BREEDING AND POPULATION ECOLOGY OF SOOTY TERNS ON ASCENSION ISLAND

by

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ABSTRACT

Seabird breeding success and population size on many oceanic islands have declined in recent years as a result of predation by non-native mammals. On Ascension Island, South Atlantic the sooty tern *Onychoprion fuscatus* breeding population declined precipitously in size in the 1970s. Despite cat eradication in 2003 and a cull of predatory mynas, the tern population between 1990 and 2012 consistently contained 350,000 birds. Shortages of small fish within foraging range of Ascension driven to the sea surface by once more prevalent tuna rather than cat predation probably caused the 1970s decline. Abundance and size of rats increased in response to cat eradication with the impact of rats on the size of the seabird population similar to the combined impact of both cats and rats. Ascension sooty terns have adopted a life-history strategy of sub-annual breeding as a viable alternative to seasonal breeding. The population consistently bred every 289 days, as did most individual birds. Despite an increase in lifetime reproductive rate resulting from sub-annual breeding, I predict a slow but sure decline in the population size unless rats are controlled. Studies of sooty tern migratory ecology are required and the species' current IUCN Red List category should be reviewed.

This contribution to the study of tropical seabirds in the United Kingdom Overseas Territory of Ascension Island is dedicated to the citizen scientists in the Army Ornithological Society who gave freely of their time to collect the field data.

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LIST OF ABBREVIATIONS

AIG: Ascension Island Government
AoN: Apparently occupied nest
AOS: Army Ornithological Society
ASR: Adult sex ratio
BBI: Boatswainbird Islet
BM: Body mass
BOU: British Ornithologists’ Union
BTO: British Trust for Ornithology
C/100TN: Captures per 100 trap nights
CMR: Capture mark recovery
ENSO: El Niño–Southern Oscillation
GPS: Global positioning system
HBL: Head and body length
IBA: Important Bird Area
ICCAT: International Commission for the Conservation of Atlantic Tuna
IUCN: **International Union for Conservation of Nature**
LRS: Lifetime reproductive success
MM: Myna Magnet - cage traps
NAO: North Atlantic Oscillation
NASA: **National Aeronautics and Space Administration**
NGO: Non-governmental organisation
PCB: Polychlorinated biphenyl
RAFOS: Royal Air Force Ornithological Society
RNBWS: Royal Naval Birdwatching Society
RSPB: Royal Society for the Protection of Birds
SIA: Stable isotope analysis
SOI: Southern oscillation index
SST: Sea surface temperature
TBW: Total body water
UK: United Kingdom
UKOT: United Kingdom Overseas Territory

PUBLICATIONS FROM THESIS WORK

(1) **Hughes, B.J**., Martin, G.R. & Reynolds, S.J. 2008. Cats and seabirds: effects of feral Domestic Cat *Felis silvestris catus* eradication on the population of Sooty Terns *Onychoprion fuscata* on Ascension Island, South Atlantic. *Ibis* **150** (Suppl. 1): 122–131.

(2) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J**.** 2010. Sooty Terns *Onychoprion fuscata* on Ascension Island in the south Atlantic are a reproductively isolated population. *Revista Brasileira de Ornitologia* **18**: 194–198.

(3) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J. 2011. The use of Google Earth™ satellite imagery to detect the nests of Masked Boobies (*Sula dactylatra*). *Wildlife Biology* **17**: 210–216.

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(5) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J. 2013. Sublingual fistula in a Masked Booby (*Sula dactylatra*) and possible role of ectoparasites in its etiology. *Journal of Wildlife Diseases* **49**: 455–457.

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(7) Ratcliffe, N., **Hughes, B.J.** & Roberts, F.A. 1999. The population status of Sooty Terns *Sterna fuscata* on Ascension Island. *Atlantic Seabirds* **1**: 159–168.

(8) Reynolds, S.J., Martin, G.R., Wallace, L.L., Wearn, C.P. & **Hughes, B.J.** 2008. Sexing sooty terns (***Onychoprion fuscata***) on Ascension Island from morphometric measurements. ***Journal of Zoology*** **274**: 2–8.

