Either resident or moves south or east of breeding range ¹	North Australian coast ¹	–
Breeding Period	Oct–Feb, latest June ^{1, 2}	Oct–Jan ¹	April–June ¹	April–Aug ¹	June–Aug ¹	Sept–March ¹	Nov–July ¹
Adult Mass (g)	46-55 ¹ , 52 ²	45 ⁴	47–63 ¹	39–52 ¹	40–45 ¹	57 ¹	40–57 ¹

	Damara Tern <i>S. balaenarum</i>	Peruvian Tern <i>S. lorata</i>	Little Tern <i>S. albifrons</i>	Least Tern <i>S. antillarum</i>	Saunders Tern <i>S. saundersi</i>	Fairy Tern <i>S. nereis</i>	Yellow-billed Tern <i>S. superciliaris</i>
Mean Clutch Size	1 ^{1,2}	2 ¹	2–3 ¹	2–3 ¹	2 ¹	2–3 ¹	2–3 ¹
Mean Egg Size (mm)	32.2 × 23.8 ²	30.9 × 23.5 ⁵	32.2 × 24.1 ⁶	31.7 × 22.25 ⁷	35.5 × 25.3 ⁷	35.5 × 25.3 ⁶	30.5 × 23.6 ⁸
Hatching Mass (g)	6.5 ²	6–7 ¹	6.5 ¹	6.5 ¹	–	–	–
Nesting Habitat	Gravel plains betw dunes, salt pans, sand and gravel plains, up to 11.5 km inland ¹	Gravel plains, broad sandy beaches, sometimes several km inland ¹	Barren/ sparsely veg sandy, shell, rocky beaches, along river banks, marshes, coral islands ¹	Vegetated sandy beaches, gravel bars, mudflats, parking lots, roof tops ¹	Coastlines, estuaries, lagoons, mudflats, high above high tide line, rarely inland ¹	Coral or sandy beaches/islands, extensive coastal dunes ¹	Riverine sandbars ¹
Nest type	Shallow scrape with shells, pebbles ¹	Shallow scrape ¹	Scrape in sand or shell ¹	Scrape in bare sand, rock, shell ¹	Scrape in sand or shell, or animal footprint ¹	Scrape in sand or shell ¹	Shallow scrape ¹
Incubation period (days)	18–23 ^{1,2}	22–23 ¹	21–24 ¹	19–24 ¹	c. 20 ⁷	20–25 ¹	–
Fledging period (days)	20–22 ¹ , 20 ²	24–29 ⁵	20–24 ¹	17–21 ¹	c. 20 ⁶	22–23 ¹	–
Productivity (young/pair)	0.16–0.35 ¹ , 0.53 ²	–	0.03–0.4 ⁹	0.2–1.5 ¹	–	0.7 ¹	1.04 ¹

	Damara Tern <i>S. balaenarum</i>	Peruvian Tern <i>S. lorata</i>	Little Tern <i>S. albifrons</i>	Least Tern <i>S. antillarum</i>	Saunders Tern <i>S. saundersi</i>	Fairy Tern <i>S. nereis</i>	Yellow-billed Tern <i>S. superciliaris</i>
Sources of nest failure	Black-backed Jackal, gulls, kestrels, human disturbance, flooding ^{1,2}	Peregrine Falcon, Grey Fox, Skunk ¹	Gulls, corvids, <i>Sterna hirundo</i> , human disturbance ¹	Flooding, human disturbance ¹	Gulls, human disturbance, flooding ¹	Rats, cats, human disturbance ¹	Flooding and human disturbance ¹
Fledging dependency	2–5 months ¹ , 10 weeks ²	–	2–3 months ¹	–	–	50 days ¹	–

¹ Gochfeld and Burger 1996, ² Simmons 2005a, ³ IUCN 2009, ⁴ C. Guerra unpubl. data ⁵ Zavalaga *et al.* 2008, ⁶ Higgins and Davies 1996, ⁷ Urban *et al.* 1986, ⁸ Escalante 1970, ⁹ Cramp 1985

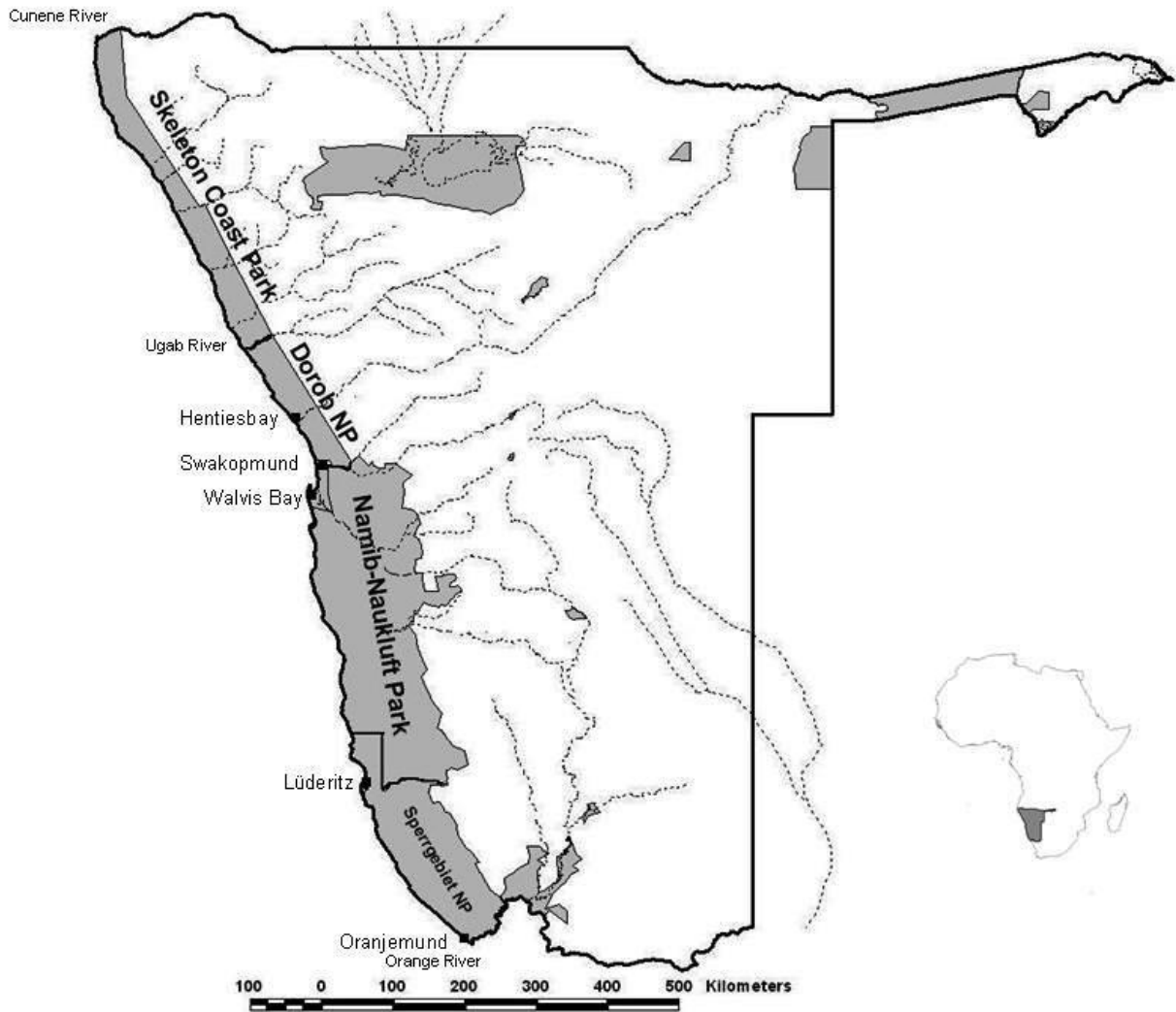


Figure 1.1: Map of Namibia, showing the division of the study area of the thesis (see text) into the Skeleton Coast Park, Dorob National Park, Namib-Naukluft Park, and Sperrgebiet National Park. All areas shaded in grey represent protected areas. Dotted lines represent ephemeral rivers. All major coastal towns are labeled. The Cunene River forms the political border between Namibia and Angola and the Orange River in the south forms the political border between Namibia and South Africa.

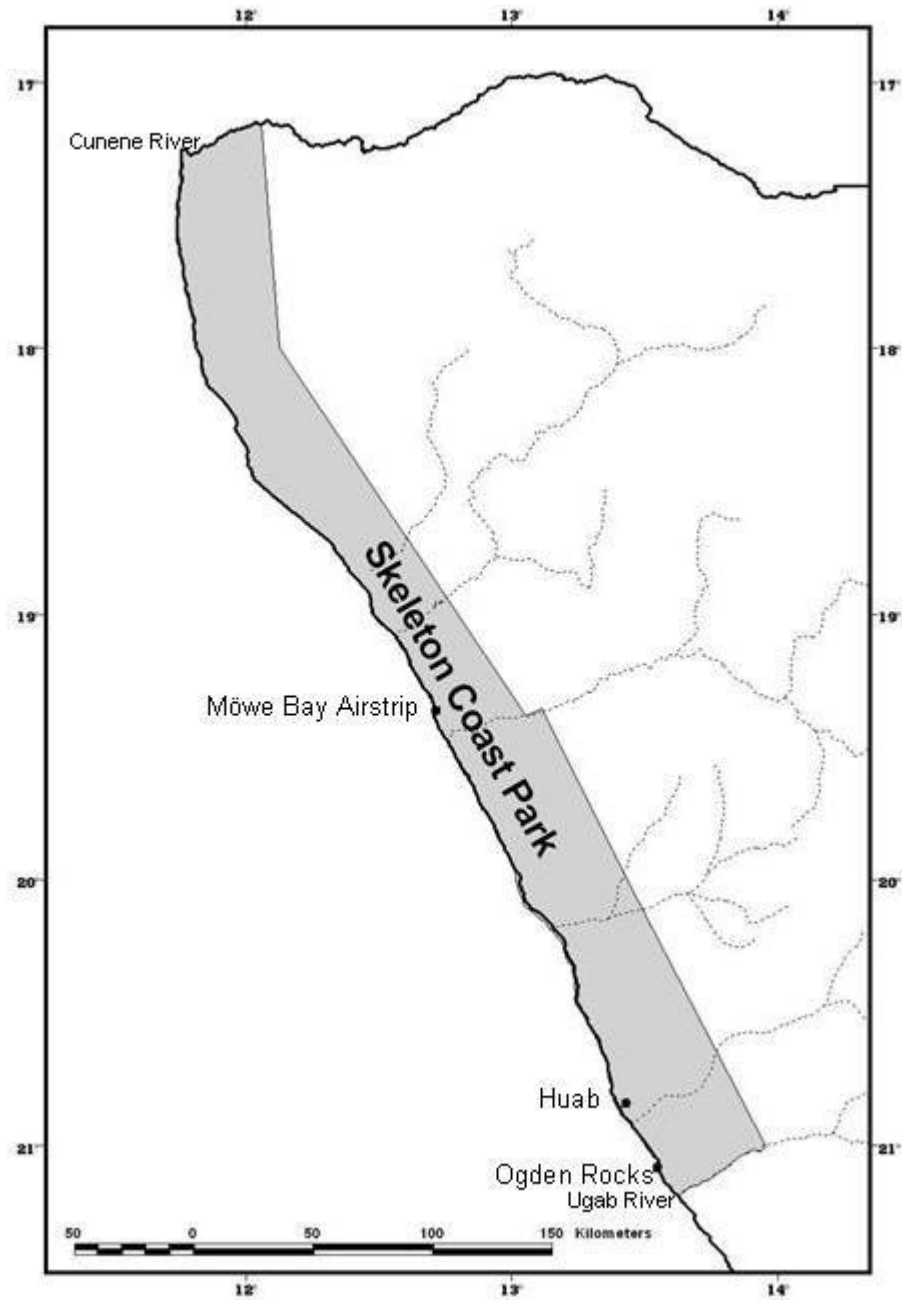


Figure 1.2: Map of the Skeleton Coast Park in northern Namibia, showing the location of the three Damara Tern breeding colonies important to this study (see text).

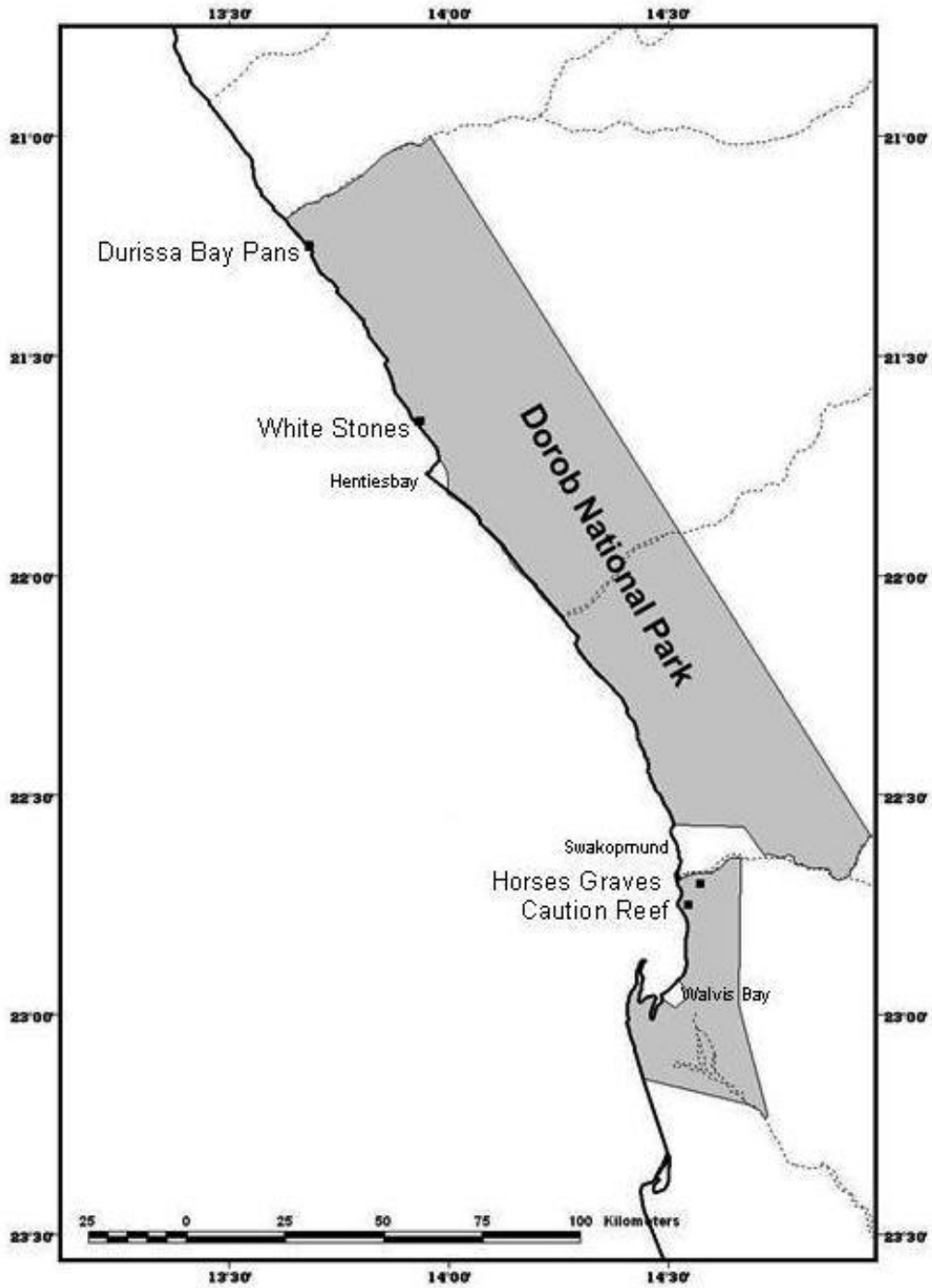


Figure 1.3: Map of the Dorob National Park in central Namibia, showing the locations of the four Damara Tern breeding colonies important to this study (see text). The location of the towns, Hentiesbay, Swakopmund and Walvis Bay are also shown.

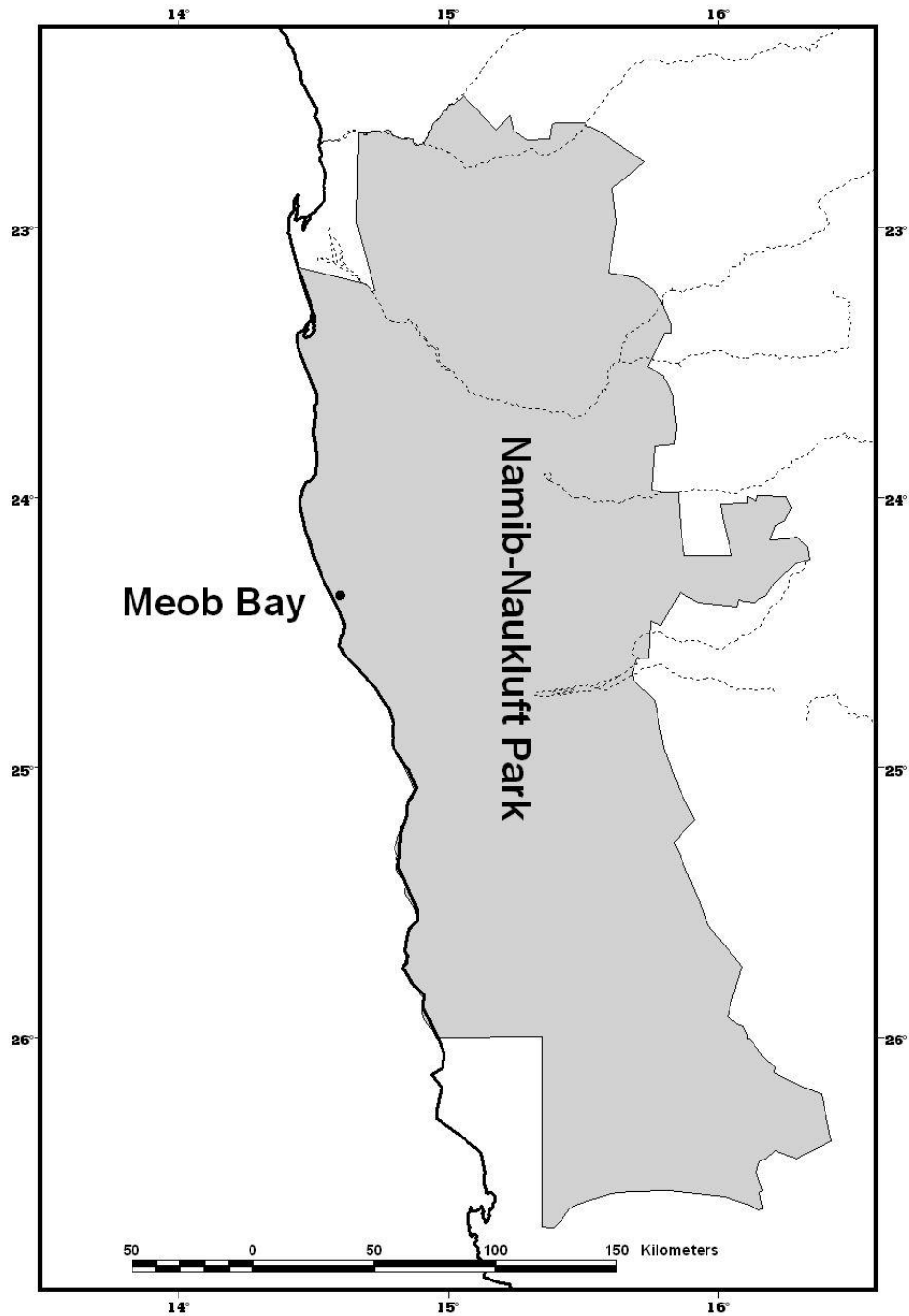


Figure 1.4: Map of the Namib-Naukluft Park in central/southern Namibia, showing the location of Meob Bay, and important Damara Tern breeding colony to this study (see text).

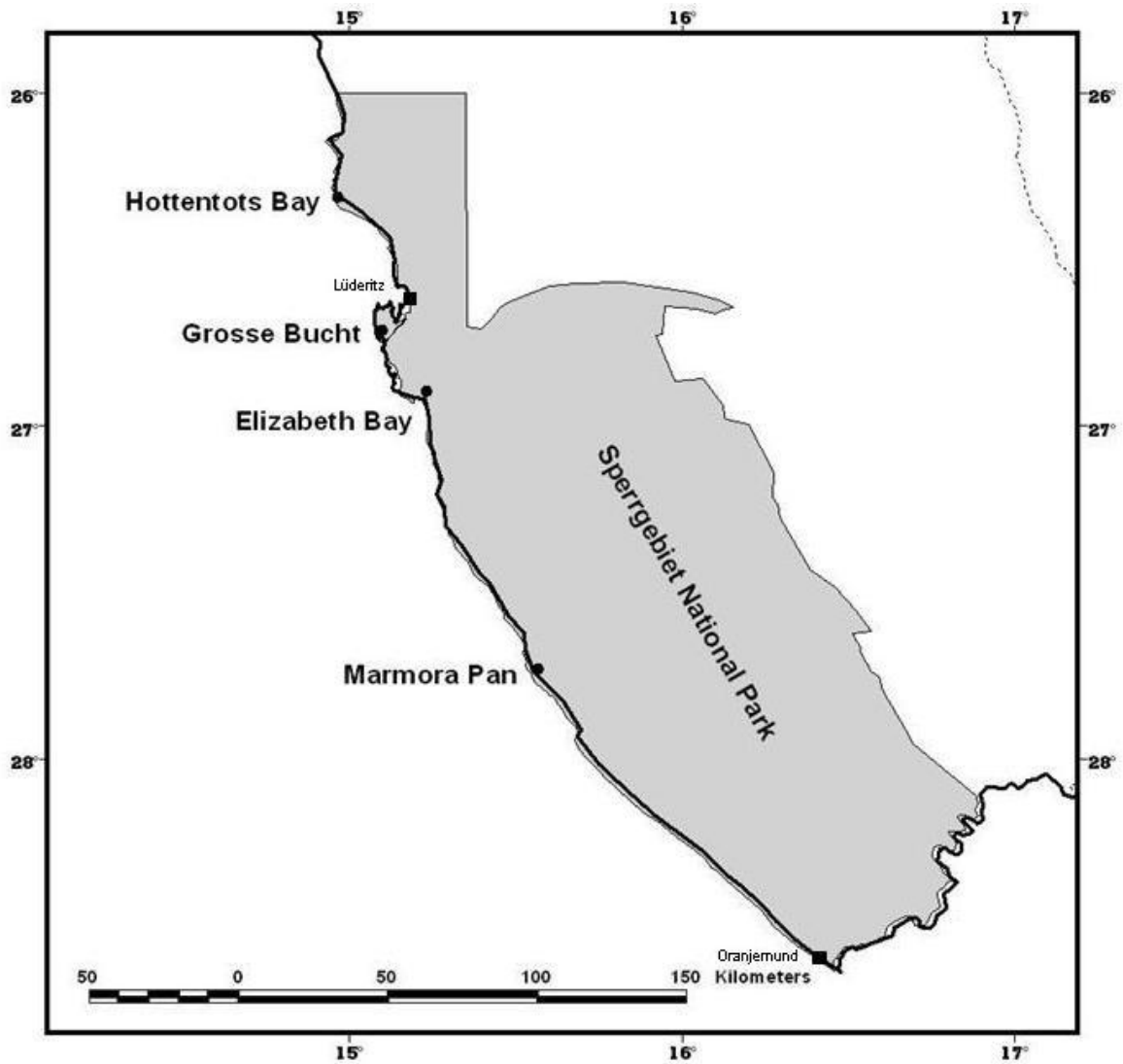


Figure 1.5: Map of the Sperrgebiet National Park in southern Namibia, showing the locations of the four Damara Tern breeding colonies important to this study (see text). The location of the towns, Lüderitz and Oranjemund, are also shown.

Chapter 2

Clutch size and breeding success of Damara Terns *Sterna balaenarum* in Namibia



Kevin Jones

Clutch size and breeding success of Damara Terns *Sterna balaenarum* in Namibia

Introduction

The key parameters in understanding the life history of a species are a knowledge of its reproductive rates, age-specific survival rates and age at first breeding. This chapter discusses the reproductive rates of Damara Terns *Sterna balaenarum*.

Arguably, what sets the Damara Tern most apart from the other small terns is that it lays only one egg (Table 1.1 in Chapter 1). Two-egg clutches are rare, and make up *c.* 1% of all nests recorded in Namibia (de Villiers and Simmons 1997). Generally, reduced clutch-size is associated either with low rates of food availability or high risks of predation (e.g. Lima 1987, Martin 1992, 1996, Hockey and Wilson 2003). The breeding range of Damara Terns is found in an area of high biological productivity (Cushing 1971, Shannon 1989), so Frost and Shaughnessy (1976) thought that food availability is unlikely to be a limiting factor. Predation risk has been hypothesized as the key factor in determining the small clutch size of Damara Terns (Frost and Shaughnessy 1976, Clinning 1978).

Damara Terns breed far inland and nest in loose aggregations (Chapter 1). Inland breeding and nesting in loose aggregations is likely to be an evolutionary adaptation to avoid nest predation (Frost and Shaughnessy 1976), mainly because predators, like the Black-backed Jackal *Canis mesomelas*, generally patrol the beaches (Simmons and Braine 1994). Inland nesting also means that nests are not vulnerable to flooding by high tides. Clinning (1978) suggested that, in light of inland breeding, increased brood

size in the Damara Tern would limit the feeding rate and protection each individual young would obtain. However, feeding rates were not obtained in that study. Frost and Shaughnessy (1976) postulated that one-egg clutches in Damara Terns may be a result of selection for faster growth rates of young as a way to overcome the high risk of predation. However, growth rates were not available to compare with those of similar species in order to test this assumption.

The incubation period of Damara Terns is known to mostly range between 18 and 22 days, but can vary from 17.5 to 30 days (Simmons 2005a). Breeding success is not well known and is estimated at 53% in Namibia (Simmons 2005a). This estimate was based on the percentage of fledged chicks in a flock of 4004 post-breeding adults observed in March 1991 in northern Namibia (Braby *et al.* 1992, Simmons 2005a). Nest losses have mainly been attributed to human disturbance, Black-backed Jackals *Canis mesomelas* and gulls (Simmons 2005a).

Many of the aspects of breeding biology of the Damara Tern have been based on small sample sizes (Clinning 1978, Simmons and Braine 1994), and/or focused on specific areas of the Namibian coastline (Clinning 1978, Braby 1995, de Villiers and Simmons 1997). Damara Terns are Near-threatened globally (IUCN 2009) and are “Specially Protected” under the draft Protected Areas and Wildlife Management Bill of Namibia. Colonies are threatened by anthropogenic activities, such as off-road driving (Braby *et al.* 2001, Chapter 8), mining (Connor 1980, Simmons 2005b), and coastal development (R.J. Braby unpubl. data). In light of this, it is becoming increasingly important to update these (and other) aspects with new and detailed information which include various colonies along the entire coastline of Namibia.

The objectives of this study are to (a) update previous information regarding clutch size, incubation period and egg measurements using larger sample sizes, (b) quantify the breeding success, and (c) determine the causes of nest losses of breeding Damara Terns in Namibia. I also review the evolutionary factors determining the clutch-size in this species.

Methods

Study Area and monitoring methods

The study areas and monitoring methods are categorized into three groups:

(a) During 1983–1993 and 19 December 2009–14 February 2010 sporadic visits were made to colonies and singleton pairs found within the Skeleton Coast Park and Dorob National Park (Figure 1.1 in Chapter 1). These visits included finding nests, nest content checks and egg measurements. These areas are referred to as “north”.

(b) In central Namibia (in the Dorob National Park), Horses Graves (S22°44 E14°32) and Caution Reef (S22°42 E14°33) were monitored for 10 consecutive years, during breeding seasons 2000/01 to 2009/10 (Figures 1.1 and 1.2 in Chapter 1). Length of monitoring varied according to length of breeding season, but usually began in September and ended in March. Daily visits included finding new nests, checking nest contents and looking for signs of possible predation if nests were empty. Effort was rarely made to relocate chicks after they successfully hatched. These areas are referred to as “central”.

(c) In southern Namibia (in the Sperrgebiet National Park) I monitored four colonies (Figures 1.1 and 1.4 in Chapter 1): Hottentots Bay (26°14'S, 14°59'E), Grosse Bucht (26°43'S, 15°40'E), Elizabeth Bay (26°55'S, 15°14'E) and

Marmorata Pan (27°45'S, 15°34'E). Monitoring took place during 15 January–31 March 2007, 22 September 2007–31 March 2008 and 1 October 2008–31 March 2009. Visits to each colony included observing adults, finding new nests, checking nest contents, measuring eggs, re-locating chicks that had left the nest, and finding signs of nest/chick losses (e.g. empty nests led to searching the vicinity for mammal tracks or other predator clues). Because of logistical reasons, more time was available to monitor the colony at Hottentots Bay in 2008/09 than in 2007/08 (414 hours were spent monitoring at Hottentots Bay in 2008/09 versus 202 hours in 2007/08). The other three colonies received the same time and search efforts over both seasons. These four areas are referred to as “south”.

At all three coastal areas, chicks were ringed with SAFRING stainless steel rings (2.8 mm internal diameter).

Egg measurements and incubation

Egg dimensions (length and breadth, mm) were measured using Vernier calipers to the nearest 0.1 mm (measurements from 1983–1993) and digital calipers to the nearest 0.01 mm. Egg masses (g) were taken using both a 10 g Pesola scale (for eggs less than 10 g), and a 100 g Pesola scale. Egg volume (cm³) was estimated from the equation

$$volume=0.000476\times length (mm) \times breadth^2 (mm)$$

as described by Bolton (1991). Incubation periods (days) were estimated for nests with known laying and hatching dates. Laying dates were determined by:

1. The observer observed a female laying her egg (i.e. there was no egg in the empty scrape before).

2. If the area was visited daily and the observer noticed a pair in the area looking like they were going to nest, and on the next day there was a nest with an egg.
3. If the area was visited daily, and the observer had not seen the nest the day before, and was certain that the nest had not existed the day before.

The maximum error associated with determining laying date was one day.

Breeding success and number of nests

Generally, nests in the north and central areas were monitored only up to the time of hatching and not during the fledging period because of the difficulty of relocating cryptic and mobile chicks. Attempts to monitor nests until the chick fledged or the nest failed were only made in southern Namibia.

However, even in southern Namibia nests (or mobile chicks) were not always found again and evidence of any predation (or other cause of death) was not always available. Hatching and fledging success was therefore estimated using the approach developed by Mayfield (1961, 1975) and extended by Underhill (submitted). The extended Mayfield method enables explanatory variables to be incorporated into nest success modeling using the standard hypothesis testing and model selection approaches used, for example, in generalized linear models. Model fitting was undertaken using the RSURVIVAL procedure of GenStat (GenStat 12 Committee 2009). For comparative reasons, one colony would be set as the baseline level.

The modelled probability of breeding success was then calculated using the inverse of the logistic transformation from the parameter coefficient.

Explanatory variables used were coastal area (i.e. north, central, south), breeding colony and breeding season. On average, Damara Terns incubate for 23 days (this Chapter) and chicks fledge 23 days after hatching (Chapter 3).

Nest days of infertile/addled eggs were counted as long as the adult was

incubating, and infertile/addled eggs were ultimately deemed as failures. Infertile/addled eggs were defined as eggs which were either not fertilized or failed to hatch because of some deformity during egg production. This generally meant that the parents would incubate while the egg failed to hatch. If an egg was abandoned, it was deemed as a failure. If the egg was predated, it was deemed as a failure. Eggs were defined as predated if:

1. There was direct evidence of predation; i.e. predators were seen taking eggs, tracks were found leading up to empty nests or shell fragments were found.
2. Eggs in initial stages of incubation disappeared, or observer knew that the egg would not have hatched yet and it had subsequently disappeared.

All eggs which failed to hatch due for any reason, were deemed as failures.

All chicks which failed to fledge were defined as failures. Chicks were determined as having been predated if:

1. There was direct evidence of predation; i.e. tracks were found around nest area and chick was still at hatchling stage.
2. Chick disappeared and even after daily searching was never found again and the colony searched was small, e.g. Grosse Bucht. Searching would include laying low and waiting for adults to come with fish to feed their chick.

If chicks disappeared, but it was not certain if they were predated or survived, their fate was deemed as unknown (i.e. no failures were observed and only nest days where the nest/chick was observed were counted).

I investigated the relationship between the Southern Oscillation Index (SOI) and the observed number of Damara Tern nests during each breeding season at Horses Graves and Caution Reef. The Southern Oscillation Index (SOI) represents a combination of climate measures, and a high SOI relates to high

marine productivity (Durant *et al.* 2010). Monthly SOI data was obtained from the Australian Bureau of Meteorology (<http://www.bom.gov.au/climate/current/soi2.shtml>), and the values for September, October and November were averaged to form a Spring SOI value for each year. This is the period during which Damara Terns would be evaluating whether to breed in a particular breeding season. The relationship was modelled using a generalized linear model with a Poisson distribution for the number of nests each season, and with Spring SOI as the explanatory variable.

Nest failures

Nest failures were observed in the north, central and south of Namibia. Evidence of predation (at egg or chick phase), such as tracks leading up to empty nests, or seeing predators take eggs or chicks, was used to explain nest losses attributed to predators. A nest was defined as abandoned if no adult was present at the nest for more than five subsequent observer visits (each visit ranged between 1 and 5 days apart), and the egg was cold to the touch. An egg was defined as infertile/addled if the adults incubated for periods longer than 45 days.

Apart from monitoring fledging success in southern Namibia, and hatching success in central Namibia, nest failure data were sporadic, erratic and spanned multiple areas. Therefore, it was not feasible to divide failures into various years and colonies.

Results

Clutch size, egg dimensions and incubation period

Of 2528 nests recorded along the coastline of Namibia from 1983 to 2010, five (0.002%) contained a two-egg clutch. Mean length, breadth and volume of 586 eggs from 585 nests, were 33.09 mm (SD=1.1 mm, range=30.55–37.12 mm)

and 23.84 mm (SD=0.63 mm, range=21.00–25.80 mm), 8.96 cm³ (SD=0.59 cm³, range=6.71–10.81 cm³), respectively. The mean fresh mass of an egg was 10.17 g (SD=0.58 g, n=12, range=9.3–11.5 g); the mean pipping (egg is starred) mass was 7.92 g (SD=0.57 g, n=68, range=6.5–9.7 g). The mean incubation period was 22.9 days (SD=2.0, n=106, range=19–31 days).

Breeding success and number of nests

The daily rates of nest loss during incubation and fledging periods were not significantly different (for example, likelihood ratio test in central Namibia, with the largest data set, allowing for interyear differences, L=17.1, chi-squared distribution with 17 degrees of freedom, P=0.45). Nest days and chick days were therefore combined in the RSURVIVAL model. The modelled rates were back-transformed (Underhill submitted) to obtain estimates of daily survival probability and raised to the power of 46, the average period (days) from laying to fledging. The breeding success was thus defined as the probability of survival of a breeding attempt from egg-laying to fledging.

A total of 1629 nest were monitored nests, with 21047 incubation days and 11632 chick days. The modelled overall probability of breeding success (BS) in Namibia was 0.356 (95% confidence interval 0.326, 0.387). There was insufficient data to ascertain breeding success at different colonies or for different years in the north. Therefore, breeding success for all colonies and years combined in the north was 0.37 (Table 2.1).

In central Namibia, where two colonies were monitored over 10 seasons, overall breeding success was 0.34 (Table 2.1). Damara Terns breeding at Horses Graves generally had larger breeding success than those at Caution Reef (Table 2.2). There were no significant differences between all breeding seasons at Horses Graves and the baseline of the model (Caution Reef in 2000/01, Table 2.2). Damara Terns breeding at Horses Graves during 2001/02

had the highest breeding success (BS=0.73, P=0.21, Table 2.2). The highest BS at Caution Reef was also in 2001/02 (BS=0.55, P=0.79, Table 2.2). In 2007/08 and 2008/09 at Caution Reef, breeding success was significantly lower than the baseline (2007/08, P=0.02; 2008/09, P=0.01; Table 2.2). These two seasons at Caution Reef also had the lowest breeding success overall (2007/08, BS=0.10; 2008/09, BS=0.08; Table 2.2). Apart from these two seasons, breeding success did not fluctuate significantly between seasons at Caution Reef (Table 2.2). Breeding success also did not fluctuate significantly between seasons at Horses Graves (Table 2.2). Jackal predations were generally associated with low breeding success at both colonies and seasons (Figure 2.1). Jackal predation was more common at Caution Reef than at Horses Graves (Figure 2.1). The number of nests fluctuated between colonies and seasons (give the range), and was largest at Horses Graves in 2002/03.

At both Horses Graves and Caution Reef, there were nine years out of the 10-year period 2001–10 for which counts of the number of nests was available (data were missing for 2000/01 at Horses Graves, and the count for both colonies for 2005/06 was incomplete). The generalized linear model suggested a negative relationship between number of nests and Spring Southern Oscillation Index (SOI) at both colonies (Figures 2.2 and 2.3). The regression coefficient for Spring SOI at Horses Graves was -0.0323 (SE=0.0064, $t_7 = -5.09$, $P < 0.001$) and at Caution Reef was -0.0120 (SE=0.0050, $t_7 = -2.38$, $P = 0.017$). At Horses Graves Spring SOI accounted for 30.8% of the deviance, and at Caution Reef it accounted for 9.3% of the deviance.