(9) Reynolds, S.J., Martin, G.R., Wearn, C.P. & **Hughes, B.J.** 2009. Sub-lingual oral fistulas in sooty terns (*Onychoprion fuscata*). *Journal of Ornithology* **150**: 691–696.

Chapter 1

GENERAL INTRODUCTION

Reproduction is one of the key life-history stages of any organism and is fundamental to the maintenance of species. For a population to remain stable or increase in size, recruitment to the breeding population must be greater than the losses from the population. Births, deaths, immigration and emigration are the demographic parameters that regulate population size (Krebs 2001). Numbers of free-living animal species and population sizes are declining at ever increasing frequency and ever increasing rates (Pimm & Raven 2000, Jenkins 2003). A decline in population size can be caused by a shortage of new recruits, adult mortality and emigration. For long-lived (*K*-selected) species capable of reproducing in many breeding seasons, a breeding adult must produce only one independent young that recruits to the breeding population to replace itself but this can fail to happen even in human *Homo sapiens* populations such as in Japan (Coulmas 2007) and Italy (Golini 2002). In these countries, the choice not to have an offspring might be the cause of population decline but for free-living non-human species food availability is believed to be the most critical factor influencing breeding success (Tilman 1982, Weimerskirch *et al.* 2001). The food availability-breeding time hypothesis suggests that seabirds and most other free-living animal taxa breed at the time of the year when food is most plentiful for their young (Martin 1987, Oro *et al.* 2004). Seabird breeding ecology, the subject of this thesis, encompasses various individual (e.g. behaviour, foraging success, breeding success) and population (e.g. size, change, timing of breeding) parameters that together inform us about the ‘health’ of the ecosystem.

1.1. Seabird breeding ecology on tropical Islands

There is an urgent need for research to provide insight into the breeding and population ecology of seabirds on tropical islands (Croxall *et al.* 2012). There are differences in the life-history parameters of seabirds at low and high latitudes. For example, in both intra-specific and inter-specific comparisons there is a tendency for average body mass of seabirds to increase with latitude (agreeing with Bergmann's rule; Allaby 1998) and for surface area:volume ratio to increase with latitude to facilitate heat loss in tropical seabirds (agreeing with Allen's rule; Allaby 1998). Breeding seasons on tropical seabirds are generally longer than those at .higher latitudes (Schreiber & Burger 2002). Tropical islands are characterised partly by their high extinction rates (Diamond 1984, Mulder *et al.* 2011) and small islands hold disproportionately high numbers of globally threatened birds (Johnson & Stattersfield 1990, Mulder *et al.* 2011). Although biodiversity has been lost on islands at a greater rate than on continental land masses, there is a dearth of current information on avian population trends on tropical islands (Senapathi *et al.* 2011). Overall, the populations of seabirds are more threatened than other avian taxa and their general population status as determined by the International Union for Conservation of Nature (IUCN) has deteriorated rapidly over recent decades (see Croxall *et al.* 2012 for more details). Pelagic seabirds spend the major part of their lives far out at sea (Weimerskirch *et al.* 2001, Jaquemet *et al.* 2007) but during their breeding season pelagic seabirds are frequently found on islands (Schreiber & Burger 2002) where their breeding populations can be monitored. However, juveniles and intermittent breeding birds (i.e. those with previous breeding experience that refrain from breeding for one or more years) do not necessarily return to land and frequently are missed in population monitoring programmes. Many islands where pelagic seabirds nest are small and remote, have few, if any, human inhabitants, typically lack local resources such as water and are administered from afar (Bertram 2004, Pienkowski 2010, Mulder *et al.* 2011).