In the south, the probability of breeding success for both seasons and all four colonies was 0.44, significantly higher than the other two coastal areas ($P = 0.009$, Table 2.1). Breeding success fluctuated significantly between colonies and between two seasons in the south (Table 2.3). Damara Terns breeding at Hottentots Bay had the highest breeding success for both seasons

(2007/08, BS=0.80; 2008/09=0.56; Tables 2.3 and 2.4). Breeding success at all colonies was significantly lower than the baseline of the model (Hottentots Bay, 2007/08, Table 2.3). Breeding success was lowest at Grosse Bucht in 2007/08 (Tables 2.3 and 2.4). Breeding success was lowest at Elizabeth Bay and Marmora Pan in 2008/09 (Tables 2.3 and 2.4).

Breeding success was significantly higher at Hottentots Bay in 2007/08 than in 2008/09 ($P=0.03$, Tables 2.3 and 2.4). Damara Terns breeding at Grosse Bucht had significantly lower breeding success in 2007/08 than in 2008/09 (2007/08, $P<0.001$, BS=0.12; 2008/09, $P=0.02$, BS=0.48; Tables 2.3 and 2.4). Damara Terns breeding at Elizabeth Bay had significantly higher breeding success in 2007/08 than in 2008/09 (2007/08, $P=0.001$, BS=0.24; 2008/09, $P<0.001$, BS=0.09, Table 2.4). Damara Terns breeding at Marmora Pan also had significantly higher breeding success in 2007/08 than in 2008/09 (2007/08, $P<0.001$, BS=0.25; 2008/09, $P<0.001$, BS=0.08; Tables 2.3 and 2.4).

Of all colonies in the south, the number of nests was highest at Hottentots Bay; Elizabeth Bay had the lowest number of nests (Tables 2.3 and 2.4). Hottentots Bay had fewer nests in 2007/08 than in 2008/09 (Tables 2.3 and 2.4). Grosse Bucht had more nests in 2007/08 than in 2008/09 (Tables 2.3 and 2.4). The number of nests was higher at Elizabeth Bay in 2007/08 than in 2008/09 (Tables 2.3 and 2.4). The number of nests was higher in 2007/08 than in 2008/09 at Marmora Pan (Tables 2.3 and 2.4).

Nest failures

Predation was the most common cause of known nest failure (79% of egg losses and 72% of chick losses, Table 2.5). The Black-backed Jackal was the most common predator of eggs and chicks (65% of egg losses, 33% of chick losses, Table 2.5).

The Pied Crow *Corvus albus* and Kelp Gull *Larus dominicanus* were each responsible for 2% of egg failures and 2% of chick failures (Table 2.5). Rock Kestrels *Falco rupicolus* were accountable for 5% of chick losses (Table 2.5). Other observed predators included the White-fronted Plover *Charadrius marginatus*, Namib Desert Gerbil *Gerbillurus tytonis* and Pale-chanting Goshawk *Melierax canorus* (Table 2.5). White-fronted Plovers were seen fatally attacking and injuring four Damara Tern chicks when both species were nesting in close proximity. Damara Tern parents would seldom mob these plovers while these activities occurred. Unknown predators could have included any of the above predators but evidence to determine which species was responsible per failure was not available. Unknown and other predators were responsible for 10% of egg losses and 30% of chick losses (Table 2.5).

Four percent of egg failures were due to egg infertility, and 9% of egg failures were caused by abandonment (Table 2.5). Only during extreme tides or unpredictable and sporadic rainfall, was there nest flooding. These events were rare, and were recorded only once at two sites, Hottentots Bay and Grosse Bucht (both in the south). Of 578 egg failures, 0.5% were attributed to nest site flooding (Table 2.5). Human disturbance involved off-road driving, trampling by horses and coastal development, and accounted for 4% of egg losses and 2% of chick losses (Table 2.5). Heat exposure killed 2% of the chicks that failed to survive. Six chicks died while hatching (1%, Table 2.5), and 7% of chicks died of unknown causes (Table 2.5).

In the south, predation was generally the most common cause of nest failure for all four colonies (Table 2.4). Predation was lowest at Hottentots Bay during both seasons and was highest at Marmora Pan during both seasons (Table 2.4). The rate of abandonment and/or egg infertility were the most common causes of nest failure at Hottentots Bay in 2007/08 and at Grosse Bucht in 2008/09 (Table 2.4). Jackal predation was most common at

Elizabeth Bay and Marmora Pan during both seasons (Table 2.4). No nests were observed to fail because of human disturbance in southern Namibia.

Discussion

The clutch-size in the Damara Tern is one, and thus different to all other small terns. The mean incubation period of the Damara Tern is 23 days. Damara Terns breeding in Namibia have a probability of success of 0.38, although breeding success varies significantly between colonies. Predation is the most common cause of nest failure in Namibia and Black-backed Jackals are the most common predators of tern eggs and chicks at most colonies.

Clutch-size

The small clutch-size in Damara Terns is a unique trait among the small terns (Table 1.1 in Chapter 1) and warrants discussion. Frost and Shaughnessy (1976) suggested that food delivery rate may be lower than in other in-shore terns because Damara Terns need to travel further distances to the foraging areas as a consequence of inland nesting. The ability of parents to provide food for their offspring is generally considered a major factor shaping reproductive strategies of birds with nidicolous young (Konarzewski *et al.* 1993). However, the mean feeding frequency for Damara Terns is 1.44 feeds/hour, the same as the Little Tern (Table 3.4 in Chapter 3). In addition, chicks often refuse food if offered too frequently (A. J. Williams *in litt.*, pers. obs). There have been no records of chicks dying of starvation (see also Frost and Shaughnessy 1976, Clinning 1978, Braby *et al.* 2001, A.J. Williams *in litt.*). Therefore food delivery rate is unlikely to be a limiting factor in determining clutch-size in Damara Terns.

Clinning (1978) suggested that an increase in brood size of the Damara Tern would limit both the rate of feeding and the amount of protection individual

young would obtain. Although adult presence decreases as the chick gets older, Damara Tern chicks are more often accompanied by a parent than Peruvian Tern *Sterna lorata* chicks (pers. obs). Predation (by natural predators) is a high risk for eggs and chicks of Damara Terns in Namibia, possibly more so than for other small terns. In fact, predation in other small terns has only increased recently as a result of anthropogenic activities (Holloway 1993, Kirsch 1996, Brunton 1997, Zuria and Mellink 2002, C. Guerra pers. comm.). Several workers have considered nest predation to be an important force in the evolution of clutch size (Skutch 1949, Cody 1966, Lima 1987). Safriel (1975) suggested that a parent's ability to defend its brood from predators may be a strong determinant of clutch-size. Frost and Shaughnessy (1976) postulated that the one-egg clutch in the Damara Tern is an evolutionary trade-off between maximizing a rapid growth rate of chicks and high risk of predation (i.e. the faster a chick fledges, the lower the risk of predation). However, growth rates of Damara Tern chicks were found to be slower than that of other small terns (Table 3.4 in Chapter 3). In addition, chick fledging period is similar to that of the Little and Least Terns (both of which have 2–3-egg clutches, Table 1.1 in Chapter 1).

The energetic content of prey fed to Damara Tern chicks may be lower than prey fed to other small tern species (Chapter 3 and 6). It is thus possible that the one-egg clutch is not only a result of the high risk of predation, but rather a combination of low energy content of food items, and predation risk. However, further studies would be required to test this hypothesis. By rearing only one chick, Damara Tern parents can allocate more time to protecting their chick from predators. Additionally, in light of a high rate of nest predation, a small clutch size would be favoured by natural selection, because it is less energetically expensive to invest in a replacement clutch (Slagsvold 1984). There has been evidence based on recent research that in some species, like gulls, egg production is the major determinant for clutch

size, because producing eggs is demanding and costly for the female (Monaghan and Nager 1997, Monaghan *et al.* 1998, Nager *et al.* 2001). In view of slow growth rates of chicks in relation to other small tern species (Chapter 3), and the possibility of low energy content of prey items compared with other small terns (Chapters 3 and 6), low food quality could also restrict egg production. A combination of the above aspects could have limited clutch size in the Damara Tern.

Breeding success and number of nests

Overall breeding success in Namibia was 15% lower than the breeding success postulated by Simmons (2005a). There was a significantly higher breeding success in the south (10% higher than central, 7% higher than north). However, these comparisons are difficult to make because each coastal area represented different years. The breeding success data from the north is now over a decade old (sporadic monitoring, 1983–1993) and jackal densities may have increased along with the northward shift in Cape Fur Seal *Arctocephalus pusillus pusillus* populations on which coastal jackals prey (Kirkman *et al.* 2007). This possible increase in jackal densities may have had a negative effect on breeding success and number of Damara Terns in northern Namibia (Chapter 9).

In central Namibia, the Horses Graves colony generally had a higher probability of breeding success than the neighbouring colony Caution Reef. Horses Graves lies further from the coast than Caution Reef and is situated in-between dunes so areas here may not have been frequented by Black-backed Jackals as often as at Caution Reef. Jackal predation of eggs was less frequent at Horses Graves than at Caution Reef. It is believed that nesting further inland is an evolutionary adaptation to avoid shoreline predators (Frost and Shaughnessy 1976, Clinning 1978, Simmons and Braine 1994).

The highest breeding success at both Horses Graves and Caution Reef was during 2001/02. During this time conservation measures had just been put in place to protect both colonies from off-road driving (Braby *et al.* 2001), although Horses Graves was not yet fenced off from the public (Chapter 8). The cause of the low probability of breeding success in 2003/04 at Horses Graves may be linked to both a higher proportion of jackal predation of eggs, and possible predations of chicks by breeding Rock Kestrels in the area, which had just arrived the season prior to this (Chapter 8). Fluctuating and low breeding success at Caution Reef was probably a result of (a) the presence of a jackal den in the vicinity, (b) fluctuating densities of Black-backed Jackals, as a result of offal from human recreation, and (c) the possibility that some jackals may have opportunistically targeted Damara Tern eggs and chicks. After jackal populations at Caution Reef were controlled (R.J. Braby unpubl. data), breeding success increased (2009/10) and predation of eggs by jackals decreased.

The number of nests at Horses Graves and Caution Reef decreased during seasons of low SOI. This infers that during Benguela Niños and warm sea surface temperatures less Damara Terns decide to breed. El Niños have been shown to impact the decision to breed in other small tern species (Massey *et al.* 1992, Zavalaga *et al.* 2008). In addition, the number of nests were probably also affected by replacement-laying after initial failures, although data for this was not directly available. Replacement clutches do occur in Damara Terns (Chapter 8, pers. obs), and are known to occur in other small tern species (Massey and Atwood 1981).

In southern Namibia, Hottentots Bay had, comparably, the largest number of nests and the best breeding success of all the southern colonies. This may be attributable to the size and substrate of the breeding area, which rendered nests both cryptic and isolated from predators (Plate 1, Chapter 7). Because it

occurs in the restricted area and is virtually inaccessible, it was also protected from human disturbance (Chapter 7, Chapter 9). The smaller number of nests and breeding success at colonies in the south from 2007/08 to 2008/09 may have been a result of food limitations, such as shortages or decreases in food quality. These are known to have an effect on breeding terns (Nisbet 1978, Monaghan *et al.* 1989). The recorded number of nests at Hottentots Bay was higher in 2008/09 than in 2007/08. However, this was due to substantially increased observer effort and it is likely that the number of nests was actually larger in 2007/08. Breeding success at Grosse Bucht was better in 2008/09 than in 2007/08 possibly because there were less jackal predations.

Predation was the most frequent cause of nest loss in Damara Terns breeding in Namibia. The Black-backed Jackal was the most common predator preying on eggs and chicks of Damara Terns. This finding is not new (Frost and Shaughnessy 1976, Clinning 1978, Simmons and Braine 1994), and jackals may be linked to evolutionary adaptations of inland nesting and one-egg clutches in Damara Terns (Frost and Shaughnessy 1976, Simmons and Braine 1994). Aerial predators like the Pied Crow, Kelp Gull and Rock Kestrel may also have taken chicks. However, little evidence for this exists. These predators are mobbed frantically when they approach breeding areas (pers. obs). Therefore, they must be considered important predators of chicks and eggs of Damara Terns. White-fronted Plovers killing Damara Tern chicks has previously been documented (Simmons 2005a). Territorial aggression in plovers is common (Simmons 1953, Cairns 1982). At a young age, Damara Tern chicks and White-fronted Plover chicks look similar. It is likely that Damara Tern chicks are mistaken as White-fronted Plover chicks by White-fronted Plover adults when adults of both species nest in close proximity.

Egg abandonment and infertility may be attributed to food shortages. In addition, chicks dying while hatching may have been due to the production of low quality eggs, also as a result of food shortages or low food quality. Egg abandonment has been indirectly linked to food shortages in Least Terns (Atwood and Kelly 1984, Atwood and Massey 1988).

Damara Terns have low fecundity as a result of a small clutch and low breeding success compared with most other small terns (Table 1.1 in Chapter 1). In light of this low fecundity, special consideration should be given towards the protection and management of breeding areas in Namibia. In addition, human disturbance was low mainly because monitoring was conducted in areas which were mostly protected and/or isolated. For instance, the breeding areas north of Swakopmund, where off-road driving is not strictly regulated, human disturbance has the potential to be an important cause of nest failure. Chicks have been observed being trampled by vehicles in these areas, even on the main road between Swakopmund and Hentiesbay (which, in some areas, Damara Tern chicks have to cross to get closer to the sea, pers. obs, Figure 1.1 in Chapter 1). Important breeding areas should be allocated protection as a step towards the conservation of breeding Damara Terns (Chapter 9). These areas should be protected from human disturbance. Human disturbances should also include indirect causes of nest failures, such as increases in jackal densities as a result of human recreation (i.e. offal left behind on beaches) on beaches. Encouraging fishermen and other recreational beach-users to take their garbage and offal with them when they leave might be one way reduce the number of jackals patrolling the beach.

Table 2.1: Results of the generalized linear model for breeding success of Damara Tern nests in Namibia in relation to coastal area as explanatory variable, with “central” set as the baseline of the model. The modelled probability of breeding success (BS) was calculated using the inverse of the logistic transformation from the parameter coefficients. Standard errors are given for the coefficients (SE).

Parameter	Coefficient	SE	t₁₉₂₈	P-value	BS
Constant	-3.739	0.050	-75.35	<0.001	-
North	-0.094	0.135	-0.69	0.49	0.37
Central	0	0	0	-	0.34
South	-0.284	0.108	-2.62	0.009	0.44

Table 2.2: Results of the generalized linear model for breeding success of Damara Tern nests at two colonies in central Namibia in relation to colony and breeding season as explanatory variables. Caution Reef in 2000/01 was set as the baseline of the model. The modelled probability of breeding success (BS) was calculated using the inverse of the logistic transformation from the parameter coefficients.

Parameter	Nest no	Coefficient	SE	$t_{1025,2}$	P-value	BS
constant		-4.193	0.499	-8.40	<0.001	
HORSES GRAVES						
2000/01	No data	No data	No data	No data	No data	No data
2001/02	59	-0.784	0.625	0.625	0.21	0.73
2002/03	122	-0.058	0.538	0.538	0.91	0.52
2003/04	89	0.839	0.525	1.60	0.11	0.21
2004/05	97	0.001	0.545	0.00	1.00	0.50
2005/06*	32	-0.400	1.12	-0.36	0.72	0.63
2006/07	69	0.036	0.547	0.07	0.94	0.49
2007/08	56	0.401	0.558	0.72	0.47	0.36
2008/09	54	0.154	0.552	0.28	0.78	0.45
2009/10	45	0.172	0.571	0.30	0.76	0.44
CAUTION REEF						
2000/01	48	0	0	0	–	0.50
2001/02	92	-0.144	0.552	-0.26	0.79	0.55
2002/03	56	0.943	0.545	1.73	0.08	0.17
2003/04	40	0.660	0.583	1.13	0.26	0.27
2004/05	60	0.277	0.562	0.49	0.62	0.40
2005/06*	13	Insuff. data	Insuff. data	Insuff. data	Insuff.	Insuff. data
2006/07	92	0.686	0.523	1.31	0.19	0.26
2007/08	52	1.232	0.531	2.32	0.02	0.10
2008/09	71	1.331	0.517	2.57	0.01	0.08
2009/10	108	0.643	0.520	1.24	0.215	0.27

* Not monitored for full season.

Table 2.3: Results of the generalized linear model for breeding success of Damara Tern nests at four colonies in southern Namibia in relation to colony and breeding season as explanatory variables. Hottentots Bay in 2007/08 was set as the baseline of the model. The modelled probability of breeding success (BS) was calculated using the inverse of the logistic transformation from the parameter coefficient.

Parameter	Nest no	Coefficient	SE	$t_{283,2}$	P-value	BS
constant		-5.359	0.407	-13.18	<0.001	-
HOTTENTOTS BAY						
2007/08	80	0	0	0	-	0.80
2008/09	187	0.967	0.447	2.16	0.03	0.56
GROSSE BUCHT						
2007/08	21	2.299	0.482	4.77	<0.001	0.12
2008/09	17	1.231	0.526	2.34	0.02	0.48
ELIZABETH BAY						
2007/08	13	1.895	0.539	3.52	0.001	0.24
2008/09	4	2.414	0.644	3.75	<0.001	0.09
MARMORA PAN						
2007/08	55	1.864	0.450	4.14	<0.001	0.25
2008/09	13	2.490	0.539	4.62	<0.001	0.08

Table 2.4: Determined nest outcomes (DNO) of total nests (TN) at four breeding colonies of Damara Terns in southern Namibia during two breeding seasons. DNO include only the nests for which outcomes (at egg or chick phase) were known. The success or cause of nest failure; predation, abandoned/addled, other, are given as percentages of the DNO. Predators included Black-backed Jackals, Pied Crows, Kelp Gulls and Rock Kestrels. Predation by Black-backed Jackals (BBJ predation) indicates nests predated only by Black-backed Jackals. “Other” indicates nest failures that include heat or wind exposure, unknown cause of death, flooding, and egg cracked.

Colonies	Season	DNO	TN	Success (%)	Predation (%)	BBJ predation (%)	Abandoned/addled (%)	Other (%)
Hottentots Bay	2007/08	7	80	77.4	16.1	3.2	18.2	9.1
	2008/09	103	187	72.8	18.4	9.7	5.8	2.9
Grosse Bucht	2007/08	18	21	22.2	55.6	33.3	0.0	22.2
	2008/09	17	17	47.1	23.5	17.6	23.5	11.8
Elizabeth Bay	2007/08	11	11	36.4	63.6	45.5	0.0	0.0
	2008/09	4	4	0.0	75.0	50.0	0.0	25.0
Marmora Pan	2007/08	53	55	26.4	87.3	59.0	0.0	1.9
	2008/09	10	13	10.0	80.0	40.0	0.0	10.0

Table 2.5: Causes of egg and chick failures based on nests with known outcomes of Damara Terns breeding in Namibia.

	EGG (n)	Percentage (%)	CHICK (n)	Percentage (%)
Total nest failures	578		44	
Black-backed Jackal	375	65	14	33
Pied Crow	11	2	1	2
Kelp Gull	11	2	1	2
Rock Kestrel	N/A	N/A	2	5
Other/ Unknown predator	56	10	13	30
Egg Infertile/ addle	21	4	N/A	N/A
Abandonment	53	9	N/A	N/A
Human disturbance	23	4	1	2
Nest site flooded	3	0.5	N/A	N/A
Sandstorm exposure	1	0.1	1	2
Heat exposure	0	0	1	2
Chick died hatching	6	1	N/A	N/A
Chick died of unknown cause	N/A	N/A	3	7

* Other predators include the White-fronted Plover, Namib Desert Gerbil, Pale-chanting Goshawk. Unknown predator is defined because the loss of the egg or chick could be attributed to a predator but a specific predator could not be identified as the cause.

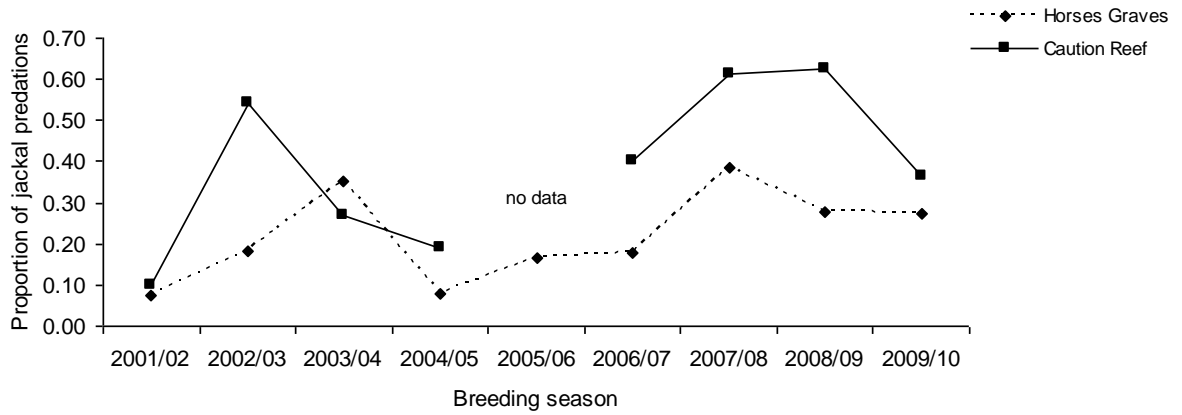


Figure 2.1: Proportion of predations on eggs attributed to Black-backed Jackals as a fraction of all known hatching outcomes (i.e. if egg hatched successfully or was predated) of Damara Tern nests at Caution Reef and Horses Graves, Swakopmund, over breeding seasons 2001/02 to 2009/10. Data were not available for 2000/01 for both colonies and 2005/06 for Caution Reef.

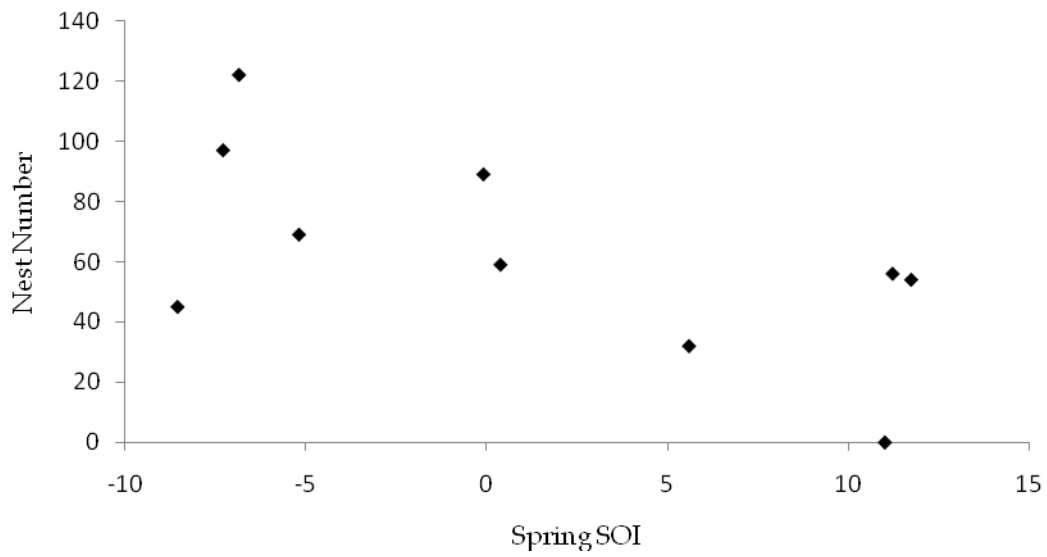


Figure 2.2: Spring Southern Oscillation Index (SOI) as compared to the number of Damara Tern nests per season (each marker represents one season) at a colony called Horses Graves in Namibia.

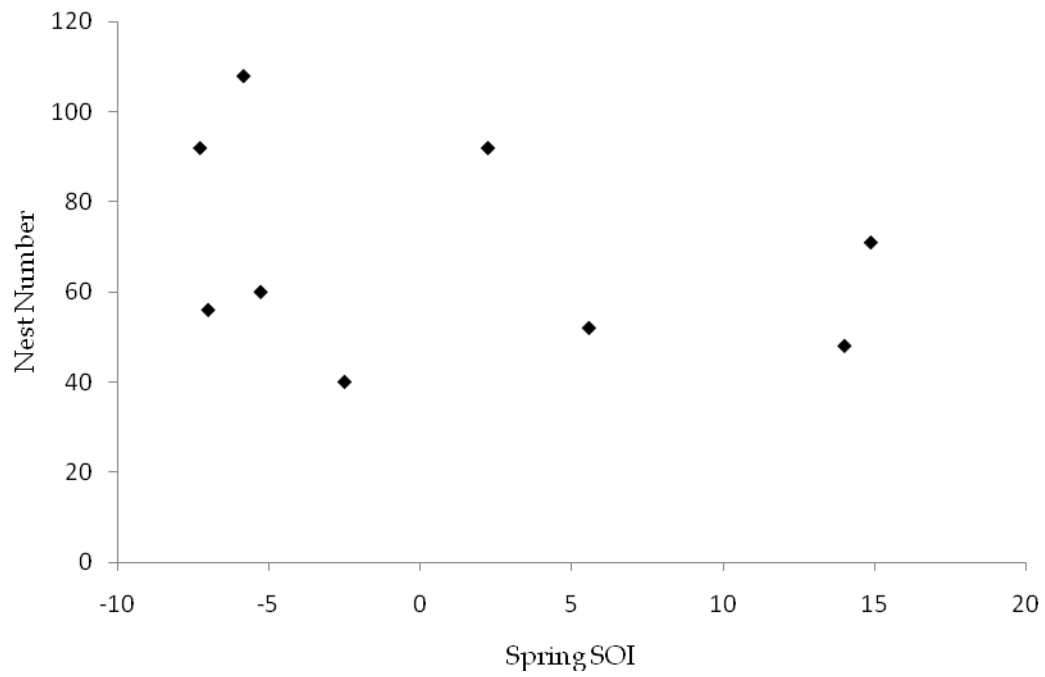


Figure 2.3: Spring Southern Oscillation Index (SOI) as compared to the number of Damara Tern nests per season (each marker represents one season) at a colony called Caution Reef in Namibia.

Chapter 3

Growth patterns, fledging period and feeding rate
of Damara Tern *Sterna balaenarum* chicks in
Namibia



Growth patterns, fledging period and feeding rate of Damara Tern chicks in Namibia

Introduction

Differences in chick growth patterns among species of terns have been attributed to food availability and other ecological factors (Ricklefs 1979, 1983, 1992, Ricklefs and White 1981). Le Roux (2006) considered the growth rates of different structures of the Swift Tern *Sterna bergii*, and found that the growth of certain structures was initially prioritized with regards to resource allocation and suggested that this might be due to predation risk.

Generally, slow growth rates, long fledging periods and small clutches are traits that have evolved as a result of food limitation (Ricklefs and White 1981, Hockey and Wilson 2003). However, predation risk can equally be argued as a limiting factor in the reproductive traits of seabirds (Cody 1966, Slagsvold 1984, Lima 1987).

Like in many seabirds, Damara Tern chicks are semi-precocial. Chicks leave the nest only two days after hatching and are highly mobile, moving large distances from one day to the next (Simmons and Braine 1994). They rely on parental feeding until at least two and a half months after fledging (Clinning 1978). Fledging periods of Damara Terns are similar to other small terns (Table 1.1 in Chapter 1). They breed in the desert environment of the Namibian coastline, where strong upwellings in the Benguela Current presents high productivity (Cushing 1971). Damara Terns generally breed far inland to avoid high predation rates (Frost and Shaughnessy 1976, Clinning 1978), and thus have to travel a relatively large distance between their breeding and foraging grounds. However, they rear only one chick and chicks often refuse food from parents (pers. obs, T. Tree pers. comm., A.J. Williams

in litt.). Feeding rates are considered to be relatively high (A.J. Williams *in litt.*).

Little is known of the growth and development of Damara Tern chicks. This chapter aims to estimate growth rates and fledging periods of Damara Terns, and investigate le Roux's hypothesis of prioritizing growth structures according to ecological factors in Damara Tern chicks. The chapter also describes the feeding frequency of Damara Tern chicks.

Study Area and methods

Chick growth rate and fledging period

Growth rates and fledging period data were collected from 11 breeding localities along the Namibian coastline (Figures 1.2–1.4 in Chapter 1):

(a) from November 1992–February 1993: Möwe Bay Airstrip (19°22'S, 12°43'E), Huab (S20°50 E13°26) and Ogden Rocks (S24°22 E24°42);

(b) during January 2006: Möwe Bay Airstrip;

(c) from 15 January–31 March 2007, 22 September 2007–31 March 2008 and 1 October 2008–31 March 2009: Hottentots Bay (26°14'S, 14°59'E), Grosse Bucht (26°43'S, 15°40'E), Elizabeth Bay (26°55'S, 15°14'E) and Marmora Pan (27°45'S, 15°34'E);

(d) from November 2009–March 2010: Durissa Bay Pans (21°15'S, 13°41'E), White Stones (21°39'S, 13°56'E), Horses Graves (S22°42 E14°33) and Caution Reef (S22°44 E14°32).

Shortly after hatching, or when found for the first time, each chick was ringed with a SAFRING stainless steel ring (2.8 mm internal diameter, and colour rings were placed on the left leg). Chicks were weighed to the nearest 1 g using a Pesola spring balance. Structural growth measurements were taken using digital calipers and included head (and bill) length, wing length,

bill length, and foot length (tarsus and toe). Wing length was measured in terms of maximum length from the curvature of the carpal joint to the end of the (down/quill) feather. Relocated chicks were measured at 2–7 day intervals. Because the growth patterns of most measurements did not conform to the standard growth curves, such as logistic or Gompertz (Reiss 1989), a descriptive statistical approach that was devised for Swift Terns in South Africa (le Roux 2006) was used. See Annex 2 for the statistical methodology as described by le Roux (2006). Fledging periods were determined from chicks for which known hatching and first flight dates were known.

Feeding rate

I observed Damara Tern chicks between hatching and just after fledging over the daylight period (06h00–20h00) during the breeding seasons October 2008–March 2009 and October 2009–March 2010 at six breeding colonies along the Namibian coastline: Durissa Bay Pans, White Stones, Horses Graves, Caution Reef, Hottentots Bay, Grosse Bucht and Elizabeth Bay (Figures 1.2 and 1.3 in Chapter 1). During continuous observations I recorded the number of times a chick was fed by its parents. Observations were either made from a car or by lying still flat on the ground and observing by binoculars (8×42) or telescope from a distance of *c.* 150 m. To avoid disturbance and thus bias results due to observer presence, chicks spotted from afar were not measured prior to starting observations. Adults would usually mob during occasions when I did measure chicks. On these occasions I only started recording my observation once observer presence was ignored, *c.* 20 mins. Simultaneous observations never exceeded two chicks, and most observations were on single chicks at any given time.

The standard observation period was 120 minutes, but some periods were shorter. I tested whether feeding rate increased with age by using a generalized linear model with a Poisson distribution and logarithmic link

function to model the number of feeds per hour, using observation time as the offset variable (McCullagh and Nelder 1989).

Results

Chick growth rate and fledging period

In total, there were 282 recaptures of 220 chicks ringed. Chicks found on the day (day=0) they hatched were defined as hatchlings. The mean mass of hatchlings was 7.05 g (SD=0.92 g, Table 3.1). The mass of hatchlings had a coefficient variation (CV) of 13.09%. Foot length (CV=4.44%) and head length (CV=5.06%) showed least variability of the structures measured (Table 3.1). Because I had no measurement data for birds that had fledged (i.e. taken first flight, chicks that were 21 days (minimum age at fledging, this chapter) and older were defined as fledglings and their measurements were used (Table 3.2). This approach suggested that the mean fledging mass was 43.5 g (SD=2.7 g) and the mean fledging wing length was 100.8 mm (SD=3.6 mm).

Measurements obtained from 401 adult Damara Terns (R.J. Braby unpubl. data) indicated that the fledgling wing length was *c.* 60% of the wing length of breeding adults (Tables 3.2 and 3.3). Fledging mass was *c.* 85% of adult mass (Tables 3.2 and 3.3). The head length of the fledglings was 72% of adult head length, but the bill length was only 58% of adult bill length (Tables 3.2 and 3.3). Foot length of adults and fledglings was similar (Tables 3.2 and 3.3).

The growth rates from hatching to fledging ranged between 1 and 2.6 g/day and peaked when chicks were between 19 and 23 g at a mean of 2.58 g/day (*c.* 7–8 days old, Figure 3.1A). At fledging mass, the mean growth rate was 1.25 g/day (Figure 3.1A). The rate of growth in mass showed large scatter (Figure 3.1B). The coefficient of variation for the peak growth rate was 36.4%. The transformation of the growth rate curve into the plot showing average

mass in relation to age indicated nearly linear growth in mass from *c.* 5–15 days and then a lower rate of linear growth from *c.* 17–25 days (Figure 3.1B). The mean growth rate of mass between hatching and fledging was 1.99 g/day.

The growth rate of the wing length showed a relatively steady increase from 1 mm/day at hatching to 3 mm/day when the wing length was 24 mm, after which there was a more rapid increase from 3.5 mm/day to a peak of 5.85 mm/day at wing length 93 mm (*c.* 22 days, Figure 3.2A). Thereafter the rate decreased very slightly towards fledging (5.72 mm/day, as the chick reached *c.* 23 days, Figure 3.2A). The growth curve for wing length against age reflected this pattern (Figure 3.2B). The wing length increased slowly until an age of *c.* 15 days, and then showed an almost linear increase towards fledging (the very slight decrease towards fledging was not visible in the growth curve, Figure 3.2B). At 15 days, the wing length was 49.13 mm, 28% of adult size. The rate of growth for wing length showed less scatter than that for mass (Figure 3.1A and 3.2A). At the point when wing length was increasing most rapidly (5.85 mm/day, SD=1.24 mm/day) the coefficient of variation was 21.21%. If the growth rate stayed relatively constant, about two more weeks would be needed for fledglings to reach adult wing length.

The growth rate of head length had its largest value, 2.68 mm/day, at hatching when the mean head length was 22.62 mm. After hatching, it decreased steadily until the head length reached 26.00 mm (2.01 mm/day, Figure 3.3A). The growth rate then showed a steady rate of decrease until it reached 0.66 mm/day at fledging, when the head length was 47.37 mm, at a mean rate 1.08 mm/day. The growth curve for head length reflected this pattern (Figure 3.3B). The head length increased rapidly until *c.* 5 days, and then showed an almost linear increase to fledging. The rate of growth for head length showed relatively large scatter (Figure 3.3A). At hatching, when head length was increasing most rapidly (2.68 mm/day), the standard

deviation of the rate of increase was 1.23 mm/day. The coefficient of variation of this was 45.8%, almost 10% higher than the coefficient of variation for peak mass growth rate.

The growth rates of bill length increased from about 0.31 mm/day (at 6.6 mm), to about 0.65 mm/day (at 17.5 mm, Figure 3.4A). Thereafter the growth rates decreased to fledging where it was 0.38 mm/day (at 18.95 mm, Figure 3.4A). This was reflected in the growth curve (Figure 3.4B), where there was linear growth up until fledging and then began to level. The growth rate plot showed large scatter (Figure 3.4A). At the peak growth rate of a mean of 0.65 mm/day at 17.5 mm, the coefficient of variation of was 49.4%.

The growth rates of foot length showed a rapid increase in growth at hatching (17.46 mm, 2.15 mm/day), and then the growth rate decreased steadily until fledging (29.4 mm, 0.12 mm/day, Figure 3.5A). This is shown in the growth curve (Figure 3.5B), where growth rate was rapid until *c.* 7 days, and slowed down to almost no growth towards fledging. The growth rate plot shows large scatter (Figure 3.5A). At peak growth rate (*c.* hatching, 17.46 mm), with a mean growth rate of 2.15 mm/day, the coefficient of variation was 46.0%. The mean fledging period for 10 Damara Tern chicks was 22.5 days (SD=0.85, range= 21–24 days).

Feeding rate

Of 34 observation bouts (30 minutes–120 minutes per bout, of chicks aged between 0 days and 22 days) of chicks being fed, the mean feeding rate was 1.44 feeds/hour (SD=0.98, range= 0–4.5 feeds/hour).

The generalized linear model used to estimate feeding rates in relation to age showed that feeding rate increased significantly with age. The regression

coefficient of the term relating to age was 0.043 (SE=0.018, $t=2.35$, $P=0.019$, one-sided test, Figure 3.6). The full model was

$$\log_e(\text{feeding rate}) = -4.281 + 0.0660 \times a + \log_e(t),$$

where a is age of chick (days) and t , the offset variable, is the observation period in minutes. Setting $t=60$, gives feeding rates per hour. The modelled feeding rate for a chick aged 0 days was 0.83 feeds/hour, increasing to 2.13 feeds/hour for a chick aged 22 days (Figure 3.6).

Discussion

This study presents the first comprehensive growth rates of Damara Tern chicks in Namibia. I also update mass and structural measurements, fledging period and feeding frequencies using larger sample sizes than have previously been available. Chicks are particularly difficult to locate because Damara Terns have small colony sizes and scattered nest distribution. In addition, chicks are camouflaged and almost always on the move. This is probably the reason why there are no earlier studies of the growth of this species, apart from Clinning (1978), who presented chick growth rates of mass, bill and wing length based on averages of one to five chicks (sample size differed between structures) of known ages. Even though I was only able to measure 220 chicks (282 recaptures) during 19 months of monitoring at 11 Damara Tern colonies, this represents by far the largest available sample of data upon which to undertake an analysis of growth for this species. In the comprehensive reviews of growth rates of terns undertaken by le Roux (2006) and Tjørve (2007), no meaningful data were available for any of the small terns.

The mean mass of hatchlings was 0.55 g larger than previously recorded (Appendix 1). The mean fledging period of 23 (rounded from 22.5) days was slightly longer than postulated by Clinning (1978). The mean mass of 43.5 g for fledglings was 3.5 g larger than previously recorded (Appendix 1). The mean mass of fledglings was 85% of the mean mass of adult terns. The mean fledging wing length was only 60% of adult wing length. Head length was 72% and bill length only 58% of adult structures. Foot length at fledging was similar to that of adults. In fact, adult foot length was reached at c. 12 days of age. At the same age, wing length was only 20% of adult wing length.

For the Damara Tern, resources are clearly channeled into leg growth in the first stages of development. This is appropriate because chicks are required to be mobile within days of hatching and move considerable distances to avoid predators (Clinning 1978, Simmons and Braine 1994). Although the attainment of flight is critical to the chick's survival, it seems that the development of wing length is postponed until legs are well-developed. As the chick nears fledging age the development of wings and the associated ability to fly received a greater allocation of resources. The main advantage that flight provides is the escape from predators such as the Black-backed Jackal *Canis mesomelas*. Furthermore, parents can more rapidly move their fledged chicks closer to the sea and to localities where food is abundant, and thus feed them more efficiently. This has energetic advantages for both the parents and the chick (le Roux 2006).

The Damara Tern feeds mainly by plunge-diving for prey (Simmons and Braine 1994, Chapter 6). The bill is therefore a critical component for prey capture success (le Roux 2006). However, bill development lags behind that of the other structures. Damara Terns, when they fledge, are unlikely able to feed efficiently for themselves. Extended post-fledging dependency enables

chicks to be fed by their parents during the time required for their bill to reach adult length.

The order of development of leg, wing and bill seems logical, and the same was found for Swift Tern chicks in South Africa (le Roux 2006). There have been no comparative studies on other small terns. Leg development is the first priority so that chicks can be mobile to avoid predators. Wing development is the next priority, so that chicks are able to move closer to food resources and better evade predators. Because parents care for their offspring at least 2.5 months after fledging (Clinning 1978), the bill can continue growing after the other growth structures are completed.

The growth rate curve plots provide a visual impression of variability of growth of the four structures measured and of mass (Figures 3.1A–3.5A). It is useful to compare the overall impressions of variability of growth in mass and the structures (Figures 3.1A–3.5A). The relative scatter was largest for foot length and least for wing length. This impression was captured by considering the coefficient of variation of growth when the growth rate was at its largest. The coefficient of variation, the ratio of the standard deviation and the mean, quantifies the concept (le Roux 2006). The coefficient of variation of growth mass was 36.4%, wing length was 21.21%. The coefficients of variation of growth of head, bill and foot length were 45.8%, 49.4% and 46% respectively. I expected mass would have had the highest coefficient of variation, mainly because mass should fluctuate more widely than structural measures (le Roux 2006). Observed mass depends on the weighing time in relation to when the chick was last fed. It is therefore unexpected that the coefficients of variation for growth of head, bill and foot length were higher than that for mass. The reason for this may be due to the difficulty of measuring the structures precisely, and that the element of observer bias existed due to different observers measuring in the field.

The mean growth rate of mass from hatching to fledging in Damara Tern chicks was lower than that of other small tern species (Table 3.4). Damara Tern chicks are highly mobile and are rarely found in the same area from one day to the next (Simmons and Braine 1994, pers. obs). This extreme mobility has not been recorded in other tern chicks. Peruvian Tern *Sterna lorata* chicks were found to be less active than Damara Tern chicks (pers. obs). It is likely that more resources are allocated to the needs of activity than the needs of growth. Alternatively, the slower growth rate of mass of Damara Tern chicks may be a result of food availability or lower energy content of food. However, feeding rates of Damara Terns are comparable to that of other small terns (Table 3.4). In addition, Damara Tern chicks often refuse food (A.J. Williams *in litt.*, pers. obs). Food availability is therefore an unlikely limiting factor in the growth of Damara Tern chicks. The energy content of prey delivered to Damara Tern chicks may be lower than that delivered to other small tern chicks. Mugilidae species fed to Damara Tern chicks in southern Namibia had low energy content (14.88 kJ/g dry mass, Chapter 6) compared to Mugilidae species fed to Little Tern *Sterna albifrons* chicks in Portugal (20.35 kJ/g dry mass, Paiva *et al.* 2006a). Further studies should investigate the comparative energy content of similar prey species of small terns to ascertain whether energy content may be a limiting factor in Damara Tern chick growth.

The feeding rate of chicks was 61% higher than previously recorded in Namibia (Reiss and Kruger 1998). This higher result is likely to be due to a substantially larger sample size (their study had eight hours of observations). A study of feeding rates of Little Tern chicks in Portugal was found to be the same as Damara Terns (Table 3.4). Feeding rates were found to significantly increase with age. This increase may be a result of higher energy requirements of chicks as they become more active with age (pers. obs). There

was insufficient data to correlate feeding rates with growth rates of Damara Tern chicks.

To ascertain why growth rates of Damara Tern chicks are slower than that of other small tern species, future studies should investigate comparative energy budget allocations, and compare energy content of food delivered to these species' chicks.

Table 3.1: Summary statistics of masses (g) and measurements (mm) of Damara Tern hatchlings in Namibia.

	Sample Size	Mean	SD	Min	Median	Max
Mass	118	7.05	0.92	4.80	7.00	9.00
Head	32	24.75	1.25	22.62	24.68	27.60
Bill	26	7.58	0.45	6.60	7.59	8.68
Wing	37	11.89	1.91	6.97	11.43	17.46
Foot	30	20.28	0.90	18.50	20.38	22.39

Table 3.2: Summary statistics of masses (g) and measurements (mm) of Damara Tern fledglings in Namibia.

	Sample Size	Mean	SD	Min	Median	Max
Mass	10	43.50	2.72	40.00	42.50	47.00
Head	3	45.01	0.99	44.34	44.54	46.14
Bill	4	17.90	1.41	15.80	18.50	18.80
Wing	5	100.82	3.57	97.00	101.00	106.00
Foot	3	28.78	0.18	28.61	28.77	28.97

Table 3.3: Summary statistics of masses (g) and measurements (mm) of breeding adult Damara Terns in Namibia.

	Sample Size	Mean	SD	Min	Median	Max
Mass	397	50.99	3.30	42.00	50.00	63.00
Head	297	62.27	2.49	48.00	62.00	72.00
Bill	349	30.10	2.34	25.50	30.10	37.00
Wing	401	172.21	4.68	152.59	172.00	175.00
Foot	10	28.25	0.98	26.78	28.25	30.52

Table 3.4: Mean growth rates of mass from hatching to fledging (g/day), and feeding rate (feeds/hr/chick) for chicks of four species of small tern.

	Mean growth rate	Feeding rate	Source
Damara Tern <i>S. balaenarum</i>	1.99	1.44	This study
Peruvian Tern <i>S. lorata</i>	2.27	–	Zavalaga <i>et al.</i> 2008
Little Tern <i>S. albifrons</i>	2.28–2.53	1.44	Paiva <i>et al.</i> 2006a
Least Tern <i>S. antillarum</i>	2.4	–	Massey 1974
	2.3		Whittier and Leslie 2005

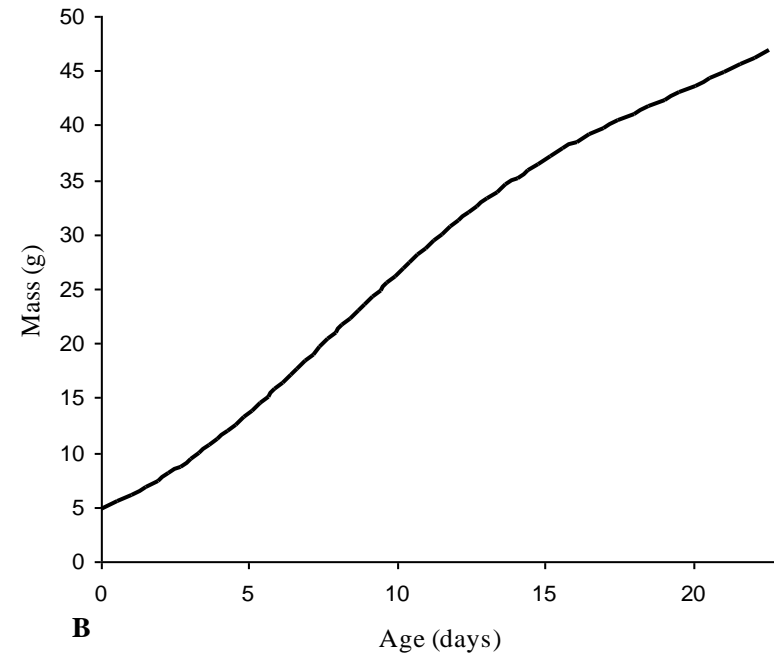
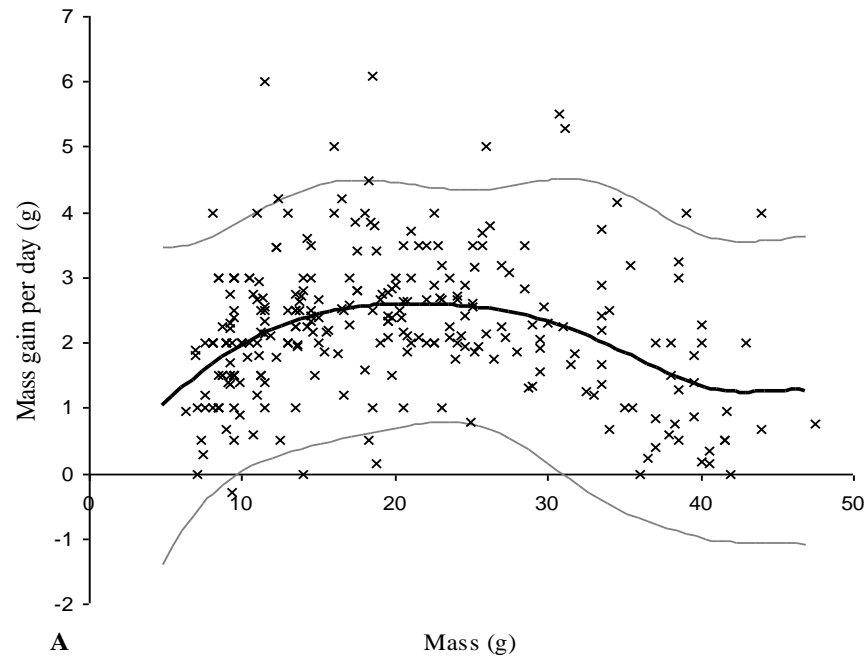


Figure 3.1: A: Growth rates (g/day) of mass of Damara Tern chicks in Namibia. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown (see text). **B:** Growth curve of mass (g) of Damara Tern chicks in relation to age in days, transformed from the trajectory of the mean in A.

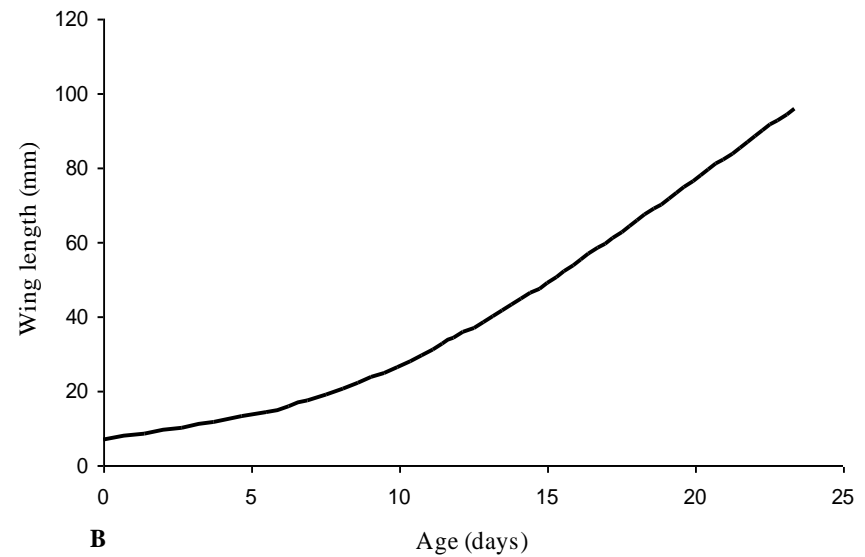
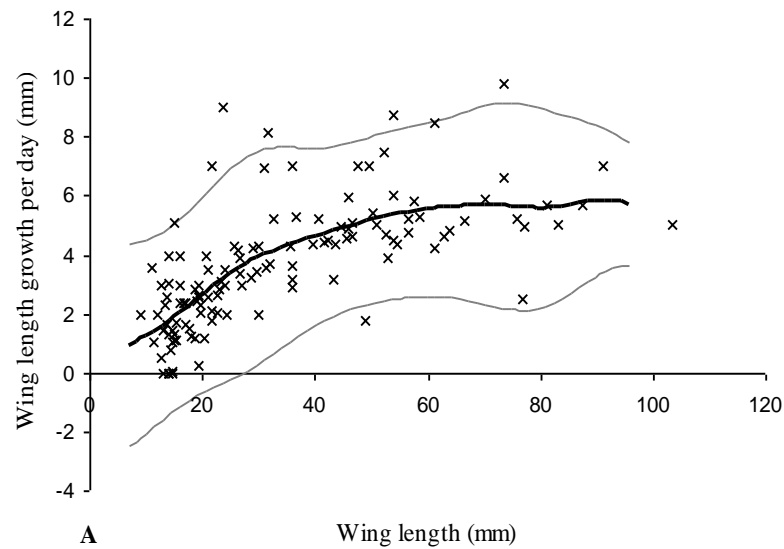


Figure 3.2: **A:** Growth rates (mm/day) of the wing length of Damara Tern chicks in Namibia. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown (see text). **B:** Growth curve of wing length (mm) in relation to age in days, transformed from the trajectory of the mean in A.

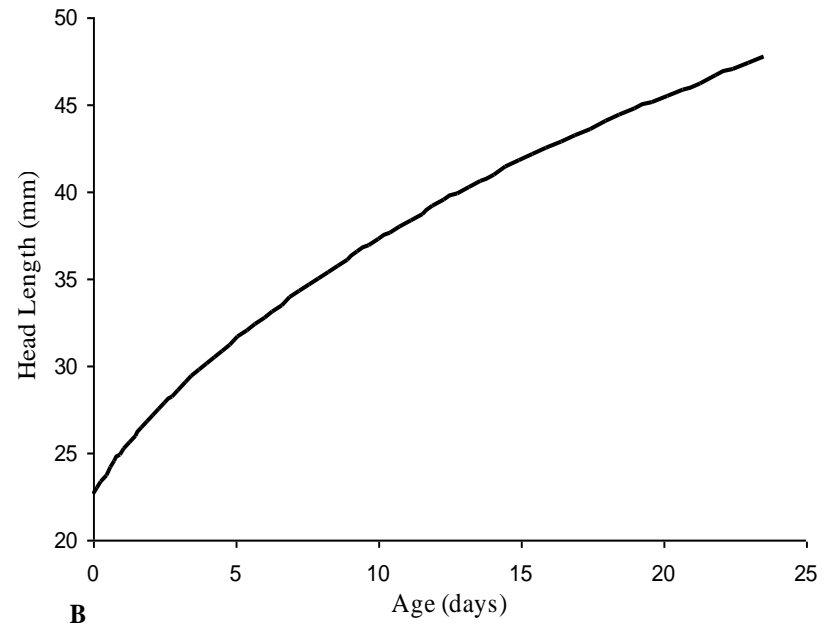
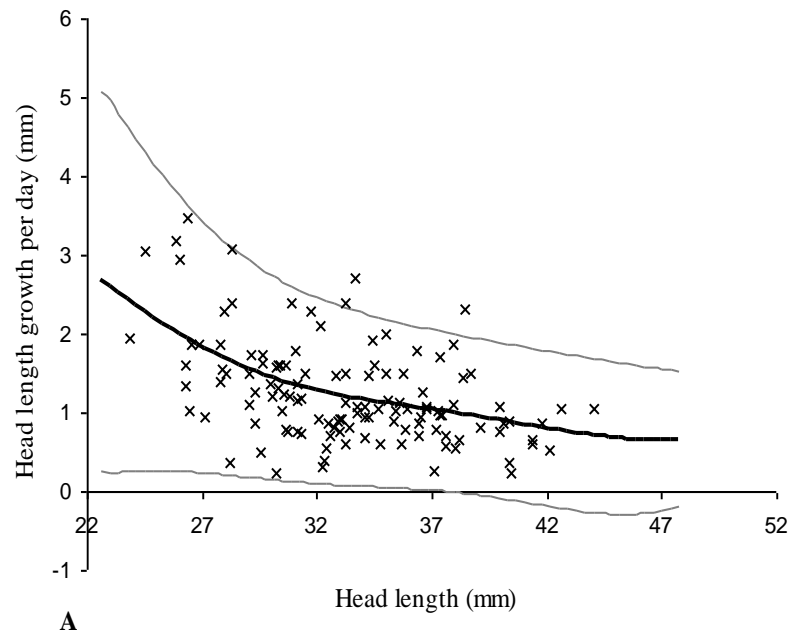


Figure 3.3: **A:** Growth rates (mm/day) of the head length of Damara Tern chicks in Namibia. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown (see text). **B:** Growth curve of head length (mm) in relation to age in days, transformed from the trajectory of the mean in A.

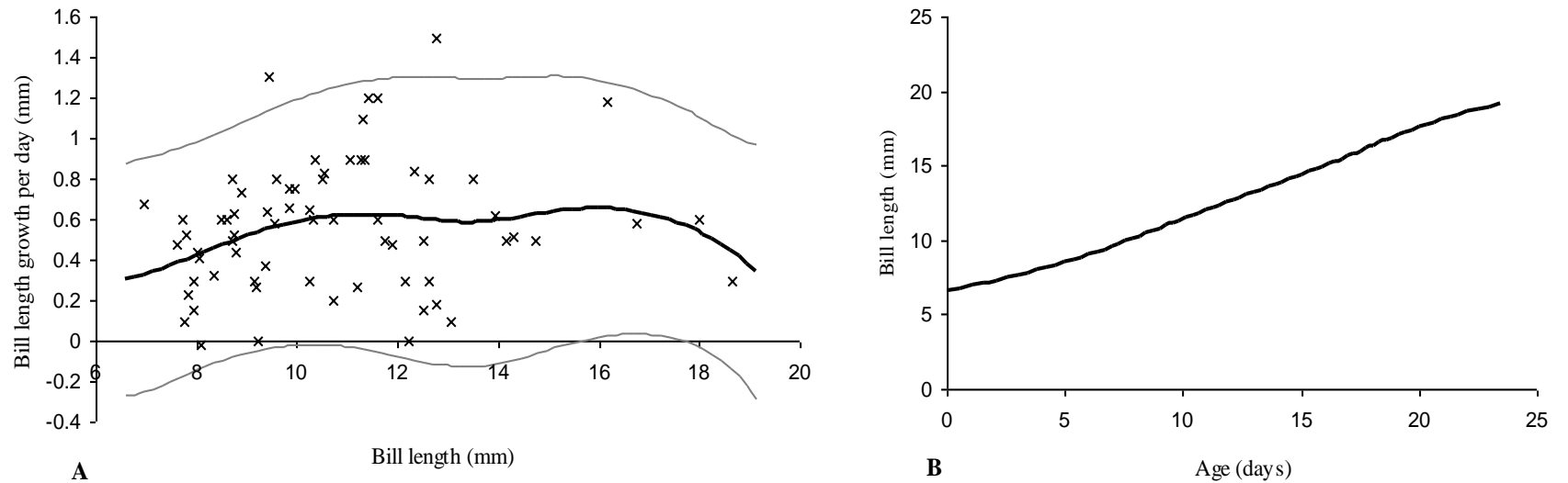


Figure 3.4: **A:** Growth rates (mm/day) of the bill length of Damara Tern chicks in Namibia. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown (see text). **B:** Growth curve of bill length (mm) of Damara Tern chicks in relation to age in days, transformed from the trajectory of the mean in A.

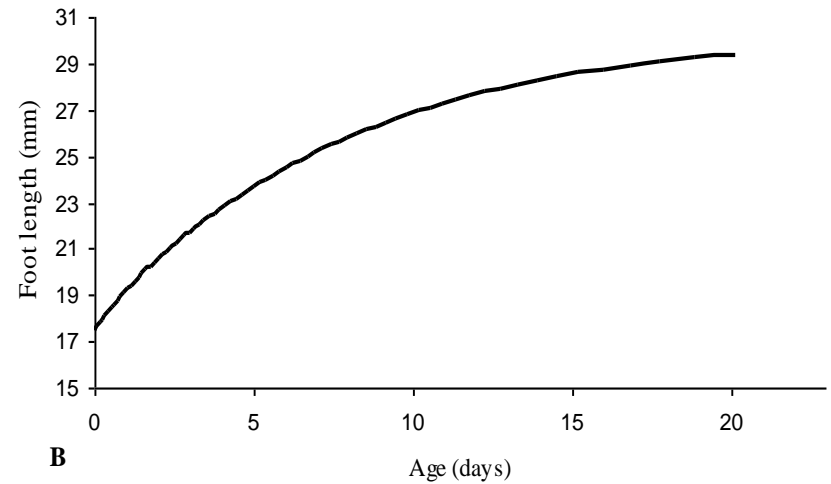
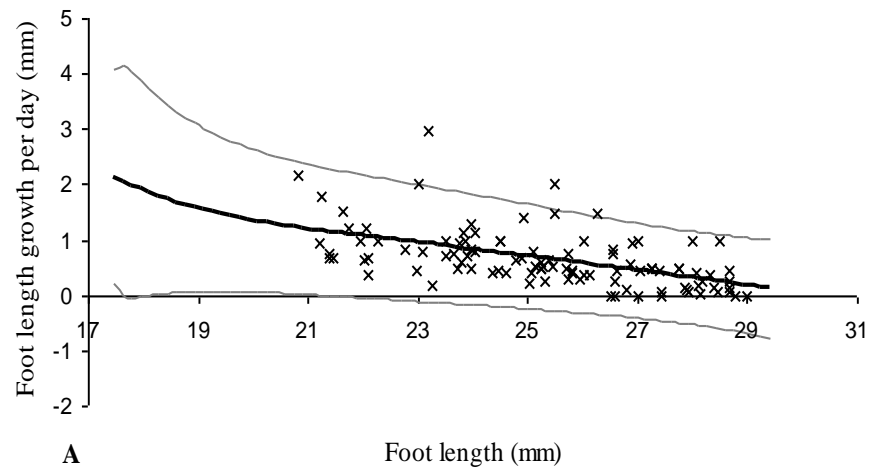


Figure 3.5: **A:** Growth rates (mm/day) of the foot length of Damara Tern chicks in Namibia. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown (see text). **B:** Growth curve of foot length (mm) of Damara Tern chicks in relation to age in days, transformed from the trajectory of the mean in A.

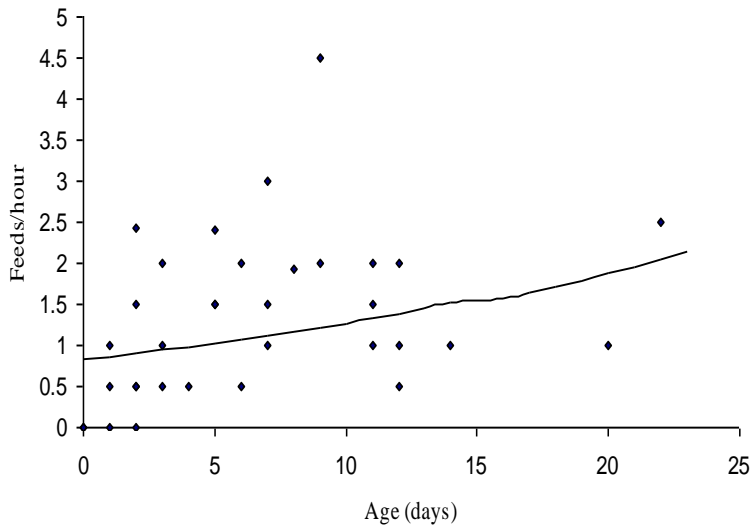


Figure 3.6: The feeding rate (feeds/hour) of Damara Tern chicks in Namibia in relation to age (days). The smoothed curve illustrates the modelled feeding rate (feeds/hour) using a generalized linear model (see text).

Chapter 4

Immature survival and age at first breeding of
Damara Terns *Sterna balaenarum*: conservation from
a non-breeding perspective



Immature survival and age at first breeding of Damara Terns: conservation from a non-breeding perspective

Introduction

To assess and ensure the long-term viability of any population requires an understanding of its life-history. Immature survival and the age at which a bird first breeds are important parameters in the life-history of seabirds (Lack 1967, Burger and Gochfeld 1986, Sandvik *et al.* 2008). However, long-term studies are required to attain these parameters. Such studies of seabirds are rare (Breton *et al.* 2006), and in small seabirds such as terns there are often methodological and logistic problems in studying their population ecology (Becker and Wendeln 1997). Because many seabirds migrate to isolated or inaccessible areas during non-breeding seasons, taking their fledged offspring with them, there are often periods of unobservability following fledging. Thus few studies have reported reliable estimates of survival rates for immatures (Ezard *et al.* 2006, Sandvik *et al.* 2008).

Age of first breeding, on the other hand, has been reported for several species of terns (reviewed by Mundkur 1992, Becker and Wendeln 1997, Becker *et al.* 2001). Age at first breeding may be influenced by a number of factors, such as physiological maturity, non-breeding migration, learning of food availability

and predation risks at breeding grounds and acquiring skills sufficient to feed offspring (Harrington 1974, Chabrzyk and Coulson 1976, Wooller and Coulson 1977, Danchin *et al.* 1991, Mundkur 1992, Ludwigs and Becker 2002). With the exception of river terns (e.g. Indian River Tern *Sterna aurantia*), which tend not to migrate and generally have permanent and reliable access to food resources (Mundkur 1992), terns exhibit delayed or deferred maturity and initiate breeding at the age of two to three years (Mundkur 1992), and up to five years for some species (Harrington 1974). Other long-lived seabird species do not breed until seven years of age (Lack 1968, Cramp 1985).

Damara Terns breed along the desert mainland of southern Africa during the austral summer and migrate to West Africa for the non-breeding season (Simmons 2005a). Successful breeding attempts result in one fledged chick per pair and fledging dependency extends for up to two and a half months (Williams and Meyer 1986). Damara Terns breed in harsh desert environments with high risks of predation and the probability of a breeding attempt being successful is less than 40% (Chapter 2). Like most terns, Damara Terns feed by plunge-diving for prey; this skill requires considerable time to perfect and explains the extended post-fledging dependency (Ashmole and Tovar 1968, Ashmole 1971, Feare 1975, Burger 1980, Cramp 1985,).

In the light of these factors I predict that Damara Terns share the life-history traits of most terns by displaying delayed (or deferred) maturity and thus relatively high immature survival. Breeding Damara Terns are threatened by habitat loss due to coastal development (R.J. Braby unpubl. data) and disturbance caused by off-road driving (Braby *et al.* 2001, Williams *et al.* 2004, Chapter 8). In addition, non-breeding and immature Damara Terns are trapped for food in their non-breeding grounds (Braby 2010, Annex 1). However, the actual number of individuals which are killed, and the impact of this mortality on the global population, is unknown (Braby 2010). It is thus important to investigate life-history parameters that deal with life-stages outside of the breeding season to find a holistic approach to the conservation of the species, both in breeding areas, and in non-breeding areas.

The objectives of this study are two-fold: to report the first information of (a) estimates of immature survival and (2) age at first breeding of Damara Terns. The study is based on 10 years of capture-mark-recapture data at two breeding colonies on the coastline of central Namibia.

Study area

This study took place at Horses Graves (22° 42'S, 14° 33'E), 4 km south of Swakopmund, and at Caution Reef (22°44S, 14°32E), 8 km south of Swakopmund (Figure 4.1). The habitat at Caution Reef consists mainly of

open and sparsely vegetated sandy plains with a raised gravel ridge through the centre (Braby *et al.* 2001), and the area comprised approximately 2.5 km². Horses Graves consists of a series of barchan, linear, and crescent dunes separated by gravel plains in which the terns breed (Braby *et al.* 2001), and the area comprised approximately 3.5 km². A more detailed description of the study area is given in Chapter 1.

Methods

Incubating adults were trapped on their nests using a netted snap-trap controlled by remote trigger from a distance of up to 200 m. Adults and chicks were trapped during the breeding seasons (October–February) from 2000/01 to 2009/10. Chicks were ringed when first found with a 2.8 mm SAFRING stainless steel rings on the right leg, and a breeding season specific colour ring on the left leg. Adults received the same combination along with an additional colour ring on the left leg specific to breeding site.

Multi-state capture-mark-recapture models were used to estimate the age at first breeding (Colbert *et al.* 1994, Lebreton *et al.* 2003). For this analysis, data on Damara Terns ringed either as nestlings (678 individuals) or adults (214 individuals) were used. The data on adult terns were included to estimate breeder recapture probabilities. Two states were defined, immature and breeder. All birds ringed as nestlings were initially assigned to the

immature state. The age-specific movement probability from the immature state to the breeder state was then used as an estimate of the probabilities of first breeding at a given age. In this analysis, the maximum age at which all individuals start to breed needs to be assumed (Lebreton *et al.* 2003). Values were explored for this parameter up to a maximum of six years.

Only breeding birds were trapped, and the recapture probability in the immature stage was therefore set to zero. As a result, yearly age-specific survival was not estimated for immature birds, but an average estimate of annual survival during that life stage was obtained.

An added complication was that nestlings were ringed at variable ages, ranging from the day of hatching until shortly before fledging. The immature survival rate thus contained a component of pre-fledging mortality. To account for the resulting heterogeneity, the age when a nestling was last seen (ranging from 0.5 to 23 days) was used as an individual covariate in the analysis. This estimate of juvenile survival corresponds to an individual with mean age when last seen in the nest; this was 4.7 days. I included nestling age as a linear covariate into the models, mainly to account for heterogeneity in observed survival caused by variable age at ringing. However, I used this relationship to also estimate expected survival for individuals that reach fledging age (23 days).

In this analysis, models in which the recapture probability of breeders was constant, year-dependent, or a linear function of effort (number of hours spent trapping) were considered. Breeder survival was kept constant and a common value for both colonies was assumed.

The fit of the most general model without individual covariates (with year specific recapture probabilities) using the median- \hat{c} procedure in program MARK (White and Burnham 1999) was examined. This test showed little sign of overdispersion ($\hat{c}=1.23$, $se=0.02$), and including the individual covariate should account for some remaining heterogeneity.

The standard optimization routine used in program MARK, based on a Newton-Raphson algorithm, did not always appear to converge properly. Therefore most models were run using the alternative optimization based on simulated annealing, also provided in program MARK. All models were run in program MARK 6.0 (White and Burnham 1999), and the sample-size adjusted Akaike's information criterion for model selection was used.

Results

Model selection favoured a model which assumed that the maximum age at first breeding was four years (Model 1, Table 4.1), that immature survival

was positively related to the age when a nestling was last seen in the nest, and that the recapture rate was positively related to field effort. This model suggested that the probability of starting to breed was zero for 1-year old birds, 0.06 (95% confidence interval (CI) =0.007–0.36) for 2-year old birds, 0.26 (CI=0.03–0.78) for 3-year old birds, and made the assumption that all birds breed at 4-years old. Data sparseness could have partly affected this result, and I interpret it as showing that most Damara Terns started breeding at either 3 or 4 years of age, with an estimated 94% (26% and 68% respectively) commencing breeding at these ages.

Average annual survival of immature terns was 0.59 (CI=0.48–0.68), and adult survival was 0.87 (CI=0.73–0.94). My estimate of immature survival contains an element of pre-fledging mortality because it is mean annual survival from mean ringing age (nestlings 4.7 days old) to breeding age. I included nestling age as a linear covariate into the models, mainly to account for heterogeneity in observed survival caused by variable age at ringing. However, this relationship can be used to estimate expected survival for individuals that reach fledging age (23 days). Based on that relationship the best estimate for annual immature survival would be 0.84 (0.64–0.94), much closer to adult survival.

The youngest record of breeding was 2 years and the oldest was 15 years. The 15-year old bird was ringed as a chick at Caution Reef in November 1993, and trapped as a breeder on its nest at Caution Reef in December 2004, and again on its nest at Caution Reef in November 2008.

Discussion

My results show that, as with many seabirds, Damara Terns display high immature survival and delayed maturity. These are the first estimates of immature survival and age at first breeding for this species.

The estimated immature annual survival rate of 0.59 was lower than the adult survival rate of 0.87. However, it was higher than those of other tern species (0.27 for immature Common Terns *Sterna hirundo*, Becker *et al.* 2001; between 0.16–0.30 for immature Roseate Terns *Sterna dougallii*, Spendelow 1991, Spendelow *et al.* 2002). My estimate of immature survival contained an element of pre-fledging mortality because it is the mean annual survival from mean ringing age (4.7 days old nestling) to breeding. The calculation required for the immature survival of 0.84 relied on the assumption that survival during the nestling stage is constant, due to the linear relationship used. However, nestling survival probably improves with nestling age. I had few individuals ringed close to fledging age. Therefore, this estimate of immature survival is likely to be too high because I was

attributing some immature mortality to the nestling stage. Nevertheless, it may be a realistic upper bound. In a study of Atlantic Puffins *Fratercula arctica*, where only juveniles that had fledged were considered, survival rates of immatures were not depressed in relation to adults (Sandvik *et al.* 2008). I predict that my estimate of 0.59 would have been higher if only immatures that had fledged were considered, especially when taking into account the high risk of predation during pre-fledging.

Of the six small terns closely related to the Damara Tern (Chapter 1), the only other species for which age at first breeding is known is the California Least Tern *Sterna antillarum browni*, which breeds at age three years, and rarely at age two years (Massey and Atwood 1981). The age at first breeding of three to four years of Damara Terns is similar. It is also typical of most plunge-diving terns where an extended period is needed to learn this skill, and immatures are much less efficient at foraging than adults (Dunn 1972, Ainley *et al.* 1986). The difficulty adults face in bringing sufficient and adequate food to their young is therefore an important factor in delayed maturity (Lack 1968, Ashmole 1971). Like many seabirds, Damara Terns migrate thousands of kilometers to non-breeding areas and immatures probably remain in these areas for at least two years before they return to their breeding grounds (Ashmole 1971, Harrison 1983, Cramp 1985).

In some tern species, it has been found that within-species variation exists in the age at first breeding with different populations of birds (Mundkur 1992). The age of breeding is decreased when more food is available and competition for nest sites is reduced in some seabird species (Lack 1968). In other seabird species, recruitment has been linked to population size (Crespin *et al.* 2006) and predation risk (Finney *et al.* 2003). Because Damara Terns do not breed in dense colonies and breeding habitat is not a constraining factor in the immense desert coastline, recruitment is unlikely to be affected by competition for nest sites. It is uncertain whether Damara Terns which breed in areas with lower predation risks start breeding at a younger age and this should be explored in further studies.

Because Damara Terns exhibit delayed maturity, high immature survival and lay only one egg with low probabilities of success (Simmons and Braine 1994, Chapter 2), the generational turn-over rate of the species is low.

Extended periods are spent by immature and pre-breeding Damara Terns in non-breeding grounds in West Africa, and breeding Damara Terns migrate along c. 4000 km of West African coastline twice a year. Given an adult survival rate of 0.87, the estimated number of adults dying per 1000 adults is 130 per year. Given the average fledging success rate of 0.36 (Chapter 2), and a juvenile survival of 0.84 per year, 500 pairs of terns would produce 180 fledglings of which an estimated 107 would survive to three years and 90 to

four years. Based on these best current estimates of survival and recruitment, it appears that the breeding productivity is insufficient for population growth.

Migratory seabirds such as the Damara Tern are trapped and sold for food in countries along their migratory route (Braby 2010, Annex 2). In light of these factors, and the apparent shortfall in recruitment, special consideration should be given toward the protection of Damara Tern populations in their non-breeding countries in addition to the conservation management of breeding areas.

Table 4.1: Summary of model selection analysis for age-at-first breeding (alpha) and survival of Damara Terns in Namibia. I examined models that assumed the maximum age to start breeding was 3, 4, 5 or 6 years. Annual survival during the immature period (Sj) was either kept constant (depicted by () in the model descriptions), or assumed to be a linear function of the age when last seen in the nest ((age) in model descriptions), to account for a variable component of nestling mortality because individuals were ringed at different ages). Immature birds could not be trapped, and I examined models where breeder recapture probability (Pa) was either constant (), varied over the years (year), or a linear function of effort (effort). K is the number of estimated parameters.