1.2. Seabirds in the United Kingdom Overseas Territories (UKOTs)

The United Kingdom has sovereignty over 14 mostly small islands in the Atlantic, Pacific and Indian Oceans. Most of the islands in the UKOTs are Important Bird Areas (IBAs) (Sanders 2006). There are 23 endemic bird species (Sanders 2006, Pienkowski 2010) and 33 species of birds that are critically endangered in the UKOTs (Hilton & Cuthbert 2010). Of the six seabird species that have gone extinct in historic times, the St Helena gadfly petrel *Pterodroma rupinarum* and the St Helena bulweria petrel *Bulweria bifax* were originally found in the UKOT of St Helena as their names imply (McCulloch 2004).

Ascension Island, the location for research documented in this thesis, is another of the islands that make up the territory of St Helena. Of the three endemic species found on Ascension, the Ascension frigatebird *Fregata aquila* has a Red List category of ‘Vulnerable’ (BirdLife International 2013) while the Ascension crake *Mundia elpenor* and the Ascension night heron *Nycticorax olsoni* (Bourne *et al.* 2003a) are now extinct. The Audubon’s shearwater *Puffinus lherminieri* no longer breeds on Ascension (Bourne & Loveridge 1978) and most of the remaining 11 species are in decline with the red-footy booby *Sula sula* close to being extirpated (Simmons 1990, Ratcliffe *et al.* 2009). All of the native species that currently breed on Ascension are pelagic seabirds. Their population sizes are small (with a mean of 3,000 birds, n = 10 species) with the exception of sooty terns *Onychoprion fuscatus*. Clearly, there is a need to monitor and manage seabird populations that are small but large populations such as sooty terns also need to be monitored as they too can be susceptible to extinction events. History tells us that even some species that were present in large populations (e.g. great auks *Pinguinus impennis,* passenger pigeons *Ectopistes migratorius*) have become extinct rapidly as a result of exploitation by humans (Gaskell 2000, Loehle & Eschenbach 2012, BirdLife International 2012a).

1.3. Ascension Island

My study was based on Ascension Island which was discovered in 1501 by Portuguese navigators. It remained uninhabited until 1815 when the Royal Marines built a garrison on the island (Ashmole & Ashmole 2000). Ascension is an isolated 97 km^2 island in the tropical South Atlantic Ocean (07º57´S, 14º24´W) midway between South America and Africa (Fig. 1.1). It lies some 800 km south of the equator, 2,000 km from continental land masses and its nearest neighbour is St Helena which is 1,400 km to the south-east. It is entirely volcanic in origin except for some beach material (Weaver 2002); composed mainly of basaltic lava flows, the highest point on the island is Green Mountain at 859 m. The island constitutes only 1% of a huge shield volcano which lies below the surface of the ocean. The surrounding oceanic crust is 3,200 m below sea level (Weaver 2002). Ascension is a very young volcanic island with the oldest exposed rocks being about 1 million years old (Weaver 2002). There are no rivers on Ascension, water is scarce and standing water occurs rarely and then only on Green Mountain (Packer 1983). Water for the present human population is obtained from desalination equipment