	Model	AICc	Delta AICc	AICc Weights	K	Deviance
1	{Sj(age)Sa()Pa(effort)alpha(age4)}	682.861	0.000	0.622	8	666.687
2	{Sj(age)Sa()Pa(year)alpha(age4)}	684.352	1.491	0.295	15	653.764
3	{Sj()Sa()Pa(year)alpha(age3)}	688.060	5.198	0.046	12	663.679
4	{Sj()Sa()Pa(year)alpha(age4)}	689.758	6.897	0.020	14	661.244
5	{Sj()Sa()Pa(year)alpha(age5)}	690.864	8.003	0.011	15	660.277
6	{Sj()Sa()Pa(year)alpha(age6)}	692.591	9.730	0.005	16	659.925
7	{Sj(nage)Sa()Pa()alpha(age4)}	698.032	15.171	0.000	7	683.896

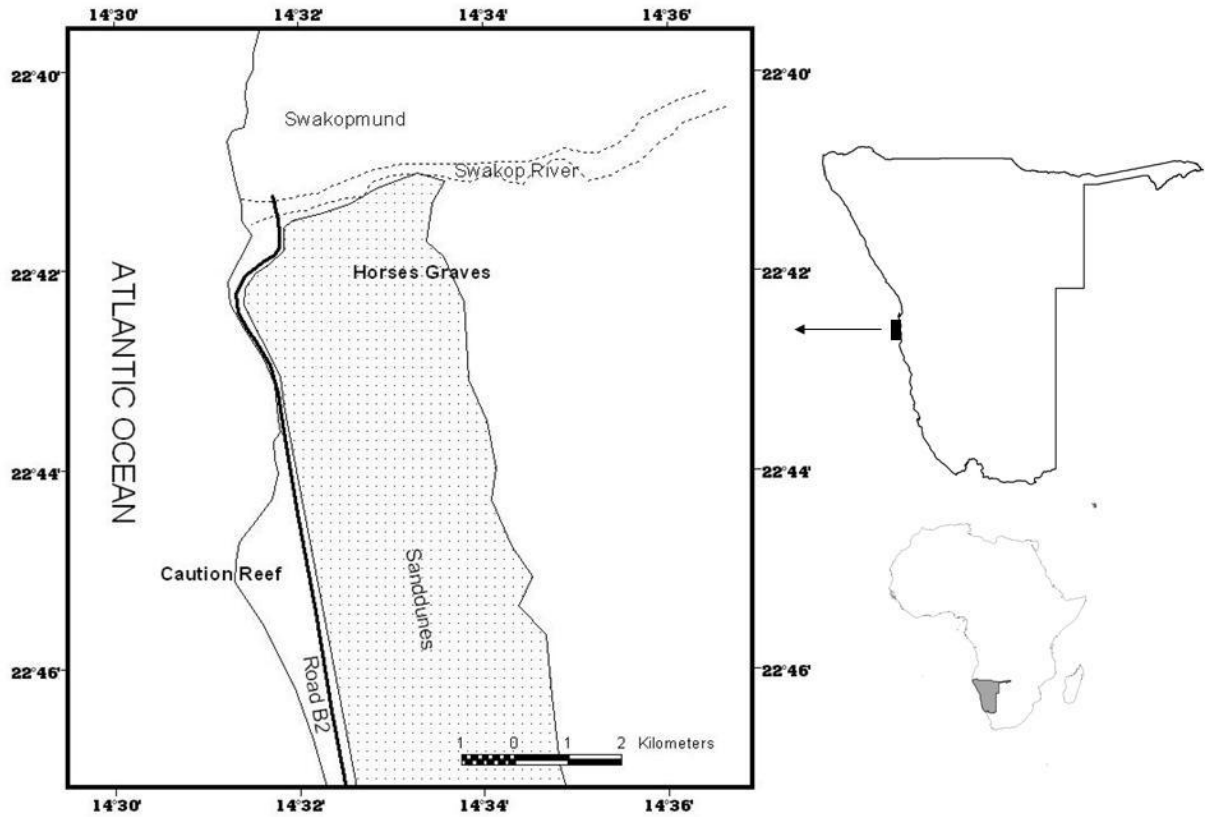


Figure 4.1: Location of two Damara Tern breeding colonies, Caution Reef and Horses Graves, in central Namibia (see Plate 3 for a satellite image).

Chapter 5

Annual survival and dispersal of a seabird adapted to a stable environment: implications for conservation



Nicole Braby

Annual survival and dispersal of a seabird adapted to a stable environment: implications for conservation

Introduction

When habitat becomes unsuitable for a species it is of great conservation interest to know if and how far the individuals will move to resettle in other suitable areas. Knowledge of dispersal is therefore vital when considering wildlife management at the landscape scale. The level to which a species displays fidelity or dispersal depends on the environmental conditions it has evolved in (McPeck and Holt 1992, Clobert *et al.* 2001). We expect such a life-history strategy is dependent on various environmental conditions, such as food availability, predation rates, and how much habitat is available.

Generally seabirds are long-lived and faithful to their breeding areas (Beadell *et al.* 2003), but species living in highly variable environments are nomadic and may suffer higher rates of mortality (Renken and Smith 1995a, b; Robinson and Oring 1997). The tendency for individuals to return to areas where they were hatched (natal philopatry), and/or previously bred (breeding philopatry), has been well-documented for a variety of seabirds, including gulls (Coulson and White 1958, Southern 1977, Southern and Southern 1980, Blockpoel and Courtney 1980, Stenhouse and Robertson 2005) and terns (Austin 1940, 1949, Atwood and Massey 1988, Becker and Wendeln 1997, Spendelov *et al.* 1995, 2008, 2010, Becker *et al.* 2001, Lebreton *et al.* 2003,

Devlin *et al.* 2008). Because prior knowledge exists on available nesting sites, food resources and predation pressures, it is often considered a safer strategy for birds to return to a previous breeding site or natal territory than to immigrate to a new area with unknown resources and/or risks (Renken and Smith 1995b). Factors such as predation, low reproductive success and changes in habitat have been implicated in causing breakdowns in fidelity (McNicholl 1975, Erwin 1977, Conover and Miller 1978). However, in spite of the obvious negative impacts of these factors, continued re-use of adversely affected sites has been reported for several seabird species (Austin 1940, 1949, Southern and Southern 1979, Peterson 1980, Southern *et al.* 1980, Southern and Southern 1982). The level to which species display fidelity to their breeding sites is important in understanding the management and protection of these species.

Damara Terns *Sterna balaenarum* breed predominantly on the coastline where the harsh Namib Desert meets the cold and dynamic Benguela current (Simmons and Braine 1994). Damara Terns feed primarily inshore where physical fluctuations result in biological patchiness and high variability (Branch *et al.* 1987). Recruitment of prey species like Anchovy *Engraulis encrasicolus* in the northern Benguela system shows high inter-annual variability (Boyer *et al.* 2001). However, the Benguela system is not as variable as say, the Humboldt system, and seabirds here are generally adapted to a more stable supply of food (Crawford *et al.* 2006). I would expect

that Damara Terns have adapted to this stable food supply by displaying high annual survival and fidelity to their breeding sites. In addition, although there is ample available undisturbed habitat along the coastline of Namibia, Damara Terns are found breeding in specific areas (Clinning 1978). However, predation rates are high and predation has been considered the major driving force in the evolution of the unique one-egg clutch trait of this tern (Frost and Shaughnessy 1976; Clinning 1978). High or fluctuating predation has resulted in lower fidelity in some other tern species, and even caused mass periodic dispersal in other species of terns (Oro et al. 1999). The Damara Tern is globally Near-threatened (IUCN 2009) and it is the only small tern that predominantly lays one egg (Simmons and Braine 1994; de Villiers and Simmons 1997). During the non-breeding season (May–September) Damara Terns migrate to West African countries such as Gabon, Cameroon and Nigeria (Williams et al. 2004). The Benguela Upwelling System is currently undergoing changes due to over-fishing and climate change (Clark 2006). In addition, Damara Tern breeding grounds are threatened by off-road driving and coastal development (Braby et al. 2001; Braby et al. 2009; RJ Braby unpubl data). It is thus becoming increasingly important to understand the life-history adopted by the species. Few demographic parameters exist for the Damara Tern and these are necessary to test whether the current management approach of protecting specific breeding sites is appropriate. The objective of this chapter is to provide estimates of (a) adult survival and (b) dispersal probabilities of Damara

Terns based on 10 years of capture-mark-recapture data of adult Damara Terns breeding at two close-proximity colonies along the central coastline of Namibia.

Study area

This study took place at Caution Reef (22°44S, 14°32E) and Horses Graves (22° 42'S, 14° 33'E) south of Swakopmund within the Dorob National Park (Figure 4.1 in Chapter 4). The habitat at Caution Reef consists mainly of open and sparsely vegetated sandy plains with a raised gravel ridge through the centre (Braby *et al.* 2001). Horses Graves comprises a series of barchan, linear, and crescent dunes separated by gravel plains in which the terns breed (Braby *et al.* 2001). For a more detailed description of the study area, see Chapter 1.

Both Caution Reef and Horses Graves are fenced off from the public to ensure minimal disturbance from off-road driving. These two areas are protected from coastal development.

Methods

Incubating adults were trapped on their nests using a netted snap-trap controlled remotely by a trigger from a distance of up to 200 m. Once

successfully trapped, SAFRING metal rings were placed on the right leg; and a unique combination of colour rings pertaining to the breeding season were placed on the left leg. Damara Terns were trapped between October and February, when they are breeding during the austral summer months. I used data collected on 214 adult terns between October 2000 and December 2009, defining the survival intervals to run from 1 October until 30 September of the following year.

Multi-state capture-mark-recapture models (Spendelov *et al.* 1995) were used to estimate adult survival rate at the two colonies, and the annual movement probabilities between them. These models are extensions of classical capture-mark-recapture models (Lebreton *et al.* 1992) and provide estimates of survival and movement while accounting for the recapture probabilities at the two colonies.

The models consist of three components. The first estimates local survival, which is the probability of surviving from one year to the next, and staying in the study area. I cannot distinguish between mortality and permanent emigration to sites not studied here, and my survival estimates will therefore tend to be biased slightly low. The second component estimates recapture, which is the probability of capturing an individual given that it is alive and in the study area. The third component estimates movement between the colonies.

The most general model that could be fitted to the data allowed all components to differ between the colonies and the recapture rates to vary over the years. Simplified versions of this model were considered and sample-size adjusted Akaike's information criterion (AICc) was used to evaluate model performance (Burnham and Anderson 2002). All models were fitted in program MARK 6.0 (White and Burnham 1999).

The models used make the assumption that individuals have similar survival, recapture, and movement probabilities. This assumption was tested for the most general model using the median- \hat{c} procedure in program MARK. This test showed little sign of overdispersion ($\hat{c}=1.19$, SE=0.03), and thus suggested that this model captured the structure in the data well. Parameter estimates in the text are given with the 95% confidence interval in brackets.

Results

Model selection based on AICc favoured a model that kept the annual survival rate constant across colonies, assumed that the recapture rate was a linear function of effort (number of hours spent trapping per season), and that movement probabilities were equal in both directions (Model 1, Table 4.1). According to this model, annual local survival was 0.88 (0.73–0.96). The annual movement probability was 0.06 (0.03–0.12), and the

recapture probabilities were positively related to effort and ranged from 0.041 (0.023–0.076) to 0.18 (0.10–0.30).

Model 2 was 2.4 times (ratio in AICc weights) less well supported by the data than the best model. According to this model, terns had lower annual survival at Horses Graves colony (0.86; CI: 0.69 to 0.95) than at Caution Reef colony (0.91; CI: 0.66 to 0.98).

Discussion

My results show that Damara Terns have high survival rates and are faithful to their breeding sites, life history traits typical of seabirds adapted to stable environments (Beadell *et al.* 2003). Despite variability of prey in the near-shore ecosystem where Damara Terns feed, the Benguela Upwelling System is abundant in prey species such as Anchovy (Crawford *et al.* 2006). The most similar upwelling system, in the Humboldt Current, experiences more frequent El Niño perturbations and seabirds feeding on the same species of prey there have a demography that enables them to recover more rapidly from population decreases due to these perturbations (Crawford *et al.* 2006). No comparative demographic parameters exist for the Peruvian Tern *Sterna lorata*, an ecological equivalent which is adapted to a more variable environment than the Damara Tern (Crawford *et al.* 2006). Such a comparison would be necessary to determine how similar species have adapted to different environments. However, my results conform with the

suggestion by Crawford *et al.* (2006) that seabirds reliant on the Benguela system are adapted to a more stable supply of food.

My annual survival estimate of 0.88, albeit with wide confidence intervals owing to a relatively small data set, is consistent with published estimates of adult annual survival in other terns and gulls, among which survival estimates are typically high (Table 5.2). The estimated annual survival probability is probably lower than the true value because I could not distinguish between mortality and permanent emigration from the study area. To determine the relative importance of permanent emigration will require a study of inter-colony movement between all major colony sites. No large colonies exist in the vicinity of our study area, but it is possible that three small colonies (<30 pairs) within 30 km of the study site may have absorbed a small number of emigrants. Reed and Oring (1993) found that expanding their study site gave a more accurate picture of site fidelity and dispersal in Spotted Sandpipers *Actitis macularius*. However, previous multi-site studies on breeding terns showed that terns nesting on colonies closer together experience higher rates of movement than those further apart (Spendelow *et al.* 1995, Devlin *et al.* 2008). The two colonies in this study were extremely close together (*c.* 4 km), and very little movement was observed between the two sites. Due to this low movement probability I assume that there is little emigration of Damara Terns from colonies, but a multi-site study would be required to test this assumption. Spendelow *et al.*

(2010) found that a small sample of Roseate Terns, even after breeding in one region for many years, may move up to 400 km to another region to breed.

The low local dispersal probability of 0.06 indicated that Damara Terns show fidelity to the same breeding area. Low dispersal probabilities may have evolved in the species as a result of previous knowledge of breeding sites, like associated predation risk factors and prey availability. Damara Terns suffer high predation rates, even at the study areas in question (Braby *et al.* 2001, Braby *et al.* 2009, Chapter 2). Generally, increased predation rates at tern colonies result in low site fidelity, or mass movement from breeding areas (Oro *et al.* 1999, Spindel *et al.* 2002). It thus comes as a surprise that Damara Terns display little dispersal from their study sites. This tern may have evolved with high rates of predation, and thus shows fidelity to sites due to learned and acquired knowledge of predation risks at these sites. Little or no change to habitat occurs at either breeding sites (Horses Graves and Caution Reef, pers. obs.) and unpredictable breeding habitat usually yields little fidelity (Robinson and Oring 1997). For instance, California Least Terns *Sterna antillarum browni*, which only occupy several secure breeding sites, display a 79% rate of return to the same breeding site yearly (Atwood and Massey 1988), but interior Least Terns *Sterna antillarum*, which breed on sandbars and islands in rivers (a habitat that is continuously changing), display yearly return rates of only 42% (Renken and Smith 1995b). Species which are not accustomed to changing habitats are generally more site

faithful and they may fail to move if their breeding habitats are impacted by humans, which would therefore reduce their ability to breed successfully (Southern and Southern 1982).

Prior to this study no details of the demography of Damara Terns were known, which in the past has (1) prevented basic population modeling, and (2) prevented meaningful comparisons with other terns. Such comparisons could help determine whether or not species considered closely related share important demographic characteristics and would better our understanding of similar life-history strategies (Stenhouse and Robertson 2005).

Demographic parameters also help us find appropriate conservation approaches to ensure the species survival. Damara Terns migrate a total of *c.* 8000 km each year and breed in harsh desert environments with high rates of predation, but feed in highly productive waters where food is abundant (Crawford *et al.* 2006). Low breeding success (probability of less than 0.4 of nests surviving predation per season per pair, Chapter 2), high annual survival and fidelity to breeding sites may have evolved as a response to these conditions. In light of this, the most important management approach for the population viability for seabirds such as the Damara Tern, which display high rates of fidelity, may be long-term maintenance and protection of current colony sites.

Table 5.1: Summary of model selection analysis for survival and movement of Damara Terns in Namibia. The model components were survival (Sh at Horses Graves colony, and Sc at Caution Reef colony), recapture probability (Ph and Pc at the two colonies, respectively), movement from Horses Graves to Caution Reef (Ψ_{hc}), and movement in the opposite direction (Ψ_{ch}). I considered variable recapture rates over the years (year), or as a linear function of effort (effort; number of hours spent trapping). K is the number of estimated parameters.

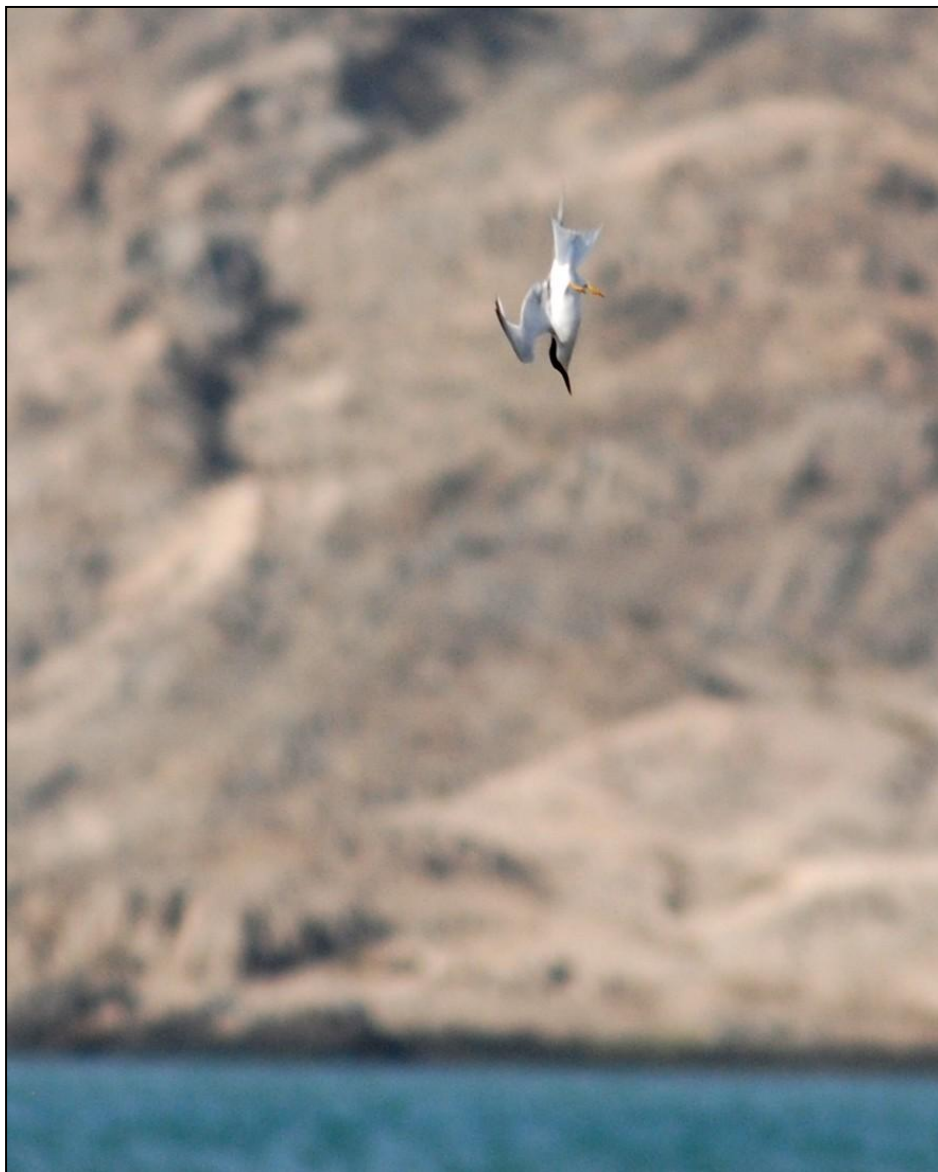
Model	AICc	Delta	AICc	Weights	K	Deviance
		AICc	AICc			
1 {Sh()=Sc()Ph(effort)=Pc(effort) Ψ_{hc} ()= Ψ_{ch} ()}	484.675	0.000	0.573	4	156.475	
2 {Sh()Sc()Ph(effort)=Pc(effort) Ψ_{hc} ()= Ψ_{ch} ()}	486.383	1.709	0.244	5	156.103	
3 {Sh()Sc()Ph(effort)=Pc(effort) Ψ_{hc} () Ψ_{ch} ()}	488.136	3.461	0.102	6	155.758	
4 {Sh()Sc()Ph(effort)Pc(effort) Ψ_{hc} () Ψ_{ch} ()}	489.924	5.249	0.042	7	155.432	
5 {Sh()=Sc()Ph(year)=Pc(year) Ψ_{hc} ()= Ψ_{ch} ()}	490.310	5.636	0.034	10	149.372	
6 {Sh()Sc()Ph(year)=Pc(year) Ψ_{hc} () Ψ_{ch} ()}	494.670	9.995	0.004	12	149.345	
7 {Sh()=Sc()Ph()=Pc() Ψ_{hc} ()= Ψ_{ch} ()}	497.103	12.428	0.001	3	170.967	
8 {Sh()Sc()Ph(year)Pc(year) Ψ_{hc} () Ψ_{ch} ()}	505.763	21.088	0.000	20	142.148	

Table 5.2: Estimates of annual survival rates of terns and gulls. 95% confidence intervals (CI), or standard errors (SE), are given when available.

	Survival Rate	Reference
Sternidae		
Damara Tern <i>Sterna balaenarum</i>	0.88 (0.73-0.96)	This study
Least Tern <i>Sterna antillarum</i>	0.85 (SE=0.06)	Reuken and Smith 1995a
Common Tern <i>Sterna hirundo</i>	0.88 (SE=0.04)	Nisbet and Cam 2002
	0.91 (0.87-0.97)	Becker et al. 2001
Arctic Tern <i>Sterna paradisaea</i>	0.74-0.84	Spendelow et al. 1995
	0.704–0.960	Devlin et al. 2008
Roseate Tern <i>Sterna dougallii</i>	0.8501	Lebreton et al. 2003
	0.0835 (SE=0.006)	Spendelow et al. 2008
	0.850	O'Neill et al. 2008
Sooty Tern <i>Onychoprion fuscatus</i>	0.91 (SE=0.01)	Feare and Doherty 2004
Royal Tern <i>Thalasseus maximus</i>	0.95	Collins and Doherty 2006
Laridae		
Kelp Gull <i>Larus dominicanus</i>	0.84	Altwegg et al. 2007
Herring Gull <i>Larus argentatus</i>	0.826-0.975	Pons and Migot 1995
Sabine's Gull <i>Xema sabini</i>	0.89 (SE=0.03)	Stenhouse and Robertson 2005
Ivory Gull <i>Pagophila eburnea</i>	0.86 (SE=0.04)	Stenhouse et al. 2004
Black-legged Kittiwake <i>Rissa tridactyla</i>	0.88 (SE=0.02)	Harris et al. 2000
	0.80 (SE=0.03)	Oro and Furness 2002
Black-headed Gull <i>Larus ridibundus</i>	0.90 (0.86-0.92)	Prévot-Julliard et al. 1998

Chapter 6

Prey capture success and chick diet of Damara Terns
Sterna balaenarum in southern Namibia



Jessica Kemper

Prey capture success and chick diet of Damara Terns *Sterna balaenarum* in southern Namibia

Introduction

The success of foraging seabirds is influenced by prey availability which is a function of both prey abundance and prey accessibility (Henkel 2006).

Especially for seabird species feeding close to the coastline, prey accessibility may be influenced by a number of environmental factors (Ainley 1977, Holm and Burger 2002, Peste *et al.* 2004, Henkel 2006, Baptist and Leopold 2010). Many terns feed by plunge-diving which is visually associated and requires considerable skill (Williams and Meyer 1986). I postulate that environmental factors affecting one plunge-diving tern, the Damara Tern *Sterna balaenarum*, include tidal phase, wind speed, water clarity, cloud cover and water depth.

Tidal phase and wind speed are known to influence the feeding ecology of terns (Dunn 1973, Cramp and Simmons 1983, Hulsman *et al.* 1989, Becker and Specht 1991, Frank 1992, Frank and Becker 1992, Becker *et al.* 1993, Brenninkmeijer *et al.* 2002, Peste *et al.* 2004, Paiva *et al.* 2008). Prey capture success or chick provisioning has generally been found to increase at low or receding tides (Peste *et al.* 2004, Brenninkmeijer *et al.* 2002, Paiva *et al.* 2006b), but some studies have shown increased success at high tide (Hulsman 1976, Burger 1982). Taylor (1983) found a decreasing capture rate at higher wind speeds, but Dunn (1972, 1973) found that capture rates increased with increasing wind speed.

Many studies have shown the effect of water clarity on the distribution and ecology of feeding seabirds (Ainley 1977, Haney and Stone 1988, Safina and Burger 1988, Abrahams and Kattenfield 1997, Holm and Burger 2002, Day *et*

al. 2003, Henkel 2006, Baptist and Leopold 2010). One would expect that in turbid water prey are more difficult to locate, but in clear water predators may be visible to prey too. Baptist and Leopold (2010) found a non-linear relationship of prey capture success in increasing water turbidity, with success least in very clear and very turbid waters, and greatest for moderate levels of turbidity.

In relation to cloud cover, Hawksley (1950, 1957) and Lemmetyinen (1972) showed that Arctic Tern *Sterna paradisaea* chicks gained weight on clear days but generally lost weight on foggy days. However, neither author considered prey capture success directly. Factors affecting prey capture success are important to study because they can influence various aspects of breeding success (Peste *et al.* 2004).

Damara Terns *Sterna balaenarum* feed mainly by plunge-diving into water (Simmons and Braine 1994). Feeding terns can be found in sheltered bays, lagoons, estuaries and in the surf zone along the open coast (Frost and Shaughnessy 1976, Clinning 1978, Williams and Meyer 1986, Braby *et al.* 1992). Small samples of prey items collected from chick regurgitations (Clinning 1978, Simmons and Braine 1994) have been found to be similar to that of related species, such as Peruvian Terns *Sterna lorata* (Zavalaga *et al.* 2008), and Little Terns *Sterna albifrons* (Bogliani *et al.* 1994, Catry *et al.* 2006, Paiva *et al.* 2006b).

I studied the prey capture success of Damara Terns breeding at two localities during two breeding seasons in southern Namibia as a function of six variables: wind speed, tidal phase, water clarity, cloud cover, water depth and locality. This chapter also presents new information on the diet of Damara Tern chicks in Namibia.

Methods and study area

Foraging observations

The prey capture success of Damara Terns was measured during two consecutive breeding seasons in 2007/08 and 2008/09 (October to March) at two breeding localities in southern Namibia: Grosse Bucht (26°43'S, 15°40'E) and Elizabeth Bay (26°55'S, 15°14'E, Figure 6.1). The environments of each area are described in Chapter 1. Both bays are affected by winds that can exceed 50 km/hour.

Observations on foraging terns were made throughout two breeding seasons, and during daylight hours. The observer watched from a vehicle or from the beach. Once a Damara Tern was recorded foraging, it was watched continuously using 8×42 binoculars. Its activities were timed (to the nearest second) until it flew back to the colony, landed, or flew out of sight. A single foraging bout consisted of a tern looking down while flying or hovering 1–5 m above the sea surface. The numbers of successful and unsuccessful dives were recorded during each foraging bout.

Five environmental conditions were recorded during each foraging bout: tidal phase, wind speed, water clarity, cloud cover and feeding location.

Tidal phase; four tidal phases were categorized: high tide (90 minutes before HT until 90 minutes after HT), receding tide (RT: next three hours), low tide (90 minutes before LT until 90 minutes after LT), and incoming tide (IT: next three hours).

Wind speed was estimated in the field (four categories; 1: calm to gentle breeze, 2: moderate breeze, 3: wind, 4: strong wind). When the observed descriptions of wind speeds were checked against the measured wind speeds at the weather station at Diaz Point (26°38'S, 15°05'E), the mean wind speeds in the four categories were approximately 10, 20, 30 and 45 km/hr

respectively. Using the midpoints between these values (15, 25 and 37.5 km/hour), as boundary points, there were only eight occasions (of 119 observations) when the assigned category differed from the measurement. For all except one of these, the wind speed at Diaz Point was greater than in the study area. Diaz Point is particularly exposed to winds, and is 11 km north of Grosse Bucht, and 33 km north of Elizabeth Bay. Wind conditions can vary considerably between these areas, depending on wind direction. Water clarity was classified on a three-point scale at Elizabeth Bay, where clarity was affected by sediments deposited into the bay as part of the diamond mining extraction process (Chapter 7). Water colour was used to estimate water clarity: a gradient was adopted, ranging from one to three, where 1=least turbid water (blue water) and three 3=most turbid water (brown waters). It must be noted that least turbid water here is still relatively turbid due to sediment deposits into the bay (and the natural turbidity of the area, CSIR 1996, 1997, 1998, Chapter 7).

Cloud cover was estimated in the field (a scale of 0–4; 0= no cloud, 4= completely overcast).

Feeding location was either Elizabeth Bay or Grosse Bucht.

Adults observed foraging were assigned to water depth; the shallows, in the surf zone, or behind the breakers.

A generalized linear model with a binomial distribution and a logistic link function was used to relate the number of successful dives (i.e. prey capture success) within the total number of dives of a foraging bout to the explanatory variables observed at the time of the bout. Within each foraging bout, the probability of success of each dive was therefore modelled as having the same explanatory variables. Variables considered were wind speed, tidal phase, water clarity, cloud cover, water depth and locality; for each variable, the first level was set as the baseline level in the generalized linear model. Analyses were performed in GenStat and the Akaike Information Criterion was used to

guide model selection (GenStat 12 Committee 2009). A generalized linear model with a Poisson distribution and logarithmic link function was used to relate the total number of dives counted during the observation period to wind speed. Because water clarity was only measured at Elizabeth Bay, the dataset for all explanatory variables (including water clarity) was analysed separately when investigating the influence of water clarity on prey capture success. The observation period was used as an offset variable (GenStat 12 Committee 2009).

Collection of prey items

Chick regurgitations and prey items dropped by adults while provisioning their chicks were collected at the following localities and time periods: Ogden Rocks (21°06'S, 13°34'E) on 19 December 1992, Durissa Bay Pans (21°15'S, 13°41'E) and White Stones (21°39'S, 13°56'E) during December 2009–March 2010, Caution Reef (22°44'S, 14°32'E) during October 1994–March 1995, Hottentots Bay (26°14'S, 14°59'E), Grosse Bucht, Elizabeth Bay and Marmora Pan (27°45'S, 15°34'E) during October 2007–April 2008 and October 2008–April 2009 (Figures 1.1–1.3 and 1.5 in Chapter 1).

Bomb calorimetry and energy content of fish

In order to estimate the energy content of the fish species fed to chicks, fresh specimens were collected using a small net from foraging areas at Grosse Bucht. Five specimens were measured (standard length), washed with fresh water and frozen. To determine the energy content, specimens were thawed and dried in an oven at 60° C until no further weight loss occurred (c. 7 days). Each dried specimen was crushed to dust in a mortar. These were converted into discs in a press and used to determine the calorific content in the Cal 2k bomb calorimeter. The energy content was given by the calorimeter in kilojoules per gram of dry mass.

Results

Prey capture success

Damara Terns were always observed foraging at sea. During 105 hours of observations for foraging terns, 389 foraging bouts, lasting a total of 16.6 hours, were observed. Within these 389 foraging bouts there were 865 dives of which 305 were successful (30.5%, SD=3.1%). The mean time spent foraging by a Damara Tern during a foraging bout was 153 seconds (SD=124 seconds, n=389).

Prey capture success increased with tide, and was highest at high tide (Modelled Probability of Prey Capture Success (PCS)=0.65, Figure 6.2A). The prey capture success at incoming tide was significantly lower than at high tide (the baseline level of the model) (P=0.008, Table 6.1; PCS=0.45, Figure 6.2A). The prey capture success at receding tide was also significantly lower than at high tide (P=0.001, Table 6.1; PCS=0.41, Figure 6.2A). In relation to high tide (baseline), the prey capture success was lowest at low tide (P<0.001, Table 6.1; PCS=0.33, Figure 6.2A).

There was a general tendency for prey capture success to increase with increasing wind speed. For wind level 1 (the baseline level of the model, c. 10 km/hr), PCS was 0.45 (Figure 6.2B). In relation to this baseline level, prey capture success was highest in wind 4 (c. 45 km/hr, P=0.001, Table 6.1; PCS=0.63, Figure 6.2B). The prey capture success was higher in wind 2 (c. 20 km/hr, PCS=0.47, Figure 6.2B) and in wind 3 (c. 30 km/hr, PCS=0.49, Figure 6.2B) than in wind 1. However, these were not significant (wind 2, P=0.769; wind 3; P=0.487; Table 6.1). The dive rate (dives per minute), however, decreased with increasing wind speed (Table 6.2). The product of the dive rate and the modelled prey capture success provides an estimate of

prey capture success rate (successful dives per minute), and this decreased with increasing wind speed (Table 6.2).

At Elizabeth Bay, water clarity was a significant explanatory variable in predicting prey capture success (Table 6.3, Figure 6.3). In relation to water clarity 1 (the baseline level of the model, least turbid water, PCS=0.37, Figure 6.3), the prey capture success was significantly lowest in water clarity 3 (most turbid water, $P<0.001$, Table 6.3; PCS=0.12, Figure 6.3). The prey capture success in water clarity 2 was also lower than the prey capture success in water clarity 1 ($P=0.008$, Table 6.3; PCS=0.24, Figure 6.3).

Cloud cover, water depth and locality (i.e. Grosse Bucht and Elizabeth Bay) were not significant explanatory variables in predicting prey capture success. Interactions between explanatory variables were not significant either.

Diet composition

A total of 55 prey items were collected at seven localities along the Namibian coast over 18 years (Table 6.4). Five could not be identified. The 50 identifiable prey items represented 15 fish species in 12 families, of which the most abundant was the Cape Silverside *Atherina breviceps* (18%, $n=10$). However, this species was not represented in any of the prey items found in the breeding colonies of southern Namibia. Species from the family Blennidae (14.2%, $n=8$), Southern Mullet *Liza richardsonii* (12.5%, $n=7$), and Cape Anchovy *Engraulis encrasicolus* (10.7%, $n=6$) were among the most abundant species collected. The mean length of 27 whole prey items was 5.67 cm (SD=2.56 cm, range=2.27–10.84 cm). The fresh masses of three items were obtained: two Cape Anchovy weighed 4 g (length=7.48 cm) and 3.48 g (length=9.26 cm) and a needlefish sp. (Belonidae) weighed 2.7 g (length=9.20 cm).

Bomb calorimetry and calorific value of fish

The five fresh specimens collected from foraging areas at Grosse Bucht were Southern Mullet. Of these five specimens, I was able to ascertain the energetic contents of four. The mean energetic content of these four specimens (mean length=5 cm) was 14.84 kJ/g dry mass (Table 6.5).

Discussion

Prey capture success

Tidal phase, wind speed and water clarity significantly affected the prey capture success of foraging Damara Terns, but cloud cover, water depth and feeding locality did not. The data showed that Damara Terns had an overall prey capture success of 30.5%. Simmons and Braine (1994) found a prey capture success of only 14% of four observations of foraging Damara Terns in northern Namibia. This low prey capture success compared to mine may be attributed to a smaller sample size in their study.

This study found that Damara Terns dived most successfully at high tide. Peste *et al.* (2004) found a higher prey capture success in foraging Little Terns during the receding tide, and Davies (1981) observed chicks being fed mostly in the last hours of the receding and incoming tide. Brenninkmeijer *et al.* (2002) estimated a better food intake rate for Little Terns during the receding tide. Because these studies were mainly conducted at lagoons, estuaries and salinas, the narrow channels of water which connect to the ocean would be greatly affected by the tide. Perhaps during the receding tide fish become more grouped and conspicuous in these channels and probably easier to catch (Peste *et al.* 2004). Paiva *et al.* (2006b) found that number of foraging Little Terns was higher during low tide; however this was not the case in this study where the number of Damara Terns was similar across all four tidal phases. Common Terns in Jamaica fed primarily during high tides

(Burger 1982). Hulsman (1976) had similar findings with Black-naped Terns *Sterna sumatrana*. However, Erwin (1977) found no effect of tides on Common Terns feeding in Maryland. Burger (1982) postulated that during low tides many areas of the bay may be exposed thus decreasing feeding habitat; and fish may tend to move back into the shallow areas of the bay with an incoming tide. Damara Terns frequently dived in shallow waters but water depth did not significantly impact prey capture success. Both Elizabeth Bay and Grosse Bucht have areas exposed at low tides and these areas are relatively shallow at high tide. Perhaps during high tide there is more feeding habitat, thus reducing competition between terns within the feeding grounds in the bays studied.

Wind speed significantly affected the prey capture success of foraging Damara Terns. Surprisingly, increased prey capture success correlated with strong winds. However, dive rate and prey capture success rate was highest in calm or light breeze conditions. Dunn (1972, 1973) found increasing prey capture success with increasing wind speed. Prey capture success in this study was higher at moderate and strong wind conditions compared with calm sea. This could be explained by the visibility of the predator, which is strengthened by the more vigorous hovering action at low wind speed and by the reflective properties of a smooth sea surface (Dunn 1973). Dive rates and prey capture success rates increased with decreasing wind speeds. Diving more frequently in calm conditions may be a result of a lower energetic cost per dive in calm conditions versus windy conditions. Taylor (1983) also found that dive rates decreased significantly with increasing wind speed in Common and Sandwich Terns *Sterna sandvicensis* but prey capture success showed no significant relationship. Paiva *et al.* (2006b) found that wind speed affected delivery rate of prey to Little Tern chicks. Stienen *et al.* (2000) reported an increasing chick provisioning rate in the Wadden Sea at increasing speeds of around 30 km/hr but found a rapid decline at speeds over

50 km/hr. This was beyond the scope of my study, but wind conditions are more likely to affect flight speed to and from the breeding area than foraging success itself. Dunn (1975) postulated that under most wind conditions, however, the fishing success of adult terns is not altered sufficiently to influence tern chicks' daily intake of food.

I found that prey capture success was highest in least turbid water at Elizabeth Bay. Previous studies have suggested that Damara Terns avoid murky, sediment-filled water (Simmons 2005a), but these have been mostly based on small sample sizes (10 foraging bouts, Simmons 2005a, b). Henkel (2006) suggested that plunge-divers should be associated to clear waters where prey can be located visually from a distance but contemplated studies that showed species like terns prefer more turbid water (Haney and Stone 1988, Safina and Burger 1988). Prey may avoid the surface layers in clear waters to escape from plunge-diving predators. Plunge-divers like terns may prefer turbid waters where prey may concentrate in the upper layers. The greatest upwelling cell in the Benguela Upwelling System is found near Lüderitz (Shannon 1989). Natural water turbidity is thus generally quite high around Grosse Bucht and Elizabeth Bay (CSIR 1996, 1997, 1998), both of which are in relatively close proximity to Lüderitz. Water turbidity at Elizabeth Bay is also increased due to discharging fines into the bay as part of the diamond mining process (Chapter 7). Damara Terns dived for prey more successfully in the least turbid water here, which arguably is still quite murky. I suspect that prey capture success would decrease if the water was very clear. This non-linear relationship was found in a study of Sandwich Terns in the North Sea (Baptist and Leopold 2010).

Chick diet and energy content

At least nine new species were found in the chick diet of Damara Terns which had not been found in two previous studies of Damara Tern chick diet

(Clinning 1978, Simmons and Braine 1994). Both Clinning (1978) and Simmons and Braine (1994) found species that were collected in this study too, including larval Blenny, Mullet, Anchovy and Needlefish. The diet of Damara Tern chicks is similar to that described by Catry *et al.* (2006) for fish fed to Little Tern chicks (e.g. *Artherina* sp., *Mugil* sp., Blennidae, Gobidae), by Elliot *et al.* (2007) for the diet of the California Least Tern *Sterna antillarum browni* (e.g. *Atherina* sp., Gobidae, *Engraulis* sp.), and by Zavalaga *et al.* (2008) for the diet of the Peruvian Tern (e.g. *Atherina* sp., *Engraulis* sp., *Scomberesox* sp.). This emphasises the ecological similarities between these small terns.

Cape Silverside occurs all along the coastline of south-western Africa (Smith and Haemstra 1986) but none were collected from chick regurgitations in southern Namibia. This absence of Cape Silverside may have been attributable to a small sample size. Most of the Cape Silverside specimens were collected from the central coastline where Damara Terns feed predominantly around the Swakop River estuary (pers. obs). A possible reason for this is that the Cape Silverside is one of the few marine fish that can withstand the reduction in salinity within the estuarine environment (Smith and Haemstra 1986) and thus may be the most common prey species for Damara Terns feeding in estuarine environments. The energy content of Southern Mullet specimens (14.84 kJ/g dry mass) was lower than that for Mugilidae species fed to Little Tern chicks in Portugal (20.35 kJ/g dry mass, Paiva *et al.* 2006b). Lower energy content of food may have implications on chick growth and other aspects of breeding biology (Chapters 2 and 3).

This study confirms the importance of the impact of environmental conditions on feeding success of plunge-divers. Environmental conditions affecting feeding success are likely to be linked to Damara Tern breeding numbers and reproductive success in any given season.

Table 6.1: Results of the generalized linear model with binomial distribution and logit link function relating the prey capture success of Damara Terns at two breeding areas in southern Namibia to two explanatory variables, tidal phase and wind speed. Both variables are categorical, with baseline categories, for which the estimated regression coefficients are set to zero.

Explanatory variable	Coefficient	S.E.	t_{388,2}	P-value
Constant	-0.209	0.283	-0.74	0.460
Tide high	0	0	0	-
Tide receding	-0.906	0.285	-3.18	0.001
Tide low	-1.270	0.303	-4.19	<0.001
Tide incoming	-0.735	0.275	-2.67	0.008
Wind 1 (calm breeze)	0	0	0	-
Wind 2 (moderate breeze)	0.071	0.241	0.29	0.769
Wind 3 (wind)	0.147	0.211	0.69	0.487
Wind 4 (strong wind)	0.754	0.232	3.25	0.001

Table 6.2: Percentage of successful dives, dive rate (dives per minute) and prey capture rate (prey captured per minute) in relation to wind speed for foraging Damara Terns in southern Namibia. The sample size is the number of foraging bouts observed.

Wind category	Sample Size	Successful dives (%)	Dive rate	Prey capture rate
Wind 1 (calm breeze)	90	24.0	1.366	0.612
Wind 2 (moderate breeze)	73	27.9	0.935	0.436
Wind 3 (wind)	126	28.4	0.814	0.395
Wind 4 (strong wind)	100	45.8	0.598	0.379

Table 6.3: Results of the generalized linear model with a binomial distribution and a logit link function showing modelled prey capture success of Damara Terns at Elizabeth Bay in southern Namibia in relation to three explanatory variables; tidal phase, wind speed and water clarity. Because water clarity was only measured at Elizabeth Bay (due to turbidity increase through diamond mining processes), a separate analysis was performed for Elizabeth Bay. All three variables are categorical, with baseline categories, for which the estimated regression coefficients are set to zero. The sample size is the number of foraging bouts observed.

Explanatory variable	Sample size	Coefficient	SE	t_{176,2}	P-value
Constant		0.279	0.385	0.72	0.469
Tide high	33	0	0	0	–
Tide receding	111	–1.120	0.403	–2.78	0.005
Tide low	107	–1.893	0.470	–4.03	<0.001
Tide incoming	138	–0.825	0.421	–1.96	0.05
Wind 1 (calm breeze)	90	0	0	0	–
Wind 2 (moderate breeze)	73	0.790	0.479	1.65	0.099
Wind 3 (wind)	126	0.631	0.359	1.76	0.078
Wind 4 (strong wind)	100	0.987	0.353	2.80	0.005
Water clarity 1 (least turbid)	49	0	0	0	–
Water clarity 2	55	–0.605	0.286	–2.11	0.035
Water clarity 3 (most turbid)	72	–1.434	0.327	–4.38	<0.001

Table 6.4: Damara Tern chick diet composition in Namibia as determined from chick regurgitations and food dropped by adults.

Family	Common name	Latin name	Prey items (n)	Place and season
Atherinidae	Cape Silverside	<i>Atherina breviceps</i>	10	Caution Reef (94/95, n=5) White Stones (09/10, n=1) Durissa Bay Pans (92/93, n=2; 09/1, n=2)
Belonidae	Needlefish sp.	*	2	Durissa Bay Pans(92/93, n= 1) Ogden Rocks (92/93, n=1)
Blennidae	Larval Blenny sp.	*	2	Caution Reef (94/95, n=2)
	Horned Blenny	<i>Parablennius cornutus</i>	6	Caution Reef (94/95, n=6)
Clinidae	Klipfish sp.	*	2	Caution Reef (94/95, n=2)
	Super Klipfish	<i>Clinus superciliosus</i>	1	Caution Reef (94/95, n=1)
Engraulidae	Cape Anchovy	<i>Engraulis encrasicolus</i>	6	Hottentots Bay (08/09, n=4) Caution Reef (09/10, n=1) Durissa Bay (92/93, n=1)
Gobidae	Goby sp.	*	1	Caution Reef (94/95, n=1)
Gonorhynchidae	Beaked Sandfish	<i>Gonorhynchus gonorhynchus</i>	1	Hottentots Bay (08/09, n=1)
Merlucciidae	Hake sp.	*	3	Hottentots Bay (08/09, n=1) Marmora Pan (07/08, n=2)
Mugilidae	Southern Mullet	<i>Liza richardsonii</i>	6	Marmora Pan (07/08, n=2) Grosse Bucht (08/09, n=2) Hottentots Bay (07/08, n=1) Caution Reef (94/95, n=1)
Scomberesocidae	Saury	<i>Scomberesox saurus scomberoides</i>	2	Hottentots Bay (08/09, n=2)
Seranidae	Comber	<i>Serranus cabrilla</i>	4	Marmora Pan (07/08, n=4)
Sparidae	Seabream sp.	*	1	Grosse Bucht (08/09, n=1)
	Blacktail	<i>Diplodus sorgus capensis</i>	3	Caution Reef (94/95, n=3)
* Unidentified sp	*	*	5	Hottentots Bay (07/08, n=2; 08/09, n=3)

*denotes species (or families) that could not be accurately identified

Table 6.5: The energetic contents (kJ/g dry mass) of Southern Mullet specimens collected at Grosse Bucht in southern Namibia. Standard length excludes the caudal fin.

Southern mullet specimen #	Standard length (cm)	Energetic content (kJ/g dry mass)
1	4.7	14.25
2	6.2	14.04
3	–	Sample too small
4	–	15.78
5	7.8	15.32

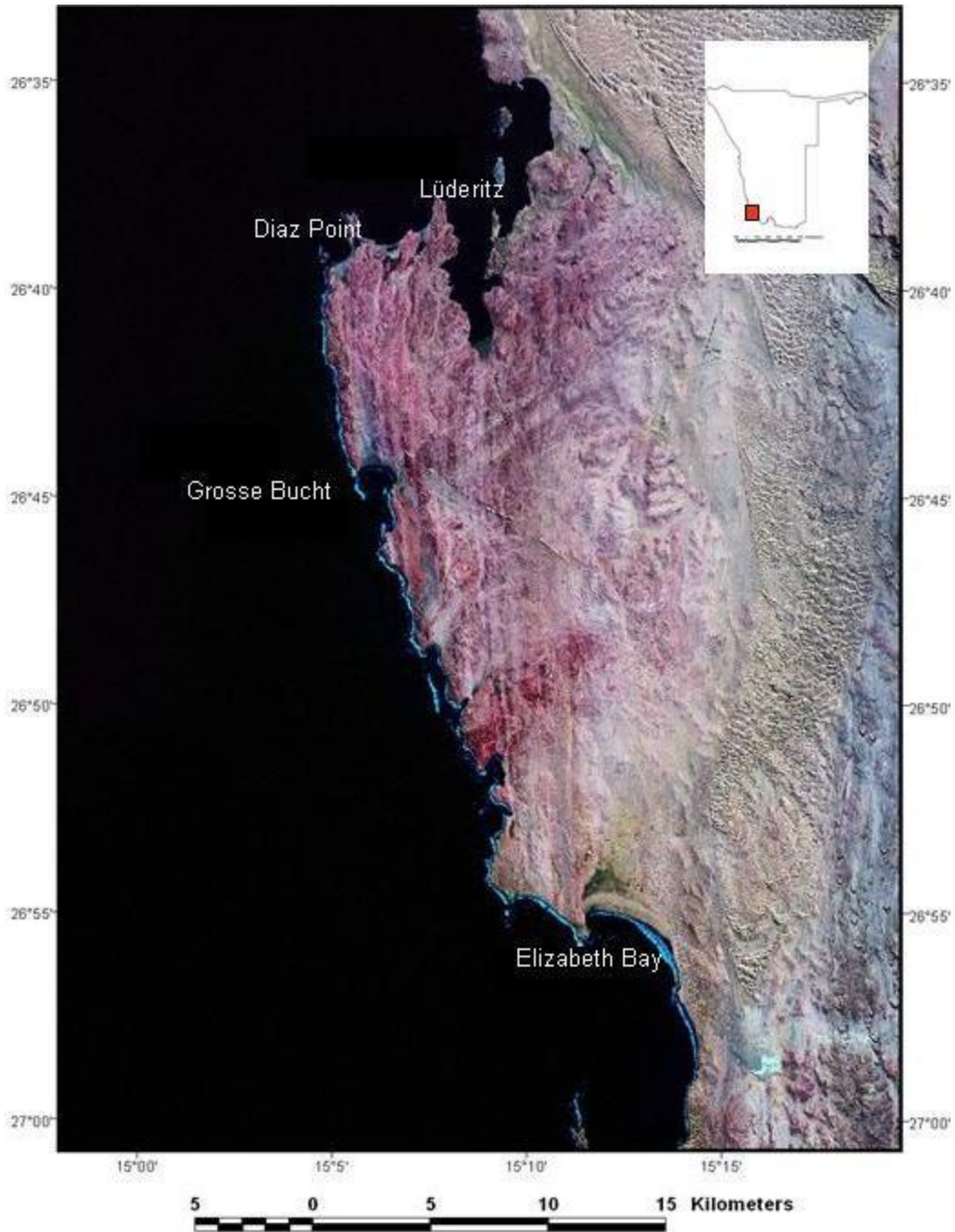


Figure 6.1: Map illustrating Elizabeth Bay and Grosse Bucht in southern Namibia, where the prey capture success of breeding Damara Terns was measured. The map also shows the location of Diaz Point, where wind speeds were measured, and Lüderitz, the nearest town.

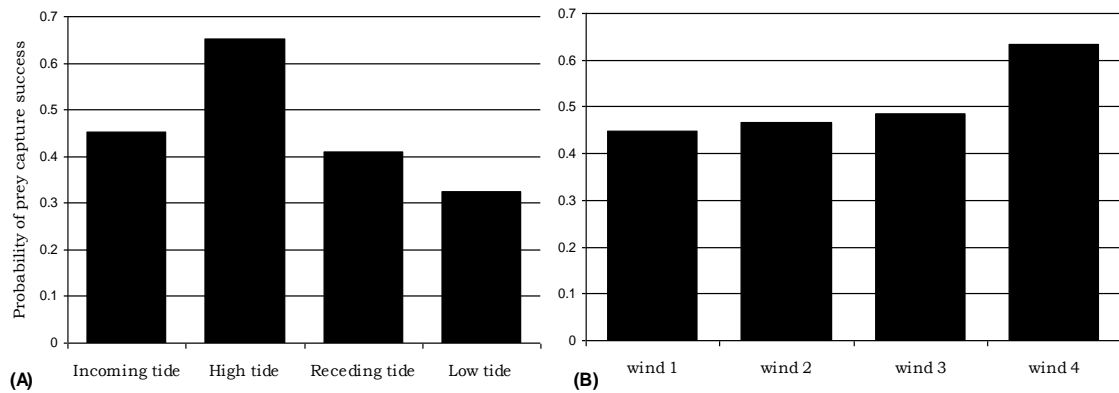


Figure 6.2: Modelled probabilities of prey capture success of Damara Terns in southern Namibia. The probabilities were calculated using the inverse of the logistic transformation from the parameter coefficients of Table 6.1. In each plot, all except one explanatory variable are held constant. Prey capture success probability is shown in relation to (A) tidal phase, with wind set to category 4 and (B) wind speed, with tidal phase set to high tide. The patterns for other combinations of the explanatory variables are similar and therefore not shown.

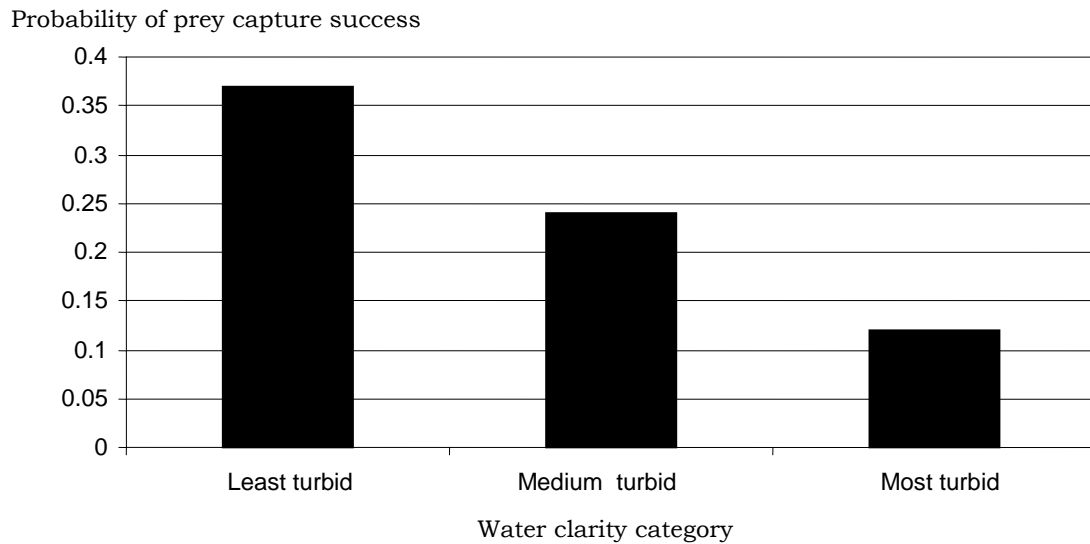


Figure 6.3: Modelled probabilities of prey capture success of Damara Terns at Elizabeth Bay in southern Namibia in relation to water clarity. Water clarity was only measured at Elizabeth Bay, the sample size was thus smaller and the graph and table for water clarity therefore had to be done separately from other analyses (see text). The probabilities were calculated using the inverse of the logistic transformation from the parameter coefficients of Table 6.3. In each plot, all except one explanatory variable are held constant. The plot indicates wind set to category 4 (c. 45 km/hr, strong wind) and tide set to high. The pattern for all other combinations of wind categories and tidal phase are similar and therefore not shown.

Chapter 7

The impacts of diamond mining activities on breeding Damara Terns *Sterna balaenarum* in southern Namibia



The impacts of diamond mining activities on breeding Damara Terns *Sterna balaenarum* in southern Namibia

Introduction

Diamond mining along the southern coastline of Namibia is of central importance to the economy of the country (Schneider 2009). Due to the possibility of diamond theft, successive governments of Namibia have restricted access to this area by the public for over a hundred years (Schneider 2009). Consequently, most of the coast between 26°S and 28°S, known as the “Sperrgebiet”, has been maintained in almost pristine condition (Pulfrich *et al.* 2003). However, the areas that have been mined have been disturbed extensively.

Terrestrial diamond mining along the Namibian coast principally involves open-cast mining, and requires the removal of overburden, including mobile barchan dunes, before the ore-body can be excavated (Pulfrich *et al.* 2003). At Elizabeth Bay, the undersized grit resulting from the diamond extraction process is deposited as a sediment-slurry directly into the sea, resulting in increased turbidity in the bay (Pallet 1995, Pulfrich *et al.* 2003). Although natural turbidity plumes occurred prior to the operation of the diamond mine, the occurrence and extent of the plumes have increased significantly (Clark *et al.* 1998), and can be seen from the air.

The Damara Tern *Sterna balaenarum*, a breeding near-endemic to Namibia and a Near-threatened species globally (IUCN 2009), has been found breeding in areas of active mining (Connor 1980, Simmons 2005b). Damara Terns breed in loose colonies, with nests rarely less than 100 m

apart, on gravel plains and salt pans in the coastal Namib Desert (Simmons and Braine 1994). Both parents provide food for the single chick by carrying single prey items from the foraging areas up to 10 km to the colony (pers. obs). Damara Terns feed mainly by plunge-diving for food (Frost and Shaughnessy 1976, Williams and Myer 1986, Simmons and Braine 1994). Like most of the other small tern species, the Damara Tern is essentially an inshore feeder (McLachlan and Liversidge 1970). Its diet consists of small fish and crustaceans (Clinning 1978, Simmons and Braine 1994, Chapter 6). Due to the nature of foraging, water turbidity may have a significant impact on prey capture success. Most studies on the influence of water turbidity on foraging terns have found that shallow plunge-divers avoid clear waters (Haney and Stone 1988, Safina and Burger 1988), probably because they are more easily detected by their prey. However, Baptist and Leopold (2010) found that prey capture success was lowest in clear and turbid waters. Terns may prefer medium turbidity where they can still see their prey, but aren't as easily detected. Simmons (2005b) postulated that increased turbidity of the water at Elizabeth Bay caused by the discharge of fine sediment negatively affected the foraging success of breeding Damara Terns. If the natural turbidity is anthropogenically enhanced, visibility of prey can be substantially reduced, thus reducing foraging ability of terns accustomed to lower levels of turbidity.

Prey capture success is likely to influence chick condition, breeding success and colony size. Other disturbances resulting from mining (such as dune-stripping, large-scale digging, off-road driving, etc) are also likely to affect success and colony size of breeding Damara Terns at Elizabeth Bay. Because the Damara Tern is to be "Specially Protected" in terms of the draft Protected Areas and Wildlife Management Bill of Namibia and is considered a species of "national conservation

importance” (Barnard 1998, Namdeb 2003), the assessment of mining impacts on the survival of this species in the Sperrgebiet has become increasingly important. This chapter investigates the impacts of diamond mining, particularly mining-related sediment discharge, on breeding Damara Terns at Elizabeth Bay. The parameters used to determine these impacts are prey capture success, chick condition (as an indicator of chick provisioning), breeding success and colony size. These parameters obtained at Elizabeth Bay are compared with those obtained from three un-mined breeding localities.

Study Area

The “Sperrgebiet” (restricted diamond area), extends from Hottentots Bay in the north to the southern border of Namibia (see the Sperrgebiet National Park, Figures 1.1 and 1.4 in Chapter 1, Figure 7.1), covering an area of 26000 km² and spanning *c.* 320 km of coastline. Four Damara Tern breeding colonies have been found in this area (Figure 1.4 in Chapter 1, Figure 7.1): Hottentots Bay (26°14'S, 14°59'E) in the northern area of the Sperrgebiet; Grosse Bucht (26°43'S, 15°40'E) near the town of Lüderitz; Elizabeth Bay (26°55'S, 15°14'E), an area where diamond mining activities take place; and Marmora Pan (27°45'S, 15°34'E) in the southern area of the Sperrgebiet. The environment of these areas are individually discussed in Chapter 1.

Methods

Foraging observations

Foraging observations were made at Grosse Bucht (control) and Elizabeth Bay (where sediment is discharged). Observations were made throughout the breeding season, during daylight hours, either from a

vehicle or from the beach for a period of one to four hours. Foraging Damara Terns were observed using 8×42 binoculars. Foraging bouts were timed to the nearest second and consisted of a tern looking down while flying or hovering 1–5 m above the sea surface. Each successful and unsuccessful dive was recorded per foraging bout. Tidal phase, wind speed, cloud cover and water clarity were recorded during every observation. At Elizabeth Bay, water clarity was recorded at every observation. The methods used to measure these variables are described in Chapter 6. The estimated amount of sediment (range: trickle, medium, full, Plate 4) being pumped by the discharge pipes into the sea at Elizabeth Bay was recorded at every observation.

Monitoring of breeding

In the seasons of 2007/08 and 2008/09, monitoring was undertaken from 1 October to 31 March. Each colony was visited at least once every two weeks and at most once a day. Two people walked separate routes through the general breeding area and searched for new nests by gauging the behaviour of adult birds. Once a nest was found, its coordinates were obtained using a GPS unit, and the site was monitored at each subsequent visit to the breeding area until the egg failed to hatch or hatched successfully. When eggs failed, evidence for the cause of failure was investigated and recorded. Once the chick hatched, the length of the head (0.1 mm), tarsus (0.1 mm) and wing chord (0.1 mm, wing chord for larger chicks was measured using a 30 cm ruler to the nearest 1 mm) were measured and its mass (g) determined with a spring balance shielded from wind. Each chick was fitted with a stainless steel SAFRING ring (2.8 mm internal diameter) on the right leg and a colour ring on the left leg. Attempts were made to find chicks again at every visit until they successfully fledged or died. This proved difficult because chicks are cryptic in plumage and behaviour, and are mobile from their

third day (Chapter 3). If chicks were not found their fate was noted as unknown. Observations of chicks found dead or being captured by predators were recorded.

Statistical Analyses

Prey capture success

Prey capture success was defined as the probability of a dive being successful (Chapter 6). A generalized linear model was used to investigate the relationship between prey capture success and a series of explanatory variables. The model used a binomial distribution and a logistic link function (GenStat12 Committee 2009). Five explanatory variables were considered. (1) The “site” was either Grosse Bucht or Elizabeth Bay. (2) Sediment discharge was either occurring or not occurring. During December 2008 and January 2009 no sediment was discharged due to mine closure, allowing a comparison of prey capture success at Elizabeth Bay between months with and without mining-related discharge. Within the season 2008/09, prey capture success was tested using the explanatory variables, “duration of sediment discharge” (October, November 2008 and February 2009), and “duration of no sediment discharge” (December 2008 and January 2009). The detailed descriptions for the remaining three explanatory variables are in Chapter 6: (3) Water clarity, (4) tidal phase, and (5) wind speed.

Body condition index

The body condition index (BCI) of an animal refers to the proportion of its body mass which is available to it in the form of metabolizable energy (Lubbe 2008). Assuming that mass reacts more strongly to variation in food supply than growth of structural components makes it possible to obtain a usable measure of condition by relating the weight of a chick to

measures of structural size (Veen *et al.* 2003, 2004). Veen *et al.* (2003, 2004) showed that total head length was the appropriate structural measure for Royal Terns *Sterna maxima* and Caspian Terns *Sterna caspia* and thus I used the same measure for Damara Terns.

The shortcomings of Veen's method, however, were two-fold. Firstly, only an upper curve was fitted to the head length versus mass scatter diagram. Secondly, this upper curve was fitted by eye. Lubbe (2008), in his study of African Penguins *Spheniscus demersus*, overcame the second shortcoming by using quantile regression (Koenker and Bassett 1978, Cade and Noon 2003) to objectively fit the upper curve, finding the 95th percentile regression. Lubbe (2008) further extended Veen's concept by also fitting the 5% percentile regression; this defines the lower limit of normal growth.

He then described BCI of a chick as the proportion of distance between the upper and lower quantiles that a particular chick falls. Lubbe (2008) found that the relationship between head length and mass for African Penguins was linear, and thus his approach was relatively simple. The relationship between total head length and mass for Damara Terns was, however, non-linear. Therefore, a weighted regression model was fitted, using the approach of Underhill *et al.* (2006). Except, in this case, the 5% and 95% quantile regressions were fitted. This generates two smoothed curves that follow upper and lower boundaries of the scatter diagram closely. The BCI of each chick is defined as

$$(M_o - P_{ML}) / (P_{MU} - P_{ML})$$

where M_o is the observed mass, and P_{ML} and P_{MU} are the estimated 5% and 95% quantiles of mass, respectively, for a chick of this total head length.

Single-factor ANOVA was used to assess differences in BCI between the four colonies. A two-sample t-test was performed to assess if there were differences between the two seasons.

Breeding success

The breeding success (BS) was defined as the probability of fledging a chick (Chapter 2). Nests (or mobile chicks) were not always found again and evidence of any predation (or other cause of death) was not always available. BS was therefore estimated using the approach developed by Mayfield (1961, 1975) and extended by Underhill (submitted). The detailed statistical methods are described in Chapter 2.

Results

Prey capture success

A total of 389 foraging bouts were observed, of which 177 took place at Elizabeth Bay. The sediment, if being discharged at full power, would affect the entire bay. Damara Terns were always found feeding in the same area – this area was most affected by the plume. Prey capture success did not differ significantly between Damara Terns foraging at Elizabeth Bay and those foraging at Grosse Bucht ($P=0.07$, Table 7.1). There was also no significant difference in prey capture success at Elizabeth Bay between the duration of sediment discharge (October 2008, November 2008, February 2009) and the duration of no sediment discharge (December 2008 and January 2009) ($P=0.888$, Table 7.2).

Prey capture success increased significantly with decreasing water turbidity ($P < 0.001$, Table 6.3 and Figure 6.3 in Chapter 6). Prey capture success was 0.37 in water clarity 1 (least turbid), 0.24 in water clarity 2, and 0.12 in water clarity 3 (most turbid) (during high tide and calm winds, Figure 6.3 in Chapter 6). Increasing water turbidity always coincided with increasing amounts of sediment being discharged by the pipes into the bay (i.e. trickle= water clarity 1, medium= water clarity 2, full= water clarity 3). Prey capture success increased significantly with increasing tide (Table 6.3 in Chapter 6). Prey capture success was significantly highest during strong winds, and significantly lowest in calm winds (Table 6.3 in Chapter 6).

Chick body condition index

The mean BCI differed significantly between colonies ($F_{3,228}=17.78$, $P < 0.001$). Chicks at Hottentots Bay had the lowest mean BCI (0.33, Table 7.3). Those at Elizabeth Bay had the highest mean BCI (0.75, Table 7.3). The mean BCI for chicks from all four colonies combined was significantly higher for 2007/08 than for 2008/09 ($t_{117}=2.56$, $P < 0.01$). There was no significant difference in the mean BCI between the two seasons for chicks at Hottentots Bay ($t_{104}=-0.22$, $P > 0.05$) and Grosse Bucht ($t_{31}=0.81$, $P > 0.05$). Seasonal comparisons could not be made for chicks from Elizabeth Bay and Marmora Pan, because of small sample sizes.

Breeding success (BS) and colony size

Breeding success at all colonies and seasons differed significantly from the baseline of the model (Hottentots Bay 2007/08, Table 2.3 in Chapter 2). Breeding success was significantly higher in 2007/08 than in 2008/09 for three of the four colonies (Table 2.3 in Chapter 2). Decreased BS

correlated with increased predation at all colonies (Table 2.4 in Chapter 2).

The number of nests fluctuated between colonies and seasons. Of all four colonies, the number of nests and BS was highest at Hottentots Bay for both seasons (Table 2.3 in Chapter 2). The number of nests at Hottentots Bay was lower in 2007/08 than in 2008/09. Breeding success was significantly higher at Hottentots Bay in 2007/08 than in 2008/09 (2007/08, BS=0.80; 2008/09, BS=0.56; $P=0.03$, Table 2.3 in Chapter 2). Of all four colonies and for both seasons, predation was lowest at Hottentots Bay (Table 2.4 in Chapter 2).

The lowest BS of all four colonies in 2007/08 was at Grosse Bucht (BS=0.21, Tables 2.3 and 2.4 in Chapter 2). Here, the number of nests was slightly higher in 2007/08 than in 2008/09 (Table 2.3 in Chapter 2). Grosse Bucht had significantly lower BS in 2007/08 than in 2008/09 (2008/09, B=0.48; $P<0.001$, Table 2.3 in Chapter 2). Predation was higher in 2007/08 than in 2008/09 (Table 2.4 in Chapter 2). Egg abandonment at Grosse Bucht was higher in 2008/09 than in 2007/08 (Table 2.4 in Chapter 2).

Of the four colonies, Elizabeth Bay had the lowest number of nests during both seasons (Table 2.3 in Chapter 2). Elizabeth Bay and Marmora Pan had equally the lowest BS of all colonies in 2008/09 (Tables 2.3 and 2.4 in Chapter 2). The number of nests at Elizabeth Bay decreased from 13 in 2007/08 to 4 in 2008/09 (Table 2.3 in Chapter 2). BS was significantly higher in 2007/08 than in 2008/09 at Elizabeth Bay (2007/08, BS=0.24; 2008/09, BS=0.09; $P=0.001$; Table 2.3 in Chapter 2). Predation was high during both seasons at Elizabeth Bay (Table 2.4 in Chapter 2).

The number of nests at Marmora Pan decreased from 55 in 2007/08 to 13 in 2008/09 (Table 2.3 in Chapter 2). BS at Marmora Pan decreased significantly from 0.25 in 2007/08 to 0.08 in 2008/09 ($P > 0.001$, Table 2.3 in Chapter 2). Of all colonies and for both seasons, predation was highest at Marmora Pan.

Discussion

Mining-related sediment discharge was not found to significantly affect prey capture success of Damara Terns breeding at Elizabeth Bay. However, prey capture success was highest in least turbid waters (and at high tide and strong wind, Chapter 6). Chick condition was highest at Elizabeth Bay, and lowest at Hottentots Bay. Chick condition was significantly higher in 2007/08 than in 2008/09 for all colonies combined. Breeding success and the number of nests were highest at Hottentots Bay for both seasons. Breeding success was mainly affected by predation.

Prey capture success

Prey capture success did not differ significantly between Grosse Bucht and Elizabeth Bay, and no significant difference in prey capture success was observed at Elizabeth Bay during months of sediment discharge and months of no sediment discharge. Therefore it is unlikely that foraging Damara Terns at Elizabeth Bay were negatively affected by sediment discharge. However, Damara Terns dived more successfully in less turbid waters, during lowered sediment discharge rates.

Previous studies have shown that shallow plunge-divers generally prefer more turbid water (Haney and Stone 1988). The greatest upwelling cell in the Benguela Upwelling System is located near Lüderitz and

surrounding areas (Shannon 1989). Water turbidity is therefore naturally high at both Elizabeth Bay and Grosse Bucht (Clark *et al.* 1998); both are in the vicinity of Lüderitz. Some turbidity may be preferred by plunge-divers because prey may concentrate in the upper layers. In addition, plunge-divers may also not be as easily detected by their prey in more turbid waters. Damara Terns breeding and foraging in these areas may be accustomed to foraging in relatively turbid waters and therefore are not greatly affected by increased turbidity generated by mining activities. A study of fish communities (especially fish that Damara Terns prey on) in Elizabeth Bay showed that elevated turbidity levels have a positive impact on fish communities in the bay (Clark *et al.* 1998). A higher abundance and diversity of fish species were found in the sediment plume at Elizabeth Bay, and the turbidity plume resulting from the fine tailings disposal may have enhanced the quality of the Elizabeth Bay surf zone as a habitat for juvenile fish (Clark *et al.* 1998). In this sense the increased turbidity may have had a positive impact.

Because Damara Terns showed higher prey capture success in the least turbid waters, during lowered sediment discharge rates, there seems to be some effect of discharging sediment on foraging Damara Terns at Elizabeth Bay. Unfortunately, no total suspended matter (TSM) concentration data, to illustrate turbidity more accurately, were available for this study. Least turbid water at Elizabeth Bay is turbid relative to what is considered clear water (i.e. the clearest water at Elizabeth Bay was *c.* 5 mg/l, measured between 1995–1997, during sediment discharge rates comparable to present discharge rates, CSIR 1996, 1997, 1998). Baptist and Leopold (2010) found that Sandwich Terns had highest prey capture success in water with TSM concentration of 5–10 mg/l. This measurement is within range of the least turbid water in my study. I postulate that my results reflect a

linear response to turbidity because the water at Elizabeth Bay probably did not include turbidities that had TSM concentration lower than 5 mg/l.

Chick body condition

The body condition of seabird chicks (such as terns) is directly related to the amount of food they get from their parents, which can be related to feeding conditions at sea (Williams and Croxall 1990, Veen *et al.* 2003, 2004). Generally, it seems that Damara Tern chicks seldom die of starvation (Figure 7.2). Chicks at Hottentots Bay had the lowest mean BCI. Compared to the other colonies, Hottentots Bay had the largest distance between nest sites and foraging grounds. Therefore breeding Damara Terns may feed their chicks less frequently because more time is spent traveling to and from foraging grounds. However, the highest mean BCI was of chicks from Elizabeth Bay, where nest sites are also relatively far from foraging grounds. Insufficient data was available to assess whether chick provisioning was affected by distance. The energy content of prey caught may have differed between colonies, but no data was available to make such comparisons.

Breeding success and colony size

Hottentots Bay had the highest breeding success, because of a lower rate of predation than at the other sites. This is likely to be due both to the size and isolation of the breeding area and to the substrate which rendered eggs and chicks particularly difficult to detect there (Plates 1 and 5). At Marmora Pan, where predation was highest, incubating adults (and eggs) are not cryptic and generally easily detected (Plates 1 and 5). The higher breeding success at Grosse Bucht in 2008/09 may be attributed to a lower rate of predation. Breeding success was mainly affected by predation at all colonies. My results showed no direct impact

of mining activities on breeding success at Elizabeth Bay. In fact, the nearest mining activities (i.e. dune stripping), occurred c. 1.5 km from the nesting grounds. Breeding success was also not negatively affected by the sediment discharge.

The breeding colony at Elizabeth Bay was the smallest of the four colonies considered here, despite the availability of large areas of suitable breeding habitat. Frost and Johnson (1977), Siegfried and Johnson (1978) and Johnson (1979) surveyed Elizabeth Bay in three consecutive years (1976, 1977, 1978) and estimated a maximum of 20 breeding pairs, but never found more than 13 nests. The colony size of 13 nests in 2007/08 is comparable with this estimate. There may have been a decline in breeding pairs there since mining began in 1991. However, the use of different census methods makes comparisons of population estimates and interpretation of apparent population trends difficult (Chapter 9). The decrease in the number of nests between the 2007/08 (n=13) and 2008/09 seasons (n=4) at Elizabeth Bay is likely to have been a function of food availability at all southern Namibian breeding localities rather than the effects of diamond mining, particularly because mining activities were greatly reduced during 2008/09 (because of the financial crisis, Babatunde 2009, Congleton 2009). Many terns may have decided not to breed at all during 2008/09 as a result of poor conditions. The decrease in nest numbers from the 2007/08 season to the 2008/09 season and the poor chick condition were indicative of the season 2008/09 being a poor breeding season. Poor feeding conditions usually result in small nest numbers (i.e. a substantial proportion of birds electing not to attempt to breed) and poor breeding success in terns (Nisbet 1978, Monaghan *et al.* 1989, Chapter 2). The increased number of nests at Hottentots Bay between the 2007/08 and 2008/09 seasons reflects a greater search effort for nests

in the latter season and it is possible that the number of nests at Hottentots Bay was higher in 2007/08 than in 2008/09 (search effort was doubled from 2007/08 to 2008/09, Chapter 2).

This study found that, although prey capture success of Damara Terns at Elizabeth Bay was lower during increased sediment discharge rates, sediment discharge had no negative effect on the overall prey capture success, chick condition, breeding success or colony size compared with that of three un-mined colonies. However, the higher prey capture success of feeding Damara Terns in least turbid waters at Elizabeth Bay indicates that sediment discharge levels should not reach levels of undesirable turbidity. Further studies should measure TSM concentrations during foraging to assess more accurate levels of turbidity during foraging observations. An investigation into the comparison of chick provisioning rates and energy content of prey at the four colonies may explain why the BCI differed between colonies.

Table 7.1: Results of the generalized linear model for prey capture success of Damara Terns in southern Namibia with “site” as a two-level explanatory variable, i.e. Grosse Bucht versus Elizabeth Bay (the baseline level of the model).

Explanatory variable	Coefficie nt	SE	t_{388,2}	P-value
Constant	-1.157	0.346	-3.35	<0.001
Elizabeth Bay	0	0	0	–
Grosse Bucht	0.778	0.429	1.81	0.070

Table 7.2: Results of the generalized linear model for prey capture success of Damara Terns at Elizabeth Bay with explanatory variable “sediment discharge”. “Months with no sediment discharge” is set as the baseline level of the model.

Explanatory variable	Coefficient	SE	t_{79,2}	P-value
Constant	-0.693	0.236	-2.94	0.003
Months with no sediment discharge	0	0	0	–
Months with sediment discharge	-0.042	0.295	-0.14	0.888

Table 7.3: The Body Condition Index of Damara Tern chicks at four colonies in southern Namibia. Each entry in the table is mean Body Condition Index (standard deviation), sample size.

Colony	2007/08	2008/09	Both seasons
Hottentots Bay	0.32 (0.24), 26	0.34 (0.32), 82	0.33 (0.33), 108
Grosse Bucht	0.66 (0.22), 16	0.48 (0.27), 19	0.55 (0.30), 45
Elizabeth Bay	0.77 (0.31), 20	0.63 (0.31), 2	0.75 (0.31), 22
Marmora Pan	0.60 (0.33), 53	0.00 (-), 1	0.59 (0.28), 54

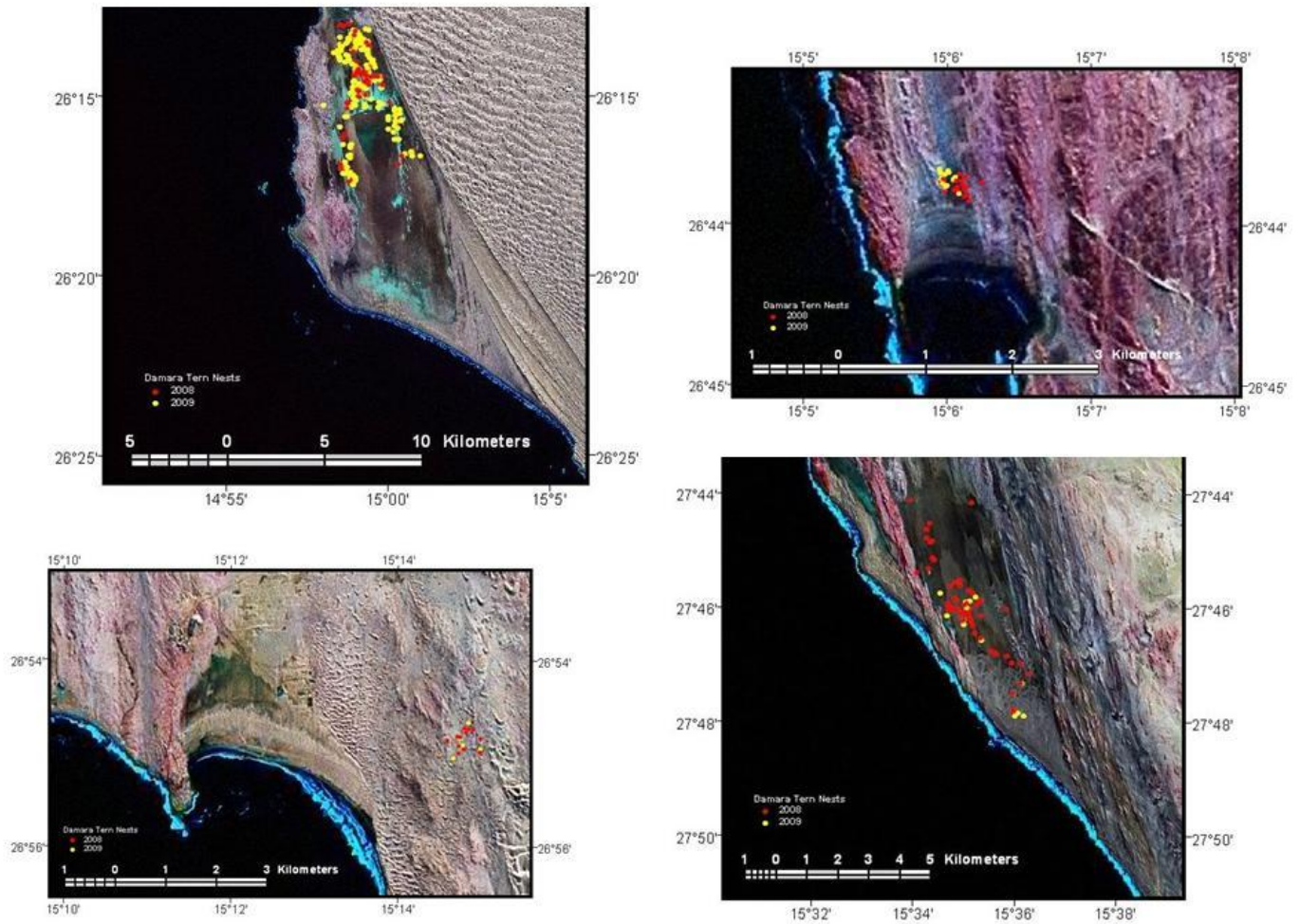


Figure 7.1: Satellite images of the location of colonies of Damara Terns in southern Namibia: Hottentots Bay (top left), Grosse Bucht (top right), Elizabeth Bay (bottom left) and Marmora Pan (bottom right). Nest distributions during 2007/08 are shown in red and 2008/09 in yellow.

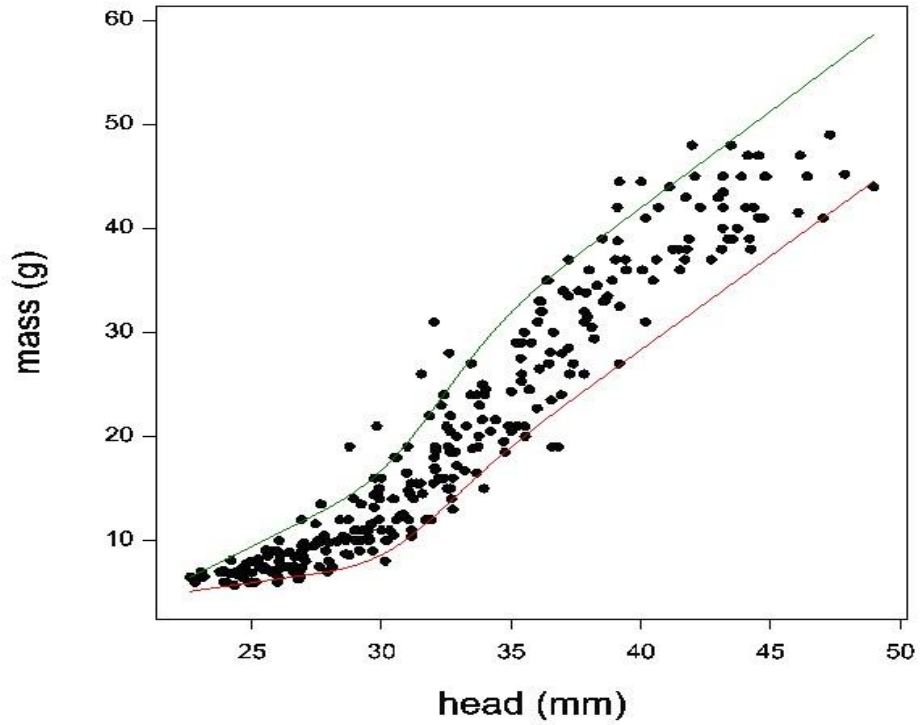


Figure 7.2: Body condition of Damara Tern chicks at four colonies in southern Namibia as measured by total body mass versus head length. The upper line is the 95th percentile, the lower line is the 5th percentile (see text).

Chapter 8

Protecting Damara Terns *Sterna balaenarum* from recreational disturbance in the Namib Desert increases breeding density and overall success



Protecting Damara Terns *Sterna balaenarum* from recreational disturbance in the Namib Desert increases breeding density and overall success

Introduction

The Damara Tern *Sterna balaenarum*, one of the smallest members of the Sternidae, is a breeding near-endemic to Namibia. Only 2% of the global population breed outside the country, along the coastlines of Angola and South Africa (Crawford and Simmons 1997). The strip of coastline between Swakopmund and Walvis Bay, two coastal towns in central Namibia *c.* 40 km apart, has the greatest density of sea- and shorebirds roosting and feeding in southern Africa (Simmons *et al.* 1998b). The Damara Tern nests adjacent to this strip, on the gravel plains that run parallel to the coast (Simmons *et al.* 1998b, Braby *et al.* 2001, Simmons 2005a).

The Damara Tern typically lays one egg in a nondescript scrape on the ground, although two-egg clutches have been recorded on rare occasions (de Villiers and Simmons 1997, Chapter 2). Unlike other terns, Damara Terns breed in loose colonies with an average density of 1–8 nests per km² (Crawford and Simmons 1997). Damara Terns are mainland coastal breeders and prefer non-vegetated gravel or sandy plains and salt pans (Simmons 2005a). They often breed up to 5 km inland, with one record breeding as far as 11.5 km inland (Braby *et al.* 2001). The main breeding season starts in September and ends in April, but nests with eggs occur as late as June (Simmons and Braine 1994) indicating that breeding can extend over nine months. During the non-breeding period Damara Terns migrate to West Africa (Elgood *et al.* 1973, Braby 2010).

Three decades ago, the Damara Tern was listed as one of the 20 bird species breeding in South Africa most in need of conservation action (Siegfried *et al.* 1976). Subsequently, its global threat status has varied between Globally Threatened to Near-threatened (IUCN 2009).

Breeding Damara Terns are particularly vulnerable to human disturbance and conservation measures have been implemented to ensure their continued survival. Human disturbance in the Namib Desert is associated with recreational activities such as off-road vehicles (ORVs), quad-bikes, horse-riding and hiking. The densest population of breeding terns is found on the central Namibian coast during the austral summer, at the same time as the number of visitors to the area is greatest. Damara Terns have been subjected to excessive disturbance and increased mortality during the breeding season in this area owing to off-road driving and quad-bike activity (Braby *et al.* 2001).

During November 2000, cable barriers were erected at a Damara Tern breeding colony at Caution Reef to prevent ORVs from traveling across the sand and gravel plains where terns bred (Braby *et al.* 2001). However, it subsequently became apparent that large numbers of Damara Terns were breeding east of Caution Reef (Braby 1995) in an area known as Horses Graves. Here terns were found breeding in gravel plains situated between dunes in an area popular with quad-bikers.

To determine the effectiveness of conservation measures, and to compare their success with that at the Caution Reef colony (Braby *et al.* 2001), the Horses Graves colony was monitored during the 2001/02 breeding season, when it was subjected to a high level of quad-bike traffic. The colony was again monitored during the following breeding season (2002/03) after interpretive sign board had been erected and strict access restrictions had

been enforced. This chapter compares Damara Tern nest numbers and densities, breeding success, and causes of mortalities before and after these measures were implemented.

Methods

The study was conducted between September and March over two breeding seasons, 2001/02 and 2002/03. I searched the study area on a quad-bike and recorded Damara Tern eggs and chicks and all vehicles or new tracks crossing the area. These searches were done daily; time of day varied from early in the morning to late in the afternoon. A record was kept of the date, time and location of all tracks and vehicles in the study area in December 2001. One route was followed through the study area to monitor breeding activities, but on occasion I explored new plains in search of potential nesting sites. A Global Positioning System (GPS) was used to record the exact location of each nest to an accuracy of *c.* 10 m. New nests were included into daily visit routines until the chick successfully hatched and was ringed or until nest failure. Breeding success was defined as the emergence and survival of a chick that moved away from its nest aged 3–4 days – a combination of hatch success and early survival. Thereafter I could not easily follow the cryptic chicks and be certain that they had perished if they were not subsequently found. The presence of potential predators such as Kelp Gulls *Larus dominicanus*, Rock Kestrels *Falco rupicolus* and Black-backed Jackals *Canis mesomelas* was recorded and failed nests were carefully examined for signs of predators, such as jackal tracks leading to empty nests. When known, the cause of nest failure was noted.

Information and interpretation sign boards were erected on 21 December 2001, in the middle of the breeding season 2001/02. Signs of human disturbance continued to be monitored. Prior to the start of the 2002/03

breeding season, cable barriers were set up at entry points to the study area that were typically used by quad-bikes (Plate 3). Quad-bike tour companies were limited to one designated route and private bike enthusiasts were warned off the gravel plain areas. Information sheets highlighting the vulnerability of Damara Terns and the position of the breeding site were handed out to private quad-bikers and other tourists.

Results

Nest abundance and density

All nests found over the study period contained one egg. In the 2001/02 breeding season, the first nest was found on 2 November and, in total, 58 nests with eggs were found over a period of two and a half months (Figure 8.1). The breeding season ended on 23 January 2002, with no more eggs or chicks seen after this date. During the 2002/03 breeding season, 122 nests with eggs were found over a four-month period, with the first egg appearing on 24 October 2002 and breeding activity recorded until 23 February 2003 (Figure 8.2). Field work occurred before these dates and until March to ensure no further egg-laying. Nest abundance more than doubled from the 2001/02 season to the 2002/03 season. The density of nests in the 2.5 km² study area increased from 23 nests km⁻² in 2001/02 to 49 nests km⁻² in 2002/03 indicating a 2.1-fold increase in breeding density following reduction in disturbance to the area. A possibility exists that nest density was larger in 2002/03 because of the longer season. I controlled for this by examining the same two-and-a-half month period (2 November to 23 January) in both seasons, when the relative densities were 23 nests km⁻² in 2001/02 and 34 nests km⁻² in 2002/03 indicating a 1.5-fold increase. There was no increase in the area occupied by the terns. Assuming that each nest represented a different breeding pair, the number of nests in 2002/03 was significantly larger than in 2001/02 (comparison of two counts, $z=4.78$,

$P < 0.001$; Zar 1999). There were, in fact, at most 15 pairs that re-laid in 2002/03, so that at least 107 pairs bred that year. The breeding population was significantly larger in 2002/03 than in 2001/02 ($z = 3.81$, $P < 0.001$).

Human disturbance

In the 2001/02 season, new vehicle tracks were seen on a daily basis and sometimes more frequently. Vehicles were common on both the gravel plains and the dunes. Quad-bike tracks were most common. In November 2001, nine ORVs were observed driving through the study area at the start of the breeding season. During December 2001, 27 new sets of quad-bike tracks, five ORVs or their tracks and one set of horse tracks (which passed within two metres of an active nest) were encountered during a 30-day period. About 30% of the quad-bike tracks were multiple tracks made by up to seven quad-bikes at a time. Tracks frequently passed within metres of nests with eggs, indicating that the bikers were unaware or uninterested in the tern nests. In six cases, vehicle tracks were found within 5 m of an active nest, but no nests were destroyed by vehicles. There was no apparent decrease in vehicle disturbance after conspicuously placed information boards were erected along all borders of the study area on 21 December 2001.

During the 2002/03 season, after additional conservation measures had been implemented, quad-bike tours were only seen following routes allocated to them. With one exception, tourists in ORVs drove only in dunes and always at safe distances from the nests. Only human or horse tracks were found in the vicinity of nests. There were no quad-bike tracks through the nesting area. Human disturbance was only witnessed on two occasions: two tourists walking through the gravel plains and an ORV driving through one breeding plain where a small number of Damara Terns nested.

Breeding attempts and overall breeding success

The number of successful breeding attempts increased from 48 nests in 2001/02 to 82 nests in 2002/03, a 71% increase (Table 8.1). However, as a percentage of nests initiated, successful nests decreased significantly from 83% (48 of 58) in 2001/02 to 67% (82 of 122) in 2002/03 ($\chi^2_1=4.1$, $P=0.043$, Table 8.1; see Chapter 2 for the probability of breeding success to fledging, 0.73 for 2001/02 and 0.52 for 2002/03). Despite the significant decrease in the proportion of nests successful before and after protection, the increased number of nests in the second year resulted in 34 more chicks surviving until 4 d of age following the implementation of protective measures.

The reduced proportion of successful nests in 2002/03 was attributable to predation by Black-Backed Jackals, as determined by tracks at failed nests (Table 8.1, Chapter 2). The number of nests failing from jackal predation increased four-fold from five nests in 2001/02 to 20 nests in 2002/03 (Table 8.1). In addition, a Rock Kestrel was periodically seen flying over the area during the 2002/03 breeding season; this species had not been observed during the previous season. A pair of Rock Kestrels was known to have bred in the vicinity of the study area in 2002/03. Subsequently, in 2005, a Rock Kestrel was observed preying on a Damara Tern chick (Chapter 2). It is thus likely that a substantial proportion of the losses attributed to 'unknown fate' (Table 8.1) involved predation by Rock Kestrels. Nest abandonment due to direct human disturbance decreased from two nests (3%) in 2001/02 to one nest (0.8%) in 2002/03 (Table 8.1).

Discussion

My results show that conservation interventions can be audited, and their benefits quantified, by measuring a number of biological parameters, such as breeding numbers, density and success of breeding, as well as intensity of

disturbance before and after the implementation of the interventions. In this study, there was a large increase in the number of Damara Terns breeding in the season following the exclusion of ORVs from the breeding area and the limitation of quad-bikes to fixed routes through it. Similarly, Braby *et al.* (2001) showed that nest density increased by 25% and that hatching success increased from 56% to 80% at the Caution Reef colony in the breeding season following exclusion of ORVs. At the southern limit of the species' breeding range, near Cape Agulhas, South Africa, all 11 pairs in the study area raised a chick to fledging in the year immediately following the ban on ORVs from beaches in South Africa (Williams *et al.* 2004). In the previous five years many pairs lost eggs or chicks during the midsummer holiday period due to disturbance attributable to ORVs. The similar results obtained in each of these three studies suggest that the protective measures played an important role in improving breeding participation and success. Non-breeding coastal seabirds also increased in number in study areas around the South African coast following the ban on ORVs (Williams *et al.* 2004).

In this study, once conservation measures were implemented, the breeding season lengthened from two-and-a-half to four months. There may be several reasons for the lengthening of the breeding season. Increased food resources to adults and chicks, known to be critical in tern breeding ecology (Nisbet 1978, Monaghan *et al.* 1989), could account for this change. At both Struisbay and in this study, the breeding season started earlier after disturbance was eliminated, so that protection may have contributed to the lengthening of the season. Breeding earlier provides fledglings with a longer period of preparation for migration (Williams *et al.* 2004).

Once vehicle disturbance was eliminated, it was found that predation was an unexpected determinant of breeding success. The reduced breeding success in the second year was attributable to increased levels of predation by jackals,

and probably by the arrival of a new predator, the Rock Kestrel (Chapter 2). Ecological factors such as these could not have been addressed through these conservation measures, but in hindsight may be expected for a ground-nesting species reliant on cryptic, well-spaced nests. Predation levels can increase naturally as nest density increases (Newton 1998), so it is useful to examine how much higher these densities were than typically encountered on the Namibian coast.

Nest densities in both seasons (23–49 nests km⁻²) were higher than previously recorded along Namibia's coast (1–15 nests km⁻², Simmons *et al.* 1998a) and at nearby Caution Reef colony (12–15 nests km⁻², Braby *et al.* 2001). The high densities at Horses Graves cannot be attributed to breeding habitat limitation, as there are vast areas of gravel plains available, nor can it be an anti-predator strategy as predation increases with higher tern densities.

Measuring the effectiveness of conservation measures is an essential but often untested step in the protection of any threatened biome, habitat or species. Managers should not simply assume that conservation efforts will be successful or that testing the effectiveness of measures is unnecessary, even if managers fear that this will reveal that resources used and expenses incurred were not justified. I recommend that funders of conservation projects set aside a portion of the funding for auditing the effectiveness of conservation interventions. In this case I demonstrated that the conservation measures enacted were effective, a result consistent with observations at two other sites in Namibia and South Africa.

Table 8.1: The outcomes of Damara Tern breeding attempts during the 2001/02 and 2002/03 breeding seasons at the Horses Graves, central Namibia

Fate	2001/02	2002/03
Jackal Predation	5 (8.6%)	20 (16.4%)
Egg addled	0 (0%)	2 (1.6%)
Chick found dead	0 (0%)	2 (1.6%)
Egg Abandoned	2 (3.4%)	1 (0.8%)
Unknown Fate*	3 (5.2%)	15 (12.3%)
Successful	48 (82.8%)	82 (67.2%)
Total nests with eggs	58	122

* 'Unknown fate' is defined by an egg or chick that was not found again but the cause of disappearance was unknown.

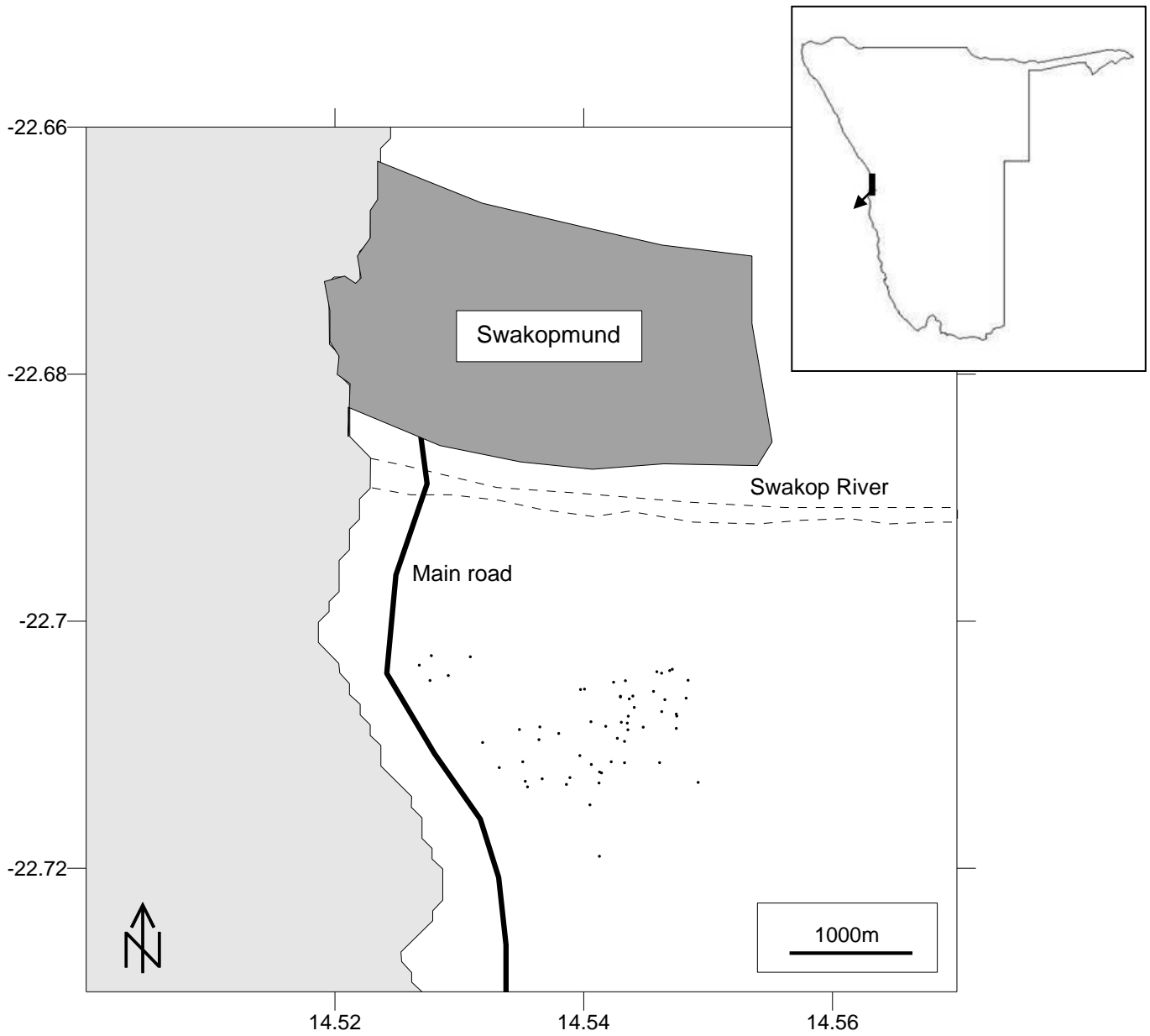


Figure 8.1: Damara Tern nesting distribution during the 2001/02 breeding season at Horses Graves, central Namibia, before the colony was fenced.

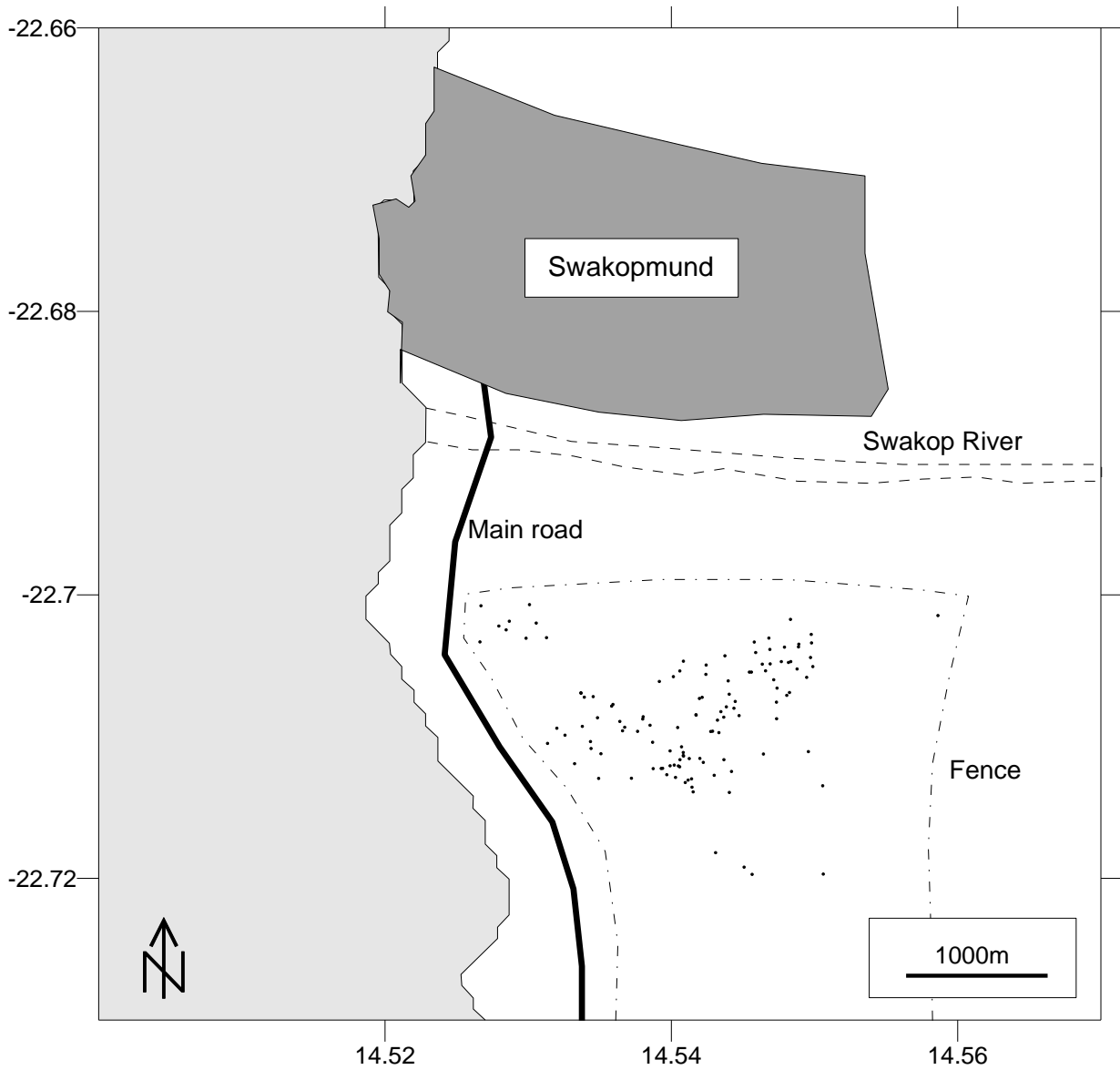


Figure 8.2: Damara Tern nest distribution during the 2002/03 breeding season at Horses Graves, central Namibia, after the colony was fenced.

Chapter 9

Population estimates, distribution and conservation
of the Damara Tern *Sterna balaenarum*



Population estimates, distribution and conservation of the Damara Tern

Introduction

The globally Near-threatened Damara Tern *Sterna balaenarum* is known to breed in three countries, from the northern Namib Desert in southern Angola (S16°58', E11°46'), through Namibia, to the Eastern Cape in South Africa (S33°30', E25°48') (Every 1979, Underhill *et al.* 1980, Randall and McLachlan 1982, Watson 1998, Simmons 2005a, 2010). Recent estimates of the global breeding population vary widely (Simmons *et al.* 1998a, Kemper *et al.* 2007), largely due to the use of various census methods and a lack of information on breeding population size throughout the species' range.

Little is known about the number of breeding individuals in Angola, and breeding was first confirmed there in 2010 (Simmons 2010). According to Crawford and Simmons (1997), 98% of Damara Terns breed in Namibia. This is probably due to its central position along the highly productive Benguela Upwelling System (Shannon 1985, 1989, Sakko 1998) that provides ample food, as well as the availability of extensive and isolated breeding habitat in the Namib Desert (Simmons *et al.* 1998a, Braby *et al.* 2001). Numbers of breeding pairs in South Africa are small and declining, and the species is classified as nationally Endangered (Barnes 2000).

The two most recent estimates of the total number of breeding Damara Terns varied widely, and taken at face value, suggest a severe decline in the breeding population from an estimated 13 500 breeding individuals in 1998 (Simmons *et al.* 1998a) to 930 pairs in 2007 (Kemper *et al.* 2007). This uncertain information suggests that a revision of breeding population estimates is timely. This chapter collates and reviews the published and

unpublished information of counts of individual birds, nest counts and locations of breeding colonies and provides revised population estimates. Threats faced by a number of breeding colonies are discussed, the conservation measures that have been put in place to protect breeding colonies are detailed, and other ways to protect the major breeding colonies of Damara Terns are suggested.

Study area and methods

This review included information from Tombua, c. 200 km north of the Cunene River in Angola (15°47'S, 12°09'E), to the Alexandria Dune Fields east of the Sundays River (22°42'S, 25°55'E) in South Africa, and included all known breeding areas within this c. 3500 km stretch of coastline (Figure 9.1). In Angola, breeding terns are found on gravel plains (Simmons 2010). In Namibia, breeding terns are found on an array of habitats including saltpans, sand and gravel plains, and gravel slacks between barchan dunes (Frost and Shaughnessy 1976, Clinning 1978, Simmons and Braine 1994, Simmons *et al.* 1998a). For the purpose of this study, Namibia was divided into four regions: Skeleton Coast Park (SCP); Dorob National Park (DNP); Namib-Naukluft Park (NNP); and Sperrgebiet National Park (SNP) (Figures 1.1–1.5 in Chapter 1) . These areas are described in detail in Chapter 1. In South Africa, breeding areas are mainly confined to dune fields where Damara Terns breed in the slacks between the dunes; however, some are found on saltpans, such as the small breeding colony at Port Nolloth, Northern Cape (29°14'S, 16°52'E), and gravel mounds, such as the breeding areas around Alexander Bay, Northern Cape (28°35'S, 14°38'E).

A “colony” is defined as a distinctive area of breeding habitat of Damara Terns to which breeding pair(s) return each year to breed. Data used to

assess breeding populations were collected using three different methods, namely:

1. Long-term monitoring, where colonies were monitored (at daily to weekly intervals) over three breeding seasons or more.
2. Short-term monitoring, where colonies were monitored (at daily to weekly intervals) for a minimum of two months to a maximum of one full breeding season (up to six months).
3. Short surveys/anecdotal nest records, where short (duration of a minimum of one day to a maximum of one week) surveys were conducted at colonies and where nests with eggs, chicks, adult and fledged Damara Terns were counted during the visit. In some cases, surveys were conducted more than once over the breeding season or over several breeding seasons.

The number of breeding pairs at each known colony was estimated. Minimum and maximum estimates are reported to account for possible fluctuations in numbers of pairs breeding between years, and to accommodate uncertainties associated with different census methods. Minimum estimates were based on minimum nest counts, irrespective of the survey method. Maximum estimates were based on maximum nest counts for long-term monitored colonies (section 3 above, however, e.g. Hottentots Bay was estimated based on breeding pair number because only a third of the area was surveyed for nests). Maximum estimates for the colonies for which short-term survey (section 3 above) information was available were estimated individually for each colony based on the following factors:

- The size of available/potential breeding habitat
- The level of disturbance (predators and human)
- Available notes on counts and behaviour of breeding adults
- The timing of the survey

Due to the vast expanse of available habitat in the Namib Desert, some pairs breed solitarily and sporadically outside of colonies (hereafter referred to as “single pairs”) along the Namibian coastline (Simmons *et al.* 1998a). The occurrence of single pairs in South Africa is unlikely, because of the restricted availability of suitable breeding habitat there. No records of these exist in Angola or South Africa. Records of single pairs along the Namibian coastline were incorporated into the overall breeding population estimate. This information was derived from surveys of breeding habitat in the SNP (January 2007–April 2007, October 2007–April 2008, October 2008–April 2009, J. Braby unpubl. data), estimates given by Braby *et al.* (2001) for the area between Meob Bay and Hottentots Bay, sporadic nests found between colonies in the DNP north of Swakopmund (December 2009–February 2010; J. Braby unpubl. data) and the entire SCP and DNP (1983–1998; MET unpubl. data).

Results

A total of 70 known breeding colonies were found to exist in Angola, Namibia and South Africa (Tables 9.1 and 9.2, Figure 9.1). Of these, eight colonies have been subjected to long-term monitoring, 20 colonies were monitored over short-terms and 42 colonies were monitored through short surveys or were anecdotal records (Table 9.1). No surveys were done for the 24 colonies in the SCP and three colonies in the DNP after 1993. No surveys were done for one colony in the NNP after 1994 (Table 9.1). No surveys exist after 1995 for five colonies in South Africa (Table 9.1).

Angola has one confirmed breeding colony, 30 km north of the Cunene River (Simmons 2010, Tables 9.1 and 9.2). Most breeding colonies are found in

Namibia (57; 24 in SCP, 23 in DNP, three in NNP, seven in SNP) and 12 colonies are found in South Africa (Tables 9.1 and 9.2).

Twenty-four colonies had maximum estimates of less than 10 pairs, 20 colonies had maximum estimates of 11–20 pairs, 10 colonies had maximum estimates of 21–40 pairs, 10 colonies had maximum estimates of 41–70 pairs, and six colonies had maximum estimates that were above 100 pairs (Table 9.2). The smallest colonies had a maximum estimate of one pair and included Ugab Saltworks Pan, Horingbay, Guano Bay in Namibia and Cape Recife in South Africa (Table 9.2, Figures 9.3, 9.4 and 9.5). These colonies differ from single pairs because they were known to return to the same area each year. A minimum estimate of zero pairs at some colonies indicate that these are likely to be extinct. All of the colonies with more than 30 pairs were in Namibia, although one was tentatively identified in Angola (Table 9.2).

The largest colony was at Hottentots Bay (187–300 pairs), followed by Durissa Bay Pans, Caution Reef and Meob Bay, all of which occur in Namibia (Tables 9.1 and 9.2). If the maximum estimate of the Angolan colony 30 km north of Cunene River is reasonably accurate, then this colony is the second largest colony globally, after Hottentots Bay (Table 9.2). However the wide range of estimates for this colony implies a large margin of uncertainty (Table 9.2).

Between 100–400 single pairs are estimated to breed between colonies in the SCP and the DNP (Table 9.2). Altogether 20 pairs were estimated between Meob Bay and Hottentots Bay (Braby *et al.* 2001, Table 9.2); the rest of the NNP is not suitable habitat. No single pairs were found outside of colonies in the SNP. Therefore, the number of single pairs in the SNP was estimated to range between 0 and 10 pairs (Table 9.2).

The global population of Damara Terns is estimated to range between 1001–2685 pairs, or 2002–5370 breeding individuals (Tables 9.2 and 9.3). The minimum estimate of 2002 individuals represents the absolute minimum. Of these minimum and maximum estimates, 1–5% (6–190 pairs) occur in Angola, 87–93% (930–2347 pairs) occur in Namibia, and 6% (65–148 pairs) occur in South Africa (Table 9.2). Within Namibia, most pairs bred in the SCP (301–770 pairs). The DNP supported 237–571 pairs, the NNP had the smallest number of pairs (47–185) and the SNP had 225–391 breeding pairs (Table 9.2).

Discussion

Breeding population estimates

The minimum estimate of 2002 breeding individuals represents an absolute minimum, because many colonies were not surveyed thoroughly and population sizes at them represent underestimates of the true population. The population is therefore more likely to approach the maximum of 5370 breeding individuals. Apart from the estimate of 7000 breeding individuals by Braby *et al.* (1992) and 13500 breeding individuals by Simmons *et al.* (1998a), most previous estimates of the total population size of Damara Terns were lower than or similar to those reported in this study (Table 9.3).

In March 1991, a group of 5068 Damara Terns was seen 178 km south of the Cunene River, of which an estimated 4004 were adults (Braby *et al.* 1992). Additional flocks, and Damara Terns still breeding during this time in northern Namibia, were added to this count, along with an extrapolated estimate of 1940 birds from Angola to give a total 7000 adults and juveniles (of which 5600 were adults and 1400 were juveniles). My study included only breeding adults (i.e. birds three to four years old and older; Chapter 4); and my estimate therefore is similar to the 5600 adults estimated by Braby *et*

al. (1992). It is also likely that the discrepancy between estimates obtained by Braby *et al.* (1992) and this study is either due to an overestimate of the Angolan breeding population by Braby *et al.* (1992) or an underestimate here. An underestimate in my study is possible, because there may be more than one colony in Angola (Simmons *et al.* 2006, Table 9.1). Alternatively, the discrepancy may reflect a decline of the breeding population since 1992.

The estimate of up to 5370 breeding Damara Terns is substantially lower than the 13500 individuals estimated by Simmons *et al.* (1998a). They sampled random blocks (measuring 1000 m each) inside and outside known colonies and extrapolated actual counts across the entire breeding habitat of the Namib Desert coastline. Damara Terns breed in colonies and display fidelity to the same sites (Chapter 5) and these sites only take up small percentages of the entire available breeding habitat (Randall and McLachlan 1982, Chapter 7). Small numbers of scattered single pairs breed outside of these colonies. Thus, extrapolating counts obtained from sampling within colonies across all suitable habitats, including those known not to support breeding Damara Terns, would overestimate the breeding population. If only those counts that were made in blocks containing scattered breeding pairs had been used to extrapolate across the entire suitable breeding habitat, added to the numbers found at each colony, the population estimate might have been similar to that obtained here.

Kemper *et al.* (2007) estimated the breeding population to number around 930 pairs. This is an underestimate, because estimates for the Angolan breeding population were not then available and there were no estimates for the area between the Cunene River and Möwe Bay. In addition, the population at Hottentots Bay was underestimated, because the extent of this colony was only ascertained after 2008. If this additional information had

been included, the total estimate by Kemper *et al.* (2007) would have been compatible with that obtained here.

The estimate of breeding pairs in Angola is based on only one confirmed colony (Simmons 2010) and is therefore likely to be biased low. Apart from the estimate of 1940 breeding individuals by Braby *et al.* (1992), no other estimates exist for that region. This estimate was based on extrapolating birds counted per kilometer in northern Namibia to similar habitat in southern Angola and may have therefore represented an upper limit. However, counts of 280 Damara Terns in breeding plumage along 203 km of coastline during December–January north of the confirmed colony implies that there could be additional colonies in Angola (Table 9.1).

Only Clinning (1978) separately estimated the Namibian breeding population of Damara Terns; his estimate was similar to that obtained here. His relatively low estimate may have been indicative of a lack of accessibility to and information on breeding sites (Table 9.3).

Previous estimates of the South African breeding population were roughly 120 pairs (Barnes 2000, Table 9.3). This is similar to the estimates of this study.

Crawford and Simmons (1997) suggested that 98% of the global breeding population occurs in Namibia. This revision concludes that up to 93% of Damara Terns breed in Namibia with substantial populations breeding in Angola and South Africa (at least 1–5% for Angola, 6% for South Africa).

Trends in the breeding population

Breeding estimates have fluctuated greatly in the past (Table 9.3) and it is difficult to discern any concrete trends, because of the different census

methods that were used. However, it is likely that the overall population has declined in the past century.

No information on possible decreases is available for Angola. In Namibia, coastal development resulted in the extinction of some colonies (Table 9.1, R.J. Braby unpubl. data). Andersson (1872) found Damara Terns breeding where Walvis Bay is presently situated, and described them as being common, as did Frost and Shaughnessy (1976) less than four decades ago. There must have been breeding colonies in areas where the towns Swakopmund and Hentiesbay are now situated. Development at Wlotzkasbaken has also resulted in the decrease or even possible extinction of the breeding colony there (Tables 9.1 and 9.2). Dolphin Beach, a colony that supported at least 32 pairs in 2005/06 is now covered with houses and apartment complexes (Table 9.1, R.J. Braby unpubl. data), and it is unlikely that birds still breed within this vicinity.

In South Africa, previous estimates of the breeding populations have decreased from 150 pairs to 120 pairs in the 1990s (Barnes 2000, Table 9.3). Estimates in this study for South Africa indicate that the population there has, at best, increased slightly, and at worst, decreased substantially. It is likely that the number of breeding pairs lies closer to the minimum estimate obtained here, suggesting that breeding birds have decreased considerably in South Africa in the past decade.

Threats to breeding colonies and populations

There are a number of threats faced by Damara Terns throughout their breeding range. These are listed below:

1. Coastal development causing colony extinctions (Vincent 1946, R.J. Braby unpubl. data). Coastal development has been the major

cause of declines in similar species, such as the Least Tern *Sterna antillarum* populations in North America and Europe (Norman and Saunders 1969, Cramp *et al.* 1974, Wilbur 1974, Massey 1974, Gore and Kinnison 1991, Koenen *et al.* 1996, Zuria and Mellink 2002, Akçakaya *et al.* 2003, Elliot *et al.* 2007). The habitat of the Little Tern *Sterna albifrons* has diminished and thus resulted in the construction of artificial breeding habitats such as salinas in Portugal (Catry *et al.* 2004) and land reclamations for breeding areas in Japan (Fujita *et al.* 2009). The largest colony of the Peruvian Tern *Sterna lorata* is losing breeding habitat to industrial development at Pampa de Mejillones in northern Chile (C. Guerra pers. comm., pers. obs.).

2. Off-road driving causing disturbance to breeding areas resulting in low reproductive success (Braby *et al.* 2001, Williams *et al.* 2004, S.J. Braby unpubl. data). Damara Terns in the DNP are directly impacted by off-road driving (Braby *et al.* 2001, Chapter 8, S.J. Braby unpubl. data, MET unpubl. data, pers. obs, N. Dreyer pers. comm.). The DNP is popular with tourists, especially off-road enthusiasts and fishermen, and the summer holiday season coincides with the Damara Tern breeding season. In South Africa, off-road driving had negative impacts in the past (Watson 1995, 1997, 1999) but beach-driving is banned as from 2001 (Williams *et al.* 2004). This resulted in increased breeding success at one colony (Williams *et al.* 2004).
3. Anthropogenic activities that result in increases in predator densities (e.g. offal from fishing attracting more Black-backed Jackals *Canis mesomelas*, R.J. Braby pers. comm.).
4. Diamond mining causing direct and/or indirect disturbance to breeding areas (Connor 1980, Brooke 1984, Simmons 2005b, Chapter 7).

Diamond mining has not recently had direct negative impacts on breeding terns in the SNP (Chapter 7). However, new diamond mining technology is focusing on inshore and surf zone mining activities in the SNP and this may have a negative impact on the feeding grounds of breeding Damara Terns. Prospecting in the SCP may cause disturbances to breeding colonies (e.g. at Sarusas, Figure 9.2). If prospecting leads to full-scale mineral extraction in the vicinity of breeding colonies in the SCP, full-scale mineral extraction is likely to have a negative impact on breeding Damara Terns.

5. Effects of climate change, including increased tidal flooding of large, low-lying colonies such as at Hottentots Bay (pers. obs), increasing fluctuations of food availability as a result of decreased upwelling and increased sea surface temperature (Roux 2003, Chapter 2).
6. The capture of Damara Terns for sale and/or food in Angola (Annex 1). No information exists regarding the scale of this trade.

Current and recommended conservation measures

There are various conservation measures that have been put in place in all three countries that assist in protecting breeding terns. These, and recommendations for further protection, are discussed below.

Angola:

The breeding area of the Damara Tern in Angola is largely uninhabited, inaccessible to humans and is legally protected as it falls within the Iona National Park (IUCN 1992). However, local people trap and kill seabirds, including (mostly migrating) Damara Terns, along the coastline, and even within the Iona National Park (Annex 1, T. de Wit pers. comm.). This practice is also conducted in other migratory countries (Braby 2010). How many

Damara Terns are killed this way, however, is unknown. Although Angola is signatory to the Convention on Migratory Species, no national law or enforcement exists that protects the Damara Tern there. It is imperative that the number of Damara Terns killed in this way be investigated in Angola and all migration countries to ascertain the level of threat of this practice to the species. Laws protecting the biodiversity and efficient enforcement of these laws would greatly reduce this practice.

Namibia:

The Damara Tern is “Specially Protected” under the draft Protected Areas and Wildlife Management Bill. Most colonies are protected because they fall within the boundaries of protected areas (Chapter 1). However, mining and prospecting is still allowed within these areas. It is mandatory for any proposed activity (like mining) to conduct an Environmental Impact Assessment under the Environmental Management Act (Act 7 of 2007) and its draft Environmental Impact Assessment (EIA) regulations and accompanying Strategic Environmental Assessment (SEA) for each coastal area.

Namibia’s first marine protected area, the Namibian Islands’ Marine Protected Area, (NIMPA), promotes the protection of feeding grounds from Meob Bay to Chameis Bay (e.g. through restrictions on mining activities, including the building of seawalls).

The entire coastline of Namibia is protected by the provisionally-named Namib-Skeleton Coast National Park, which includes the Skeleton Coast Park, Dorob National Park, Namib-Naukluft Park and Sperrgebiet National Park (and effectively a transfrontier park as it will incorporate the Iona National Park in Angola and the Richtersveld National Park in South Africa). Within this mega-park, the significant breeding areas of Damara Terns will

receive special protection because they will fall under Important Bird Areas (IBA) that are conservation priority zones. These will be protected by SEA and park management plans.

Off-road driving continues to be a problem on the Namibian coastline, and is at its largest level in the DNP during holiday season. There has been some conservation success by prohibiting access to two colonies between Swakopmund and Namibia, Horses Graves and Caution Reef (Braby *et al.* 2001, Chapter 8). However, many off-road drivers are unaware of the level of disturbance and destruction they cause (Plate 2). ORV disturbance is considered a significant threat to breeding Damara Terns, therefore it is important to continue awareness campaigns and prohibit access to important breeding areas during breeding season. A permit system is in place to protect breeding areas and prevent irreparable damage to the desert coastline of Namibia, but this is weakly enforced. The area between Swakopmund and the Ugab River (in the DNP) is heavily utilized by ORVs and there are virtually no enforced restrictions on drivers (Plate 2). Strengthened enforcement of ORV regulations by Namibia's Ministry of Environment and Tourism in the DNP could decrease ORV destruction and better protect breeding areas. Off-road regulations in isolated areas of the SCP and SNP should also be enforced through induction courses for prospectors and mining personnel driving in areas where Damara Terns may breed.

Recreational beach-users should be actively encouraged through Communication, Education and Public Awareness (via the Ministry of Environment) to not leave their offal on the beach when they depart. This may be one way to decrease the densities of jackals patrolling the beach.

South Africa:

Off-road driving has been banned on South Africa's beaches and breeding Damara Terns have responded positively to this (Williams *et al.* 2004). The National Environmental Management Act (Act 107 of 1998) and its associated regulations, which have been updated in 2010 (published under Government Notice R543–546 on 18 June 2010), and the National Environmental Biodiversity Act (Act 10 of 2004) , ensure the legal protection of the Damara Tern in South Africa. However, many colonies occur in restricted diamond mining areas in the Northern Cape and the protection of the species in these areas is weakly enforced, if at all. The mining companies in these areas should be encouraged to cordon off breeding areas and protect them from disturbance, and areas that have been disturbed (e.g. Alexander Bay, Table 9.1, Figure 9.4), should be rehabilitated.

Data: limitations, weaknesses and recommendations

There are various gaps and shortcomings in the available data on population size estimates. These need to be discussed along with recommendations to ensure reliable estimates and thus allow the accurate calculation of population trends in future:

Angola:

The estimates of breeding pairs in Angola in this study may be slightly low, because they are based on only one confirmed colony (Simmons 2010). Two potential colonies were found in 2009 (Simmons 2010) and it is possible that other small colonies exist there. Concerted efforts need to be made to survey this area properly and to verify the northern limit of the species' breeding range, thought to be as far north as Namibe (15°10'S 12°10'E, R. Sakko pers comm.).

Nambia:

There is a need for a comprehensive survey of the entire Namibian coastline to ascertain proper estimates of breeding populations within and outside of colonies. This was first suggested at the Namibian Coastal-Marine Bird Action Plan workshop in April 2008 (NACOMA 2008). The areas in urgent need of surveys are outlined below:

1. SCP

The colonies in the SCP have not been monitored or surveyed since the mid-1990s. Incidental observations since then have confirmed that most colonies are still present (Paterson pers. comm., Table 9.1). However, there has been a large-scale shift in Cape Fur Seal *Arctocephalus pusillus pusillus* distribution northwards into the SCP (Kirkman *et al.* 2007). This is likely to increase food availability for scavenging Black-backed Jackals that in turn may result in an increase in jackal densities in this area. Jackals are the most common predators of Damara Tern eggs and chicks and an increase in predator population is likely to negatively impact breeding success and numbers of terns in the SCP. A thorough survey needs to be conducted of all the colonies in the SCP to attain current estimates and to ascertain any decreases in breeding populations.

2. DNP

While Horses Graves and Caution Reef colonies have been monitored intensively for over a decade, there are some colonies for which information on breeding pair numbers is outdated (Table 9.1). Although short-term surveys have indicated that these colonies still exist (Table 9.1), more intensive surveys should be completed during the height of the breeding season to obtain more up-to-date information, especially at Durissa Bay Pans, White Stones and Mile 72.

3. NNP

Data for Conception and Meob Bay are lacking apart from a few short-term surveys and anecdotal reportings. This area, especially Meob Bay, is likely to hold a substantial population of breeding Damara Terns and needs to be monitored to ascertain threats, success and breeding numbers. Jackal densities are relatively high in these areas (R.J. Braby pers. comm.), thus the breeding success needs to be measured to investigate the importance of this colony and to assess the need and viability of implementing worthwhile conservation measures here.

4. SNP

Intensive and long-term monitoring has been conducted for the SNP north to Hottentots Bay over two and a half breeding seasons. For various reasons, only about a third of the possible breeding area of Hottentots Bay could be monitored and therefore the remaining two thirds of the breeding area should be surveyed.

South Africa:

Although the proportion of Damara Terns breeding in South Africa is low, its status as a locally endangered species (Barnes 2000) highlights the necessity for a comprehensive inventory of breeding colonies and good quality population size estimates. Colony sizes range from one to a maximum of 30 pairs (Table 9.2), but most have been poorly searched. The breeding population at Brandfontein and de Hoop are likely to be small, however a survey during the height of the breeding season should be conducted here to ensure accuracy. The information for Alexander Bay and the surrounding breeding areas is outdated (last surveyed for nests in 1996). In addition, surveys were not conducted over a long enough time period to acquire more accurate counts. These areas need to be surveyed thoroughly to obtain more current and accurate estimates.

Recommendation regarding conservation status

The Near-threatened IUCN status for the Damara Tern was based on the population estimate of 13500 mature individuals by Simmons *et al.* (1998, IUCN 2009). The estimate of this study of up to 5370 mature individuals suggests a decline of more than 60% in the past 12 years. This suggested decline, along with the small number of mature individuals, and uncertainties of future declines, fulfill the IUCN criteria for the Damara Tern to be uplisted to Vulnerable (IUCN 2000). However, this study suggests an overestimate by Simmons *et al.* (1998a) and that the population has, in fact, not declined to this reflected extent. In addition, most of the species breeding ground is (or will be) found in protected areas, thus lowering the risk of catastrophic extinction in the future. I suggest that the species remain listed as Near-Threatened. However, a re-evaluation of the species conservation status should be performed after an urgent survey of the entire breeding population is completed.

Table 9.1: Nest counts and surveys, including counts of adults and fledglings, at all known breeding colonies of Damara Terns in Angola, Namibia and South Africa. Method number refers to survey effort (1=long-term monitoring, 2=short-term monitoring, 3=short surveys/anecdotal nest records) as detailed in the Study area and Methods. Fledglings are young birds that have recently fledged and are thus assumed to have been hatched at the colony they were found, juveniles are young birds that have fledged that season and *may* have been hatched at another colony if counted at a colony during migration months (e.g. from January onwards). MET stands for Ministry of Environment and Tourism of Namibia.

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
ANGOLA						
Tombua to Baia dos Tigres and surrounds	c. S15°47 E12°09 to S16°26 E11°43	3	20 Dec 1998–4 Jan 1999	Simmons <i>et al.</i> 2006	–0	280 adults, 203 km of coastline
30km North of Cunene	S16°58 E11°46	3	24–26 January 2009	Simmons 2010	6	573 (7.5% juveniles) Damara Terns
NAMIBIA						
Skeleton Coast Park/ Northern Namibia						
Cunene Surrounds	S17°16 E11°44	3	5 Feb 1992	MET unpubl. data	2	
40km South of Cunene	S17°30 E11°44	3	6–7 Feb 1992	MET unpubl. data	3	9 adults
100km South of Cunene	S18°09 E11°54	3	7 Feb 1992	MET unpubl. data	3	100 adults
Between Angra Fria and Cape Frio	S18°17 E11°58	3	8 Feb 1992	MET unpubl. data	3	144 adults, 9 juveniles

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		3	8 Feb 1992	MET unpubl. data	–	15 - 20 adults
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Sarusas	S18°44 E12°21	3	8 Feb 1992	MET unpubl. data	2	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Westies Mine	S19°11 E12°37	3	8–9 Feb 1992	MET unpubl. data	2	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
5km North-East of Möwe Bay	S19°19 E12°43	3	Feb–Mar 1991	MET unpubl. data	3	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Möwe Bay Airstrip	S19°22 E12°43	3	December 1990 - March 1991	MET unpubl. data	8	
		2	Feb 1993	MET unpubl. data	62	
		3	January 2006	Patterson unpubl. data	6	no thorough search for nests were made
13km South of Möwe Bay	S19°27 E12°44	3	Mar –Apr 1995	MET unpubl. data	4	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
30km South of Möwe Bay	S19°32 E12°47	3	10 Feb 1992	MET unpubl. data	5	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
50km South of Möwe Bay	S19°44 E12°55	3	26 Jan–19 Mar 1991	MET unpubl. data	8	

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
60km South of Möwe Bay	S19°49 E12°57	3	14 Mar 1981	MET unpubl. data	1	
		2	21 Dec 1990–11 Apr 1991	MET unpubl. data	27	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Salt pans North of Terrace Bay Landing Strip	S19°55 E13°00	3	14 Mar 1981	MET unpubl. data	1	
		3	5–12 Jan 1987	MET unpubl. data	8	16 adults, gulls and crows present and high risk
		3	10–11 Feb 1992	MET unpubl. data	6	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Terrace Bay surrounds	S19°58 E13°03	3	10 Feb 1992	MET unpubl. data	2	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Swallow Breakers surrounds	S20°03 E13°03	3	17 Feb 1981	MET unpubl. data	9	
		3	7 Jan 1987	MET unpubl. data	7	
		3	11 Feb 1992	MET unpubl. data	18	not much more
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
6km North of Torrabay	S20°14 E13°13	3	18 Jan 1987	MET unpubl. data	4	
		3	11–12 Feb 1992	MET unpubl. data	2	

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Torrabay	S20°18 E13°14	3	6 Jan 1984	MET unpubl. data	1	
		3	30 Mar–7 Apr 1985	MET unpubl. data	2	
		3	4–5 Dec 1991	MET unpubl. data	11	+ 3 suspected nests
		n/a	2009	J. Patterson pers. comm.	–	Colony still exists
Henriette Pashette Saltpan	S20°21 E13°15	3	3–6 Feb 1990	MET unpubl. data	1	
		3	9–12 Dec 1991	MET unpubl. data	4	
		3	12 Feb 1992	MET unpubl. data	3	small colony on fringes of pan
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Black Gravel Plains North of Koigab	S20°26 E13°16	3	16–20 Jan 1984	MET unpubl. data	1	+ 1 pair mobbing
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
		3	12 Feb 1992	MET unpubl. data	1	
Montrose Saltpan	S20°32 E13°18	3	Feb 1981	MET unpubl. data	–	31 adults, 4 fledglings
		3	31 Mar 1986	MET unpubl. data	11	
		3	8 Dec 1991	MET unpubl. data	2	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Red Plains	S20°38 E13°21	3	26 Dec 1983, 1 Jan, 14 Jan 1984	MET unpubl. data	2	30 adults, very noisy

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		3	9 Dec 1984–18 Feb 1985	MET unpubl. data	6	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Toscanini Saltpans	S20°47 E13°23	3	28 Jan 1984	MET unpubl. data	1	
		3	20 Jan 1985	MET unpubl. data	1	
		3	10 Mar–1 Apr 1986	MET unpubl. data	4	6 adults, 2 juveniles
		2	Nov 1991–Feb 1992	MET unpubl. data	22	
		3	23 Nov–13 Dec 1992	MET unpubl. data	1	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Huab	S20°50 E13°26	3	3–27 Jan 1985	MET unpubl. data	4	
		3	15 Jan–12 Feb 1987	MET unpubl. data	5	
		2	Nov 1992–Jan 1993	MET unpubl. data	39	85 adults, 3 fledglings
		n/a	2009	J. Patterson pers. comm.	–	colony still exists
Ugab River to Ogden Rocks	S21°05 E13°33	3	Dec 1983 – Apr 1984	MET unpubl. data	14	
		3	Dec 1984–Jan 1985	MET unpubl. data	7	
		3	Feb–Mar 1986	MET unpubl. data	3	
		3	Jan – Feb 1987	MET unpubl. data	10	
		3	24 Nov–7 Dec 1991	MET unpubl. data	2	
		2	Nov 1992–Jan 1993	MET unpubl. data	24	
		n/a	2009	J. Patterson pers. comm.	–	colony still exists

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
Dorob National Park						
SCP fence	S21°11 E13°36	3	14 Jan 1985	MET unpubl. data	1	8 adults
6km South of Ugab	S21°13 E13°40	3	20 Jan 1985	MET unpubl. data	1	6 adults
Durissa Bay Pans	S21°15 E13°41	3	28 Dec 1983–3 Mar 1984	MET unpubl. data	11	
		3	26 Dec 1984–28 Mar 1985	MET unpubl. data	18	
		3	28 Feb–4 Mar 1991	MET unpubl. data	1	
		3	21 Nov 1991–31 January 1992	MET unpubl. data	17	
		2	1 Nov 1992–8 Jan 1993	MET unpubl. data	123	
		3	29–30 Dec 1997	MET unpubl. data	3	
		3	Dec 2009–Feb 2010	J. Braby unpubl. data	24	
Ugab Saltworks Pan	S21°22 E13°46	3	8–15 Jan 1984	MET unpubl. data	1	
		3	21 Jan 2010	J. Braby unpubl. data	0	
Mile 108	S21°28 E13°50	3	Dec 1983–Jan 1984	MET unpubl. data	5	
		3	Nov 1984 – Jan 1985	MET unpubl. data	7	
		3	19 Dec 2009	J. Braby unpubl. data	–	6 adults
Mile 100	S21°31 E13°51	3	10–19 Jan 1984	MET unpubl. data	1	
		3	8–9 Jan 1985	MET unpubl. data	3	
		3	5 Jan 1995	MET unpubl. data	2	
		3	13 Feb 2010	J. Braby unpubl. data	1	2 adults, 1 fledgling

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
Horingbay	S21°34 E13°53	3	10–11 Jan 1984	MET unpubl. data	1	
		3	Jan–March 2010	J. Braby unpubl. data	0	
White Stones	S21°39 E13°58	3	9 Jan 1985	MET unpubl. data	1	
		3	Jan–Mar 2010	J. Braby unpubl. data	11	22 adults, 5 fledglings
Cape Cross surrounds	S21°45 E13°58	3	31 Dec 1977	Underhill and Whitelaw 1977	–	2 adults
			1990s	MET unpubl. data	3	no extensive searches made
Mile 72 Camp and Saltpan	S21°53 E14°05	3	28 Nov – 9 Dec 1992	MET unpubl. data	3	
		2	20 Dec 1994–19 Jan 1995	MET unpubl. data	36	
		3	13 Feb 2010	J. Braby unpubl. data	10	20 adults
Mile 72 Saltworks Pan	S21°54 E14°06	3	11 Jan 1977	Underhill and Whitelaw 1977	–	48 adults
		2	Dec 1992–Jan 1993	MET unpubl. data	30	
		2	Dec 1994–Jan 1995	MET unpubl. data	16	
		3	13 Feb 2010	J. Braby unpubl. data	0	1 adult, 3 fledglings
North of Hentiesbay	S22°01 E14°14	3	11 Jan 1984	MET unpubl. data	3	nests widely dispersed
		3	3 Dec 1981	MET unpubl. data	2	
		3	21 Jan 2010	J. Braby unpubl. data	0	6 adults
Jakkalsputz	S22°12 E14°21	3	11 Jan 1984	MET unpubl. data	1	
		3	3–5 Mar 1986	MET unpubl. data	2	
		2	Nov 1991–Jan 1992	MET unpubl. data	14	

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		2	28 Nov–8 Dec 1992	MET unpubl. data	4	
Shipwreck	S22°14 E14°21	3	10 Jan 2010	J. Braby unpubl. data	0	11 adults, 2 fledglings
		3	21 Jan 2010	J. Braby unpubl. data	0	11 adults, 2 fledglings
		3	6 Feb 2010	J. Braby unpubl. data	0	11 adults, 2 fledglings
		3	12 Mar 2010	J. Braby unpubl. data	0	208 adults, 34 juveniles
Pebbles	S22°16 E14°23	2	Jan 1984–Feb 1984	MET unpubl. data	2	
		3	21 Jan 2010	J. Braby unpubl. data	0	3 adults
Mile 30	S22°18 E14°24	2	14 Nov 1991–5 Jan 1992	MET unpubl. data	9	2 juveniles
		3	Jan–Mar 2010	J. Braby unpubl. data	0	
Wlotzkasbaken	S22°21 E14°25	3	4, 9 Jan 1977	Underhill and Whitelaw 1977	–	21 adults
		2	Nov 1991–Jan 1992	MET unpubl. data	17	
		2	Nov 1992–Jan 1993	MET unpubl. data	10	
		3	Jan–Mar 2010	J. Braby unpubl. data	0	Possibly extinct due to housing development
Mile 8	S22°31 E14°29	3	4 Jan 1977	Underhill and Whitelaw 1977	–	8 adults
		3	Jan–Feb 2010	J. Braby and M. Boorman unpubl. data	2	20 adults, 1 juvenile
Mile 4	S22°35 E14°31	3	1 Jan 1977	Underhill and Whitelaw 1977	–	24 adults
		2	Austral Summers 2007/08, 2008/09, 2009/10	M. Boorman pers. comm.	n/a	10–20 pairs

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
Horses Graves	S22°42 E14°33	1	Sept 2001–March 2002	Braby <i>et al.</i> 2009 (Chapter 8)	59	
		1	Sept 2002–March 2003	Braby <i>et al.</i> 2009 (Chapter 8)	122	
		1	Sept 2003–Mar 2004	R.J. Braby unpubl. data (Chapter 2)	89	
		1	Sept 2004–Mar 2005	R.J. Braby unpubl. data (Chapter 2)	97	
		2	Sept 2005–Mar 2006	S.J. Braby unpubl. data (Chapter 2)	32	
		1	Sept 2006–Mar 2007	S.J. Braby unpubl. data (Chapter 2)	69	
		1	Sept 2007–Mar 2008	S.J. Braby unpubl. data (Chapter 2)	56	
		2	Sept 2008–Mar 2009	S.J. Braby unpubl. data (Chapter 2)	54	
		1	Sept 2009–Mar 2010	S.J. Braby unpubl. data (Chapter 2)	45	
Caution Reef	S22°44 E14°32	3	1 Jan 1977	Underhill and Whitelaw 1977	–	6 adults, beach count
		1	Sept 1994–Mar 1995	Braby 1995	120	
		2	Dec 1997–Jan 1998	Reiss and Kruger 1998	48	
		1	Sept 2000–Mar 2001	R.J. Braby unpubl. data (Chapter 2)	48	
		1	Sept 2001–March 2002	R.J. Braby unpubl. data	92	

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
				(Chapter 2)		
		1	Sept 2002–March 2003	R.J. Braby unpubl. data (Chapter 2)	56	
		1	Sept 2003–Mar 2004	R.J. Braby unpubl. data (Chapter 2)	40	
		1	Sept 2004–Mar 2005	R.J. Braby unpubl. data (Chapter 2)	60	
		2	Sept 2005–Mar 2006	S.J. Braby unpubl. data (Chapter 2)	13	
		1	Sept 2006–Mar 2007	S.J. Braby unpubl. data (Chapter 2)	92	
		1	Sept 2007–Mar 2008	S.J. Braby unpubl. data (Chapter 2)	52	
		1	Sept 2008–Mar 2009	S.J. Braby unpubl. data (Chapter 2)	71	
		1	Sept 2009–Mar 2010	S.J. Braby unpubl. data (Chapter 2)	108	
Dolphin Beach	S22°50 E14°32	3	2 Jan 1977	Underhill and Whitelaw 1977	–	12 adults, beach count
		3	6–7 Jan 2004	R.J. Braby unpubl. data	4	
		2	Nov 2004–Jan 2005	R.J. Braby unpubl. data	32	most failed due to development, breeding area now consists of housing development

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
Pelican Point	S22°56 E14°25	3	6 Jan 1977	Underhill and Whitelaw 1977	–	1 adult
		2	Regular visits during summer 2007–2009	N. Dreyer pers. comm.	n/a	8–15 pairs
Namib-Naukluft Park						
Sandwich Harbour	S23°09 E14°28	3	7 Jan 1977	Underhill and Whitelaw 1977	–	60 adults
		3	14–16 Dec 1993, 6–7 Jan 1994	MET unpubl. data	18	6 adults, 2 juveniles
		3	20 Dec 1997	MET unpubl. data	6	
		2	Regular visits during summer 2007–2009	N. Dreyer pers. comm.	n/a	15–35 pairs
Conception Bay	S23°51 E14°28	3	5–10 Dec 1994	MET unpubl. data	14	12 adults
Meob Bay	S24°22 E24°42	3	11–18 Dec 1994	MET unpubl. data	18	3 adults + 70 adults between Moeb and Conception
		3	27 Feb 1997	MET unpubl. data	3	
		3	02 Jun 2008	R.J. Braby unpubl. data	1	30 adults, more nests suspected
		3	08 Oct 2008	R.J. Braby unpubl. data	0	>20 pre-breeding adults
Sperrgebiet National Park/Southern Namibia						
Hottentots Bay	S26°19 E14°58	3	? Dec 1977	Siegfried and Johnson 1978	9	
		3	18 Dec 1991	de Villers and Simmons 1997	11	more nests suspected

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		3	11 Jan 1995	MRMR unpubl. data	est. 50	3 adults
		3	5–8 Jan 1996	MET unpubl. data	12	
		3	Jan–Mar 2007	J. Braby unpubl. data (Chapters 2,7)	17	
		2	Oct 2007–Mar 2008	J. Braby unpubl. data (Chapters 2,7)	80	
		2	Oct 2008–Mar 2009	J. Braby unpubl. data (Chapters 2,7)	187	596 adults (maximum count in surveyed area of pan)
Guano Bay	S26°39 E15°06	2	Jan–Mar 2007	J. Braby unpubl. data	1	
		1	Oct 2007–Mar 2008	J. Braby unpubl. data	0	
		1	Oct 2008–Mar 2009	J. Braby unpubl. data	0	
Grosse Bucht	S26°43 E15°40	3	31 Dec 1995–18 Jan 1996	MET unpubl. data	11	
		2	Jan – Mar 2007	J. Braby unpubl. data (Chapters 2,7)	7	
		1	Oct 2007–Mar 2008	J. Braby unpubl. data (Chapters 2,7)	21	
		1	Oct 2008–Mar 2009	J. Braby unpubl. data (Chapters 2,7)	17	
Elizabeth Bay	S26°54 E15°14	3	10–18 Dec 1976	Frost and Johnson 1977	5	30 adults, 2 juveniles, 12 - 15 pairs
		3	1–7 Dec 1977	Siegfried and Johnson 1978	10	possibly 5 more nests, ca. 20 pairs

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		3	8–10 Dec 1978	Johnson 1979	13	possibly 4 more, c. 20 pairs
		3	11–15 Jan 1996	Simmons 2005b	2	
		3	2 Feb 1997	MFMR unpubl. data	–	31 adults
		3	22 Nov 2002	Simmons 2005b, R.E. Simmons unpubl. data	3	4 juveniles, one courting pair, 8 adults, >8 pairs
		2	Jan–Mar 2007	J. Braby unpubl. data (Chapters 2,7)	3	40 adults, juveniles incl.
		1	Oct 2007–Mar 2008	J. Braby unpubl. data (Chapters 2,7)	13	
		1	Oct 2008–Mar 2009	J. Braby unpubl. data (Chapters 2,7)	4	
Possession Island	S27°05 E15°11	2	Sept 2004–Dec 2004	MFMR unpubl. data	0	12 adults, some may be from Elizabeth Bay
		2	Oct 2005–Jan 2006	MFMR unpubl. data	0	10 adults, some may be from Elizabeth Bay
		2	Oct 2006–Apr 2007	MFMR unpubl. data	2	12 adults, some may be from Elizabeth Bay
		2	Sept 2007–Mar 2008	MFMR unpubl. data	2	6 adults, some may be from Elizabeth Bay
Marmora Pan	S27°44 E15°34	3	Jan 1996	R.E. Simmons pers. comm.	10	
		3	5 Feb 2007	J. Braby unpubl. data (Chapters 2,7)	2	38 adults, at least 2 juveniles

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		1	Oct 2007–Mar 2008	J. Braby unpubl. data (Chapters 2,7)	55	
		1	Oct 2008–Mar 2009	J. Braby unpubl. data (Chapters 2,7)	13	
Chameis Pan	S27°54 E15°41	3		R.E. Simmons and I. Cordes unpubl. data	10	
		3	10 Jan 2008	J. Braby unpubl. data	1	3 adults
SOUTH AFRICA						
Alexander Bay	S28°29 E16°29	3	31 Dec 1995	J. Cooper and L.G. Underhill, unpubl. data	–	29 adults, 4 juveniles
		3	Jan–Feb 2007	J. Braby unpubl. data	–	30 adults
Port Nolloth Pan	S29°14 E16°52	3	18 Dec 1995	J. Cooper and L.G. Underhill, unpubl. data	5	15 adults
		2	Jan 2006	J. Cooper and L.G. Underhill, unpubl. data	6	16 adults
		1	Austral summer 2006/07	J. Lonser unpubl. data	10	20 adults
		1	Austral summer 2007/08	J. Lonser unpubl. data	10	20 adults
Oubeep Pan	S29°19 E16°57	3	18 Dec 1995	J. Cooper and L.G. Underhill, unpubl. data	3	5 adults
Dreyerspan	S29°31 E17°04	3	18 Dec 1995	J. Cooper and L.G. Underhill, unpubl. data	2	4 adults
		3	Sporadic 1990s	A. van Wyk pers. comm.	n/a	c. 20 pairs

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
Karaspan	S29°34 E17°01	3	18 Dec 1995	J. Cooper and L.G. Underhill, unpubl. data	2	15 adults
Brandfontein	S34°46 E19°53	3	1990s, date unknown	P. Steyn pers. comm.	2	
Struisbay	S34°43 E20°00	1	Austral summers 1996–2002	Williams <i>et al.</i> 2004, Williams in prep.	11–13	11–13 pairs
De Hoop	S34°29 E20°27			R.E. Simmons pers. comm.	n/a	c. 2 pairs
Gouritz	S34°18 E21°52	3	9 Jan 1976	R.W. Summers, L.G. Underhill and P.G.H. Frost, unpubl. data	–	6 adults, 1 juvenile
		3	Dec 2009–Mar 2010	P. la Grange pers. comm.	0	
Cape Recife	S34°08 E25°48	3	5 Jan 2000	Tree 2000	–	2 adults, 1 juvenile
		2	Dec 2001–Jan 2002	Martin and Taylor 2000	1	3 fledglings
		3	28 Sept 2006	Crawford <i>et al.</i> 2009	–	13 adults courtship feeding
Coega	S33°46 E25°42	3	13 Dec 1990	Crawford <i>et al.</i> 2009	1	2 separate adults
		3	1 Dec 1999	Crawford <i>et al.</i> 2009	–	2 adults
		3	30 Nov 2007	Crawford <i>et al.</i> 2009	3	4 separate adults
		3	Austral summers 2007/08, 2008/09	P. Whittington pers. comm..	n/a	3–5 pairs
Alexandria Dune Fields	S33°42 E25°55	3	17 Jan 1979	Underhill <i>et al.</i> 1980	–	6 adults, Sundays River estuary
		1	Nov 1980–Mar 1981	Randall and McLachlan 1982	12	+5 adults
		1	Austral summer 1991/92	Watson <i>et al.</i> 1997	28	

Breeding colonies	Geographical Position	Method number	Date(s)	Source	No of nests	Extra Information
		1	Austral summers from 1991–1994	Watson 1995	n/a	15–20 pairs
		3	Dec 2005	Whittington and Klages 2006	1	12 adults, 1 juvenile
		3	Austral summer 2008/09	P. Whittington and T. Tree, unpubl. data	5	
		1	Austral summer 2009/10	P. Whittington and T. Tree, unpubl. data	20	40 adults roosting on beach at night on 10 Feb 2010

Table 9.2: Minimum and maximum estimates of breeding pairs of Damara Terns at all known breeding colonies in Angola, Namibia and South Africa

Breeding colonies	Minimum estimate	Maximum estimate
ANGOLA		
30km North of Cunene	6	190
Sub-total (Angola)	6	190
NAMIBIA		
Skeleton Coast Park (SCP)		
Cunene Surrounds	2	20
40km South of Cunene	5	20
100km South of Cunene	3	50
Between Angra Fria and Cape Frio	15	70
Sarusas	2	20
Westies Mine	2	20
5km North-East of Möwe Bay	3	6
Möwe Bay Airstrip	62	120
13km South of Möwe Bay	4	30
30km South of Möwe Bay	5	30
50km South of Möwe Bay	8	30
60km South of Möwe Bay	27	60
Salt pans North of Terrace Bay Landing Strip	8	16
Terrace Bay surrounds	2	2
Swallow Breakers surrounds	18	20
6km North of Torrabay	4	10
Torrabay	14	30
Henriette Pashette Saltpan	4	10
Black Gravel Plains North of Koigab	2	10
Montrose Saltpan	11	16
Red Plains	15	30
Toscanini Saltpan	22	50
Huab	39	50
Ugab River to Ogden Rocks	24	50

	Minimum	Maximum
Breeding colonies	estimate	estimate
Sub-total (SCP)	301	770
Dorob National Park (DNP)		
SCP fence	1	8
6km South of Ugab	1	6
Durissa Bay Pans	80	123
Ugab Saltworks Pan	0	1
Mile 108	3	7
Mile 100	2	3
Horingbay	0	1
White Stones	16	50
Cape Cross Surrounds	3	10
Mile 72 Camp and Saltpan	10	36
Mile 72 Saltworks Pan	3	16
North of Hentiesbay	3	12
Jakkalsputz	1	14
Shipwreck	2	11
Pebbles	1	3
Mile 30	0	11
Wlotzkasbaken	0	17
Mile 8	3	15
Mile 4	10	20
Horses Graves	30	60
Caution Reef	60	100
Dolphin Beach	0	32
Pelican Point	8	15
Sub-total (DNP)	237	571
Namib-Naukluft Park		
Sandwich Harbour	15	35
Conception Bay	14	50
Meob	18	100
Sub-total (NNP)	47	185
Sperrgebiet National Park (SNP)		
Hottentots Bay	187	300
Guano Bay	0	1

	Minimum	Maximum
Breeding colonies	estimate	estimate
Grosse Bucht	15	17
Possession Island	2	2
Elizabeth Bay	7	10
Marmora Pan	13	55
Chameis Pan	1	6
Sub-total (SNP)	225	391
Single pairs		
SNP	0	10
NNP	20	20
DNP and SCP	100	400
Sub-total (single pairs)	120	430
Sub-total (Namibia)	930	2347
SOUTH AFRICA		
Alexander Bay	15	30
Port Nolloth Pan	7	10
Oubeep Pan	3	6
Dreyerspan	2	20
Karaspan	2	16
Brandfontein	2	10
Struisbay	11	13
De Hoop	2	10
Gouritz	0	2
Cape Recife	1	1
Coega	3	5
Alexandria Dune Fields	17	25
Sub-total (South Africa)	65	148
Total estimated breeding pairs	1001	2685

Table 9.3: Previous and current population estimates of Damara Terns.

Unless stated otherwise, the numbers represent individual breeding Damara Terns.

Source	Estimated Population			
	Global	Angola	Namibia	South Africa
Johnson and Frost (1978)	3000 (excl. Angola)	–	–	–
Clinning (1978)	3500–4000	–	2000	–
Brooke (1984)	–	–	–	c. 150 pairs
Collar and Stuart (1985)	1000–2000 pairs	–	–	–
Williams and Meyer (1986)	<4000	–	–	–
Braby <i>et al.</i> (1992)	7000 (20% juveniles)	1940 (including juveniles)	5755 (including juveniles)	
Simmons <i>et al.</i> (1998a)	13500	–	–	–
Barnes (2000)	–	–	–	120 pairs
Kemper <i>et al.</i> (2007)	930 pairs (excl. Angola)	–	–	–
Simmons (2010)	–	max. 190 pairs	–	–
This study	2002–5370 (1001–2685 breeding pairs)	12–280 (6–190 breeding pairs)	1860–4994 (930–2347 breeding pairs)	130–296 (65–148 breeding pairs)

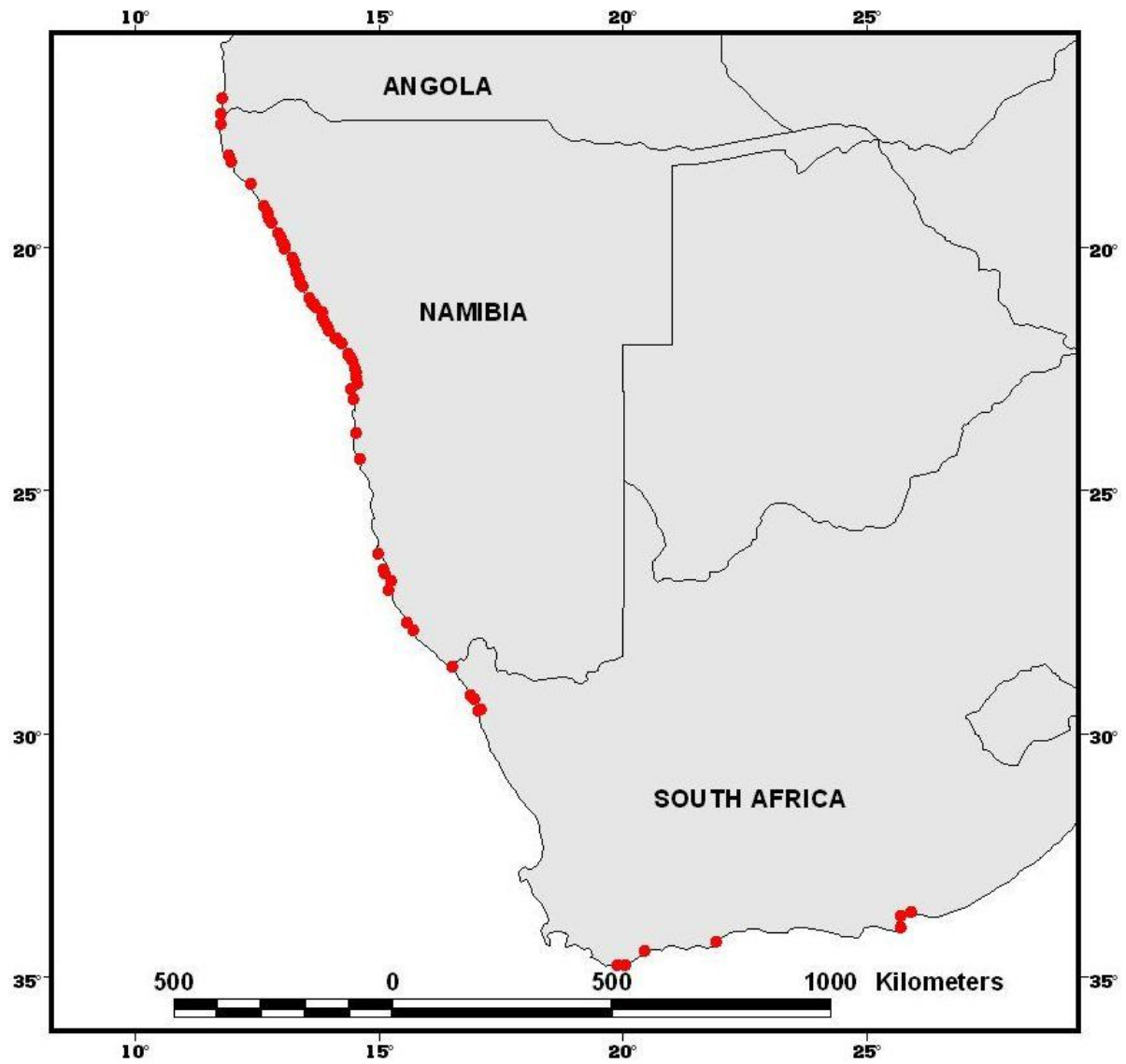


Figure 9.1: Distribution and location of all known Damara Tern breeding colonies in Angola, Namibia and South Africa.

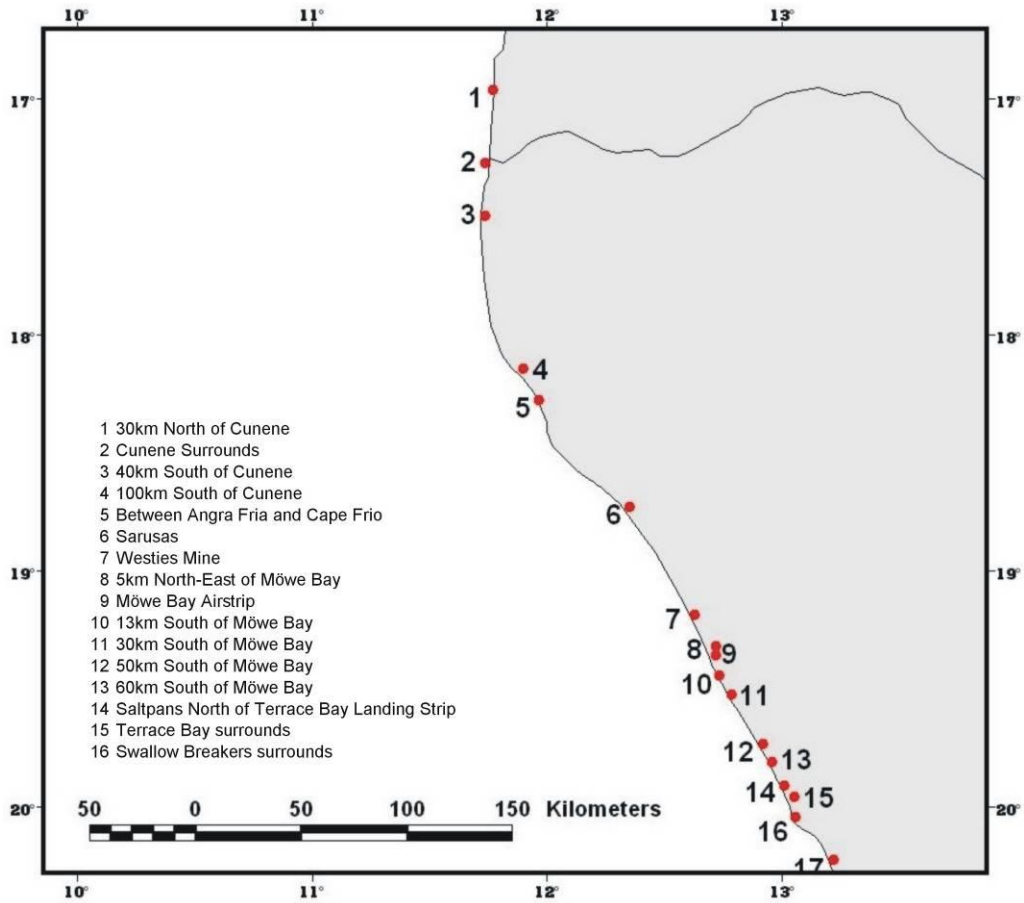


Figure 9.2: Distribution and location of Damara Tern breeding colonies in Angola and part of the Skeleton Coast Park, Namibia.

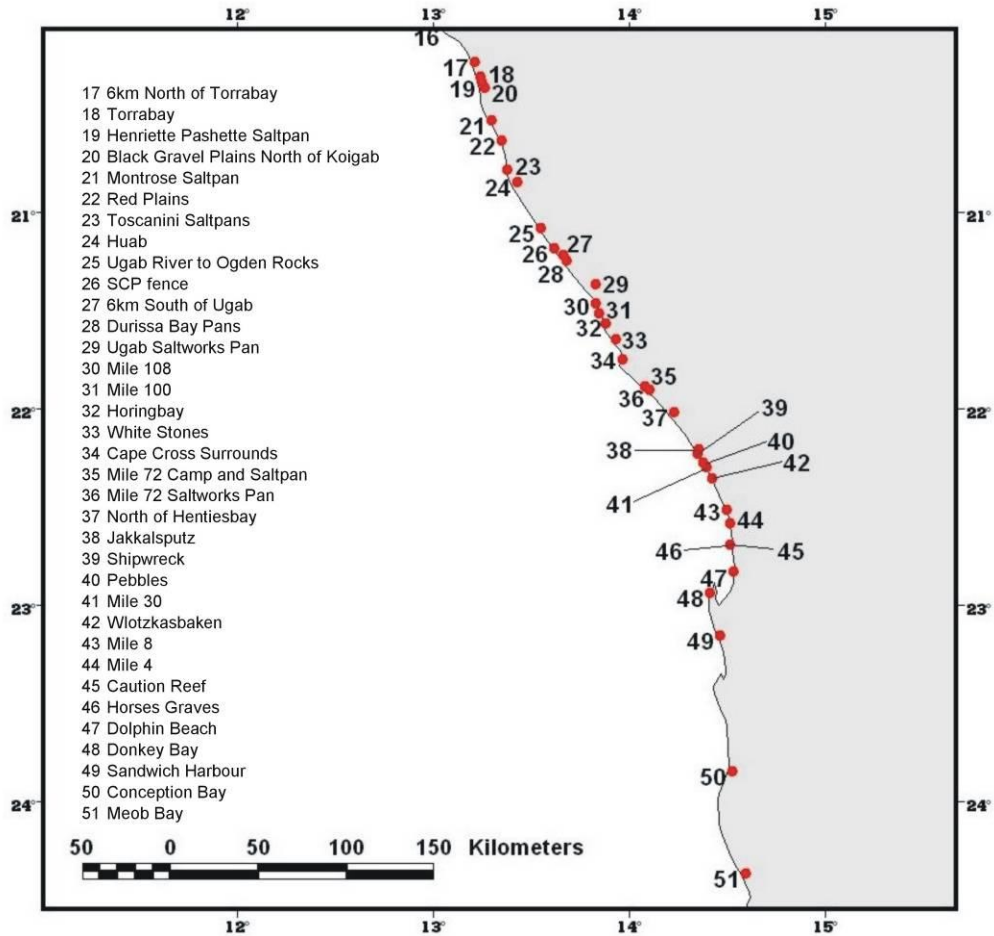


Figure 9.3: Distribution and location of all known Damara Tern breeding colonies in the southern part of the Skeleton Coast Park, the Dorob National Park, and the Namib Naukluft Park, Namibia.

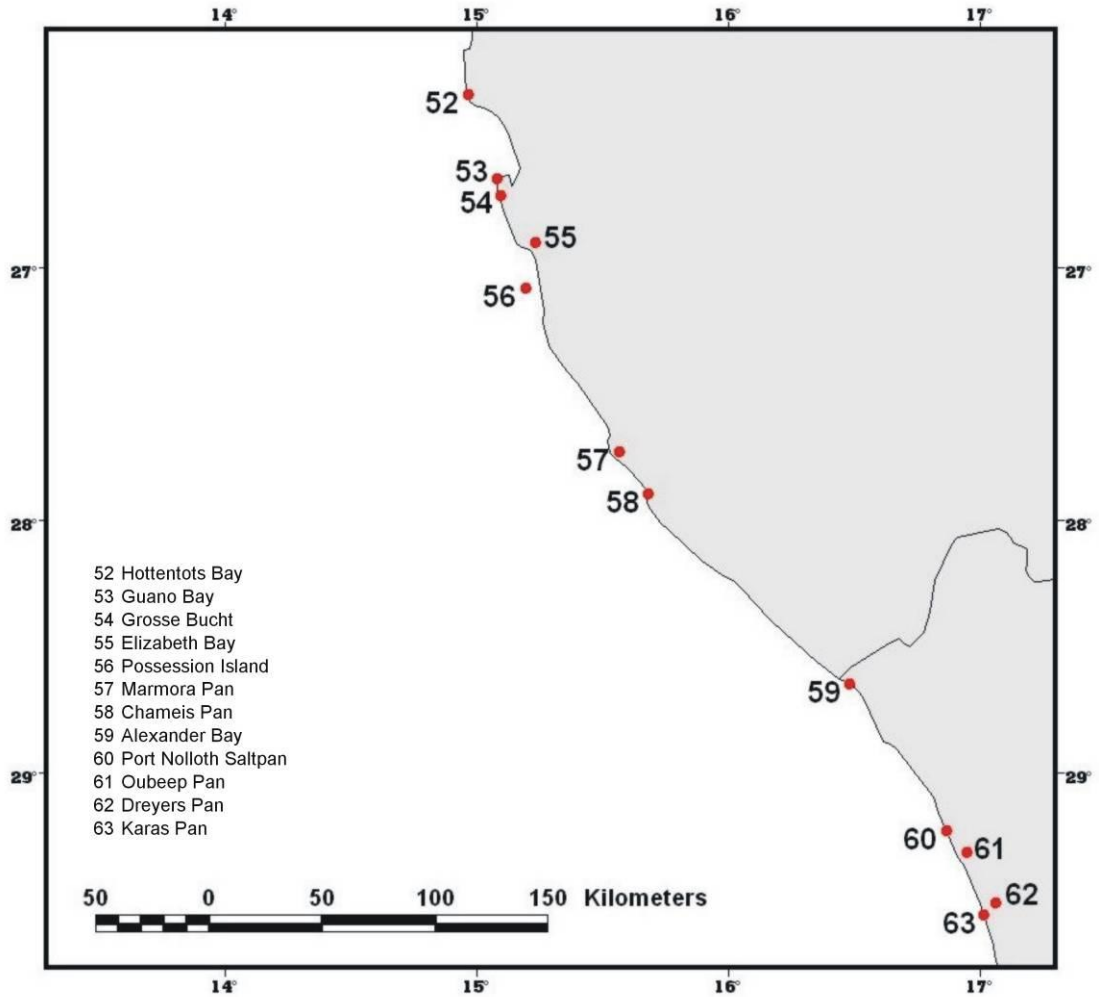


Figure 9.4: Distribution and location of all known Damara Tern breeding colonies in the Sperrgebiet National Park, Namibia and the Northern Cape, South Africa.

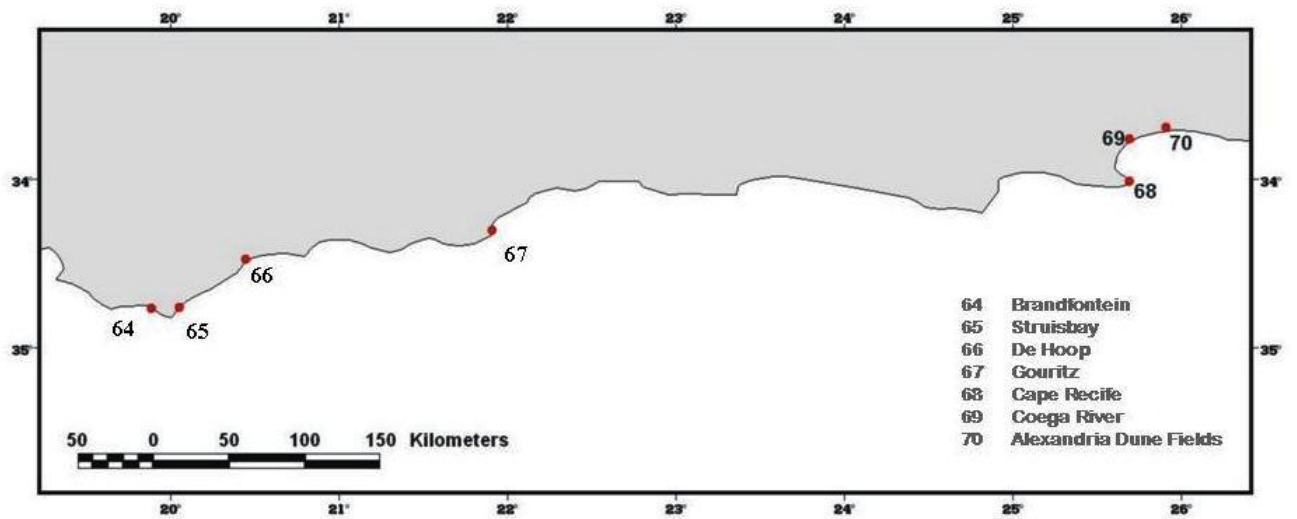


Figure 9.5: Distribution and location of all known Damara Tern breeding colonies in the Western and Eastern Cape, South Africa.

Chapter 10

Synthesis and recommendations



Synthesis and recommendations

Synthesis

The Damara Tern, with its scattered distribution in a barren desert mainland and its long distance migration to West Africa, remains an elusive species to study. This thesis used almost three decades of data collection, observations of the species in migratory countries like Nigeria, and observations of ecologically equivalent Peruvian Terns *Sterna lorata* in Chile. The study has provided new and updated information and greatly increased our knowledge base of the species. Its most important contributions include:

Chapter 1: A comparative description and review of all small terns using published information.

Chapters 2 and 3: New and detailed information of the breeding biology of Damara Terns for update of the description of the species; including the evolution of the small clutch size, egg dimensions and masses, incubation and fledging periods, breeding success in Namibia and for individual colonies, chick hatching and fledging measurements, chick growth patterns and rate, and chick feeding rates.

Chapter 4: The first information on immature survival and age at first breeding of Damara Terns.

Chapter 5: The first information on annual breeding dispersal and adult survival of Damara Terns.

Chapter 6:

1. Overall prey capture success of Damara Terns at two colonies in southern Namibia, and descriptions of the effects of environmental variables on prey capture success.
2. The most detailed description of Damara Tern chick diet to date.

Chapter 7: The effect of diamond mining on feeding and breeding Damara Terns, especially the effect of increased turbidity as a result of sediment discharge into feeding grounds.

Chapter 8: The audit of conservation management at a Damara Tern colony in central Namibia negatively affected by off-road driving.

Chapter 9:

1. A new estimate of the breeding population and an account (and gazetteer) of all known breeding colonies in Angola, Namibia and South Africa (i.e. globally).
2. Recommended survey methods to improve and update population estimates.
3. A review of conservation measures enacted for breeding populations, and recommendations for future conservation.

Recommendations

Gaps in our knowledge

Because the Damara Tern remains a difficult and time-consuming species to study, gaps in our knowledge that could not be filled in my thesis due to insufficient data still remain. These include:

1. Data for energy content of prey fed to Damara Tern chicks to compare with the energy content of similar tern species. This information would be useful to understanding the small clutch size and slower chick growth rate of Damara Terns (Chapters 2, 3 and 6).
2. Energy allocations and activity budgets of Damara Tern chicks to investigate if more energy is spent on activity/movement in Damara Tern chicks than chicks of other small tern species. This information would also contribute to our understanding of slower growth rates of chicks (Chapter 3).
3. Further investigation into dispersal using increased study areas and including more colonies (Chapter 5). This would, however, be methodologically difficult due to the size of the area and the time needed.
4. The relationship of environmental variables, prey capture success and its effect on chick provisioning (feeding) rates (Chapters 6 and 7).
5. Increased information on diet of chicks, and a study of adult diet would help our understanding of important prey species, especially in light of predicted reductions in food availability as a result of climate change (Roux 2003) (Chapter 6).
6. An investigation of the effect of nest distance to sea on chick provisioning rates (Chapter 7).
7. A comparison of energy content of prey fed to chicks at different colonies to test whether energy content has an effect on body condition at these colonies (Chapter 7).
8. Surveys to assess the continued existence of colonies that were last visited prior to 2000 need to be undertaken. This is particularly the case for the colonies along the coast of South Africa (Chapter 9).
9. Up-to-date surveys of Damara Tern breeding populations are urgently needed to assess the size of the global breeding population more

- accurately. This is necessary to re-evaluate the species' IUCN conservation status (Chapter 9).
10. Monitoring of breeding colonies adversely affected by off-road driving, especially colonies between Ugab River and Swakopmund (Plate 2).
 11. An investigation into the trapping and eating/trading of Damara Terns in Angola and migratory countries and its effect on the global population (Annex 1).

Conservation Management

The conservation of breeding populations has already been discussed in detail in Chapter 9. However, the most important points will be re-iterated along with recommendations for protection of non-breeding populations of Damara Terns.

Breeding populations

The most effective approach regarding the protection of breeding populations is the protection and management of important breeding areas (Braby *et al.* 2001, Chapters 5, 8). Colonies that make up more than 1% of the breeding population should be protected from human disturbance.¹ Although at least 95% of the breeding population can be found in protected areas, their conservation remains difficult. This is mainly because human activities that create disturbances are still allowed in these areas (Chapter 9). For instance, Iona National Park in southern Angola is not effectively protected and illegal killing of protected species is ongoing there (T. de Wit pers. comm.). Mining occurs in every protected area along the coastline of Namibia. Although no direct evidence has suggested that mining has had detrimental effects on breeding Damara Terns, the possibility of finding profitable mining deposits at important colony sites may threaten breeding Damara Terns. Other disturbances as a result of mining include mining-related activities at feeding

¹ As part of the criteria for listing an area as an Important Bird Area (IBA, Fishpool *et al.* 1998).

grounds (for more detail see Chapter 9). Off-road driving, the seemingly biggest human disturbance, remains a problem, especially in the Dorob National Park (DNP) of Namibia. Only two colonies in the entire DNP have been cordoned off to protect breeding terns, and this method of protection has resulted in antagonism by off-road drivers. Cutting fences and traversing across breeding grounds remains a regular occurrence, even eight years after fences were first erected (pers. obs). The coastal area between Ugab River and Swakopmund has been detrimentally affected by off-road vehicles (Plate 2), and although permit systems are in place, enforcement has been weak and drivers are either unaware of or refuse to obey the regulations. With the recent proclamation of the Dorob National Park, greater restrictions will be enforced to regulate off-road drivers. Banning off-road driving on beaches and other sensitive areas had direct positive impacts on various seabirds in South Africa (Williams *et al.* 2004). Banning of off-road vehicles on the coast of Namibia would result in major opposition by the coastal community. However, without a decrease in destruction to the desert landscape and its biodiversity caused by off-road driving, it may have to be an eventual option to consider.

Non-breeding populations

The trapping and killing of Damara Terns in their migratory countries has been documented only recently (Braby 2010, Annex 1). The extent of this killing and its impact on the global population of Damara Terns is largely unknown. Virtually the entire population of Damara Terns cross these countries at least once a year, roosting and feeding along the coast. Therefore, it is likely that Damara Terns are significantly affected by this activity. Successful measures were put in place by the program “Save the Seashore Birds Project” to reduce similar activities in Ghana in the 1990s (Yaa Ntiamoa-Baidu 1990). These measures were three-fold, and included:

1. Research to better define the extent of these activities on tern populations.
2. Education and public awareness campaigns that led to the formation of Wildlife Clubs in Ghana to draw attention to the problem and encourage positive action.
3. Legislation that put all terns on Ghana's list of protected species and also gave legal backing to re-enforce protection action.

If human livelihoods are, to some extent, dependent on the trapping of seabirds, then alternative avenues of income acquisition need to be explored for communities involved. Ghana had large success in reducing these activities (Yaa Ntiamoa-Baidu 1990), and similar initiatives should be conducted in all affected countries. Ultimately there should be an integrated and holistic approach led by all migratory countries in West Africa.

Conclusion

This thesis presents information that highlights the importance of an integrated approach to conservation that includes the protection of important breeding (and feeding) sites, and the protection of migrating Damara Terns along the West African coastline. The proclamation of national parks in coastal Namibia and southern Angola is a major step illustrating the commitment made by governments towards the protection of species like the Damara Tern. However, without effective enforcement and awareness, national parks are merely deemed 'paper parks' and are not fulfilling their mandate toward the conservation of biodiversity. Enforcement is needed to implement the legal restrictions set out by park rules, and increased awareness and education is vital in order to shed light on why these restrictions are necessary.

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Appendix 1

Appendix 1: New and updated information on the aspects of breeding biology of the Damara Tern *Sterna balaenarum* (b) compared with information provided by Simmons RE (2005a) (a).

	Sample size		Mean		Range	
	a	b	a	b	a	b
Clutch size	577	2528	1 (99%)	1 (99.998%)	n/a	n/a
Egg length (mm)	263	586	32.2	33.09	29.6–36.2	30.55–37.12
Egg breadth (mm)	263	586	23.8	23.84	22.1–25.3	21.00–25.8
Volume (ml)	7	586	8.57	8.96	7.26–10.77	6.71–10.81
Egg mass (fresh) (g)	7	12	9.3	10.17	–	9.3–11.5
Egg mass (pipping) (g)	7	68	7.5	7.92	–	6.5–9.7
Incubation period (days)	8	106	18-22	23	17.5–30	19–31
Fledging period (days)	1	10	20	23	–	21–24
Overall breeding success (Namibia)	–	–	0.53	0.38	–	–
Feeding rate (fish/hr/chick)	8	36	0.5	1.44	0.4–1.25	0-4.5
Mean chick growth rate (mass, g/day)	–	282	–	0.99	–	–
Chick at hatching						
Mass (g)	18	118	6.5	7.05	4.8–7.6	4.8–9
Bill (mm)	2	26	7.7	7.58	–	6.60–8.68
Wing length (mm)	–	37	–	11.89	–	6.97–17.96
Head length (mm)	–	32	–	24.75	–	22.62–27.60
Foot length (mm)	–	30	–	20.28	–	18.50–22.39
Chick at fledging						
Mass (g)	1	10	40	43.5	–	40–47
Bill (mm)	1	4	17.3	17.9	–	15.80–18.8
Wing length (mm)	1	5	88	100.82	–	101–106
Head length (mm)	–	3	–	45.01	–	44.34–46.14
Foot Length (mm)	–	3	–	28.78	–	28.61–28.97
Adult						
Mass (g)	46	397	51.8	50.99	46.5–62.5	42-63
Bill (mm)	46	350	29.7	30.1	27.7–32.8	25.5–61
Wing length (mm)	45	401	166.05	172.21	155–176	152.59–175
Head length (mm)	–	297	–	62.27	–	48–72
Foot length (mm)	–	10	–	28.25	–	26.78–30.52
Tarsus (mm)	45	237	12.8	16.6	11.6–14.7	11.10–19.50
Immature survival	–	214	–	0.59	–	–
Age at first breeding	–	214	–	3,4	–	–
Adult survival	–	214	–	0.88	–	–
Breeding dispersal	–	214	–	0.06	–	–

Annexes

Annex 1: Excerpt of an article found on the Southern African Bird Atlas 2 Project Website (http://sabap2.adu.org.za/news_list_all.php). This article was reproduced and translated from the original Afrikaans letter (and photo) sent to the newspaper "Republikein" (19 November 2010) by Mr. T. de Wit, a tourist visiting Angola.

Terns trapped and kept alive, sold fresh for food in Angola



Justine Braby is an ADU PhD student, based in Swakopmund. One of the Namibian newspapers, **Die Republikein**, has a column entitled "Dinge wat krap" (things that alarm/irritate). Justine found the following story in this column on 19 November 2010, together with this picture, taken by a resident of the northern Namibian town of Tsumeb.

The citizen reports: "This photo was taken a week ago in Tomwa, Angola, during a visit. These birds are Damara Terns *Sterna balaenarum* which are caught and sold by the local people. They use a baited hook on a fishline. The wings are broken and the birds are buried in the sand so that just the head sticks out. They are kept alive and sold later to eat. We saw other places along the coast where larger birds were caught for the same purpose. Absolutely tragic. I plan to report this to the authorities on my next visit to

Angola."

Although the birds in the picture were identified as Damara Terns most of them look more likely to be Common Terns. But we are fairly certain that there are some Damara Terns among them. Regardless of what species is involved this represents a serious conservation problem. A similar issue arose in Ghana about 20 years ago, and the problem there was tackled by establishing "wildlife clubs" at many villages along the coast. The Common Terns on passage southward along the Angolan coastline at this time of the year would be mainly from the Baltic Sea region, with the birds having bred in countries such as Sweden, Norway, Finland, Poland, Estonia, Lithuania, Latvia and Denmark. Damara Terns, in contrast, breed mainly along the desert coastline of Namibia. They don't breed along the shoreline, but several kilometres (up to 10 km) inland, so they can reduce the risk of predation from jackals, which patrol the coastline for dead and sick seals, and anything else they can scavenge. They breed from November to February, and then migrate north to spend the nonbreeding season in West Africa, in countries such as Ghana and Nigeria. So Damara Terns passing along the Angolan coastline now would be pretty close to their breeding destinations in Namibia.

The editor, Chris Jacobie, of Die Republikein gave permission for this picture, and the accompanying story, to be reproduced here. He commented: "A collusion of the article and the knowledgeable must help in some way".

Annex 2: The following excerpt is reproduced from the methodology written by le Roux (2006) for the study of growth in Swift Terns *Sterna bergii*:

“Statistical analysis for growth curves for Swift Terns

The growth patterns of most measurements did not conform to the standard growth curves, such as logistic or Gompertz (Reiss 1989). A new descriptive statistical approach was therefore devised. For all chicks that were captured more than once, growth rates were calculated between each pair of captures for mass and for each structure: wing length, head length, culmen length, tarsus length and foot length. The average of the pair of measurements was also calculated. For example if successive masses at times t and u were m_t and m_u , the growth rate over this time period is $g = (\text{change in size})/(\text{time period}) = (m_t - m_u)/(t - u)$ and the average of the pair of measurements is $a = (m_t + m_u)/2$. All the pairs of values (a, g) were plotted. This was done for mass and for each length measurement. Identical “growth-rate vs size” plots were produced by Schoener and Schoener (1978) in their analysis of growth rates of lizards. These growth-rate vs size plot are referred to as “growth rate plots”.

The initial focus was on growth in mass. For a set of target masses at small increments between hatching mass and fledging mass, the average growth rate at each of these masses was estimated. This was achieved by using weighted regression. For the target mass at which growth rate needed to be estimated, weights for all the pairs of observations were calculated (a, g) in such that values close to the target mass had large weights and values farther away had increasingly smaller weights. If the target mass was m^* , then the weight w attached to observation (a, g) was $w = \exp(-((a - m^*)/\sigma)^2)$ where σ was chosen to be 8.0. This is about 2.4% of the adult mass (see below). This results in weights attached to observations 8 g distant from the target mass being substantial (weight 0.37), at 12 g distant the weight (0.105)

is small, and at 16 g distant the weight (0.018) is tiny. Observations more than 16 g distant from the target mass thus have negligible weights to the regression calculations. The weighted linear regression was fitted to predict growth rate from mass using these weights, and this regression line, fitted by GenStat8 (Payne *et al.* 2005) was used to predict the growth rate g^* at the target mass. Using this weighted approach, this estimated growth rate then depends on observed growth rates in the neighbourhood of the target mass.

By varying σ , the length of the influential neighbourhood can be modified. The smaller the value of σ , the shorter the neighbourhood, the fewer observations are effectively included, and the estimated growth rate at the target masses are based on small samples and tend to be unstable. The larger the value of σ , the wider the neighbourhood and the more stable the estimates; however, the inclusion of growth rates distant from the target mass can result in biases. There is thus a trade-off between values of σ which are large enough to prevent instability of the estimates and values which are small enough that the estimate refers to a small neighbourhood of the target mass. A similar compromise has to be made in various statistical smoothing methods (Silverman 1986), where the amount of smoothing depends on the size of the smoothing window (frequently referred to as “bandwidth”); too small a window results in little smoothing, too large a window results in over-smoothing, with important aspects of the data being obscured. There are automatic methods to choose the width of the smoothing window, but the best approach remains visual inspection of the results (Silverman 1986). The visual inspection approach was used to choose $\sigma = 8$; however, the results do not depend critically on the choice of a particular value for σ , the experimentation showed that if a chosen value was twice as large or half as small, the results would have been nearly identical.

An approximate standard deviation of mass at each target mass was estimated. The same weights used for the regression were used to estimate a weighted standard deviation s_{m^*} ; the formula $s_{m^*} = (1/\sum w)((w(g-g^*)^2)$ was used.

An approximate coefficient of variation for each target mass was calculated as $CV^* = 100 \times (s_{m^*}/m^*)$. This coefficient of variation provides a measure of the variability of the growth rate for each target mass.

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

For each successive pair of measurements on a chick, a comparison was made between the observed growth rate and the expected growth rate in the interval between the two measurements. The expected growth rate was computed at the average of the two measurements, and its approximate standard deviation calculated as described above. The standardized growth rate was then computed using the conventional approach to standardization – dividing the difference between the observed and expected growth rate by the standard deviation. In symbols, if the observed growth rate is g , the predicted growth rate is g^* and the estimated standard deviation at this growth rate is s^* , then the standardized growth rate z is defined to be $z = (g - g^*)/s^*$. For large samples, the overall mean of all z -values is asymptotically zero; negative values indicate below average growth rates and positive values indicate above average growth rates. The z -values can be interpreted as an index of the extent to which growth in the interval is above or below expected; through the mechanism of dividing by the standard deviation, the index is independent of the stage of growth. In other words, the z -values, which are dimensionless, represent a common currency to measure

departures from “average” growth, which are independent of whether growth is measured early when the absolute growth rates (g/day or mm/day) tend to be small, at the maximum growth spurt, when growth rates tend to be large, or late in growth, when growth rates tend to be decreasing.

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

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

Plates



(a)

(b)



(c)

(d)

Plate 1: Photographs of nests illustrating the importance of substrate in egg camouflage at each colony in southern Namibia, (a) Hottentots Bay, (b) Grosse Bucht, (c) Elizabeth Bay, and (d) Marmora Pan.



Rod Braby

(a)



Rod Braby

Plate 2: Aerial photographs showing off-road vehicle tracks (a) between the main road and the beach, and (b) east of the main road. Both pictures were taken in the Dorob National Park, between the Ugab River and Swakopmund, Namibia.



Sigi Braby



Sigi Braby

Swakopmund



www.nacomana.org.na

Horses Graves

Caution Reef

Plate 3: Photographs of conservation measures put in place at Horses Graves and Caution Reef in central Namibia.



(a)



(b)



(c)

Plate 4: Photograph illustrating the level of discharge of sediment into the sea as a result of diamond mining at Elizabeth Bay in southern Namibia, (a) full, (b) moderate, and (c) trickle.



(a)



(b)



(c)



(d)

Plate 5: Photographs illustrating different breeding habitats of Damara Terns in southern Namibia; (a) Hottentots Bay, (b) Grosse Bucht, (c) Elizabeth Bay, and (d) Marmora Pan.



Hatchling



c. One week



c. Two weeks



c. Three-four weeks

Plate 6: Damara Tern chicks in different stages of development.



(a)



(b)



Kerry Steinberner

Photo: Kerry Steinberner

(c)

Plate 7: The most common predators of Damara Tern eggs and chicks, the (a) Black-backed Jackal *Canis mesomelas*, (b) Pied Crow *Corvus albus*, and (c) Kelp Gull *Larus dominicanus*.