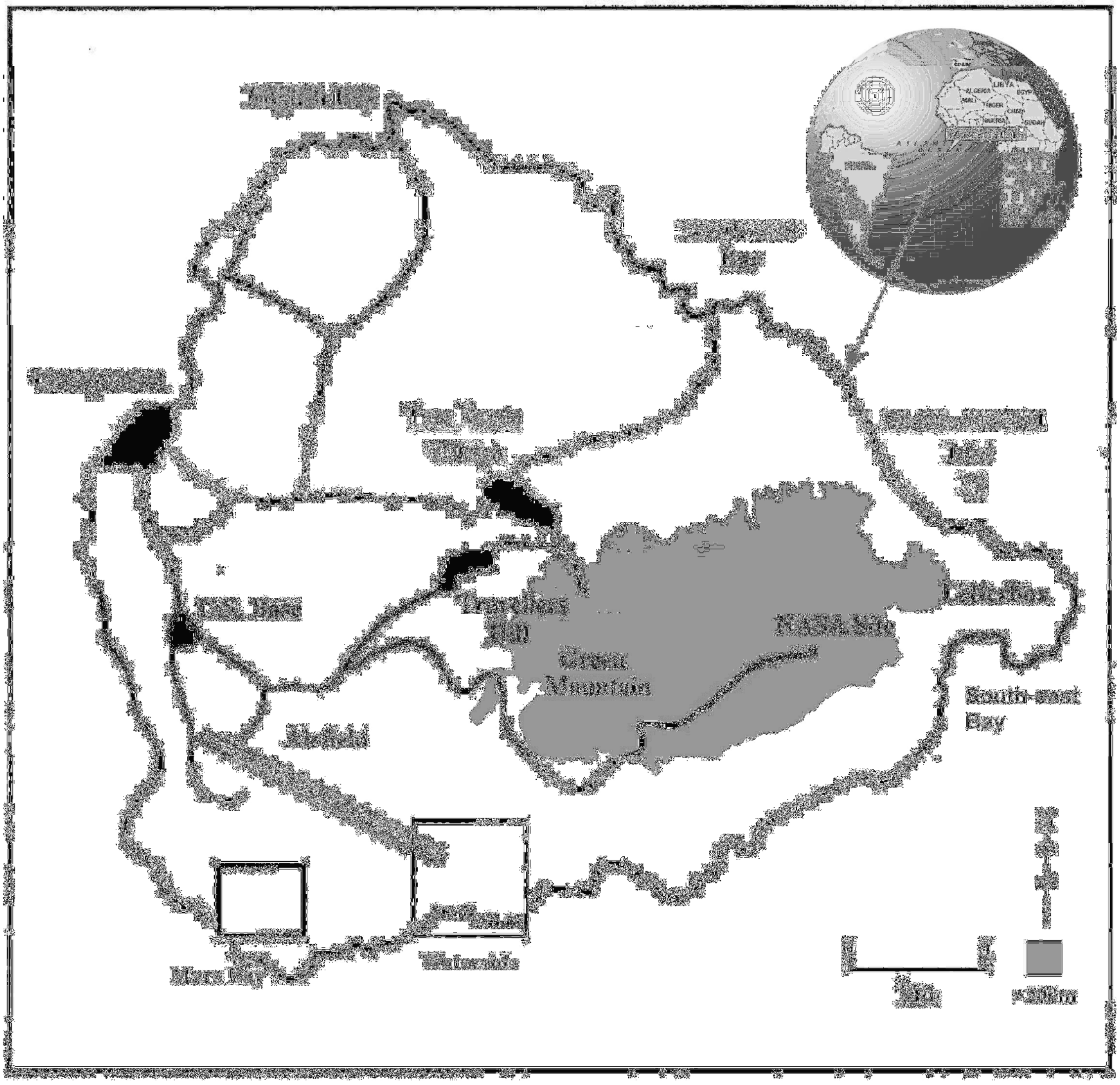

Figure 1.1. Location of Ascension Island in the South Atlantic and a map of the island showing Green Mountain, sites of human habitation and locations of the sooty tern colonies at Mars Bay and Waterside. Historically, seabird colonies were located on the plain that lies to the west of Travellers Hill and Two Boats village. Boatswainbird Islet and the 14 offshore stacks support a significant proportion of the Ascension Island population of 11 seabird species.

(McQueen 2005). The climate of Ascension Island lacks extremes of heat and humidity, and shows little seasonal variation. With regards to rainfall, the island has three seasons: January to April – the wettest period with a monthly average rainfall of 24.0 mm; May to August – broken cloud with a monthly average rainfall of 12.1 mm; and September to December – occasional drizzle with a monthly average rainfall of 9.9 mm (Anon 1998). Daytime temperature ranges from 26–31°C and overnight 21–25°C. The warmest period of the year is December to April. Strong south-east tradewinds blow across the island year-round (Anon 1998). The productivity of the waters surrounding Ascension is low and there is no evidence of seasonal variation in the abundance of zooplankton (Latif & Grötzner 2000). In offshore waters the Sea Surface Temperature (SST) ranged annually between 28°C in April and 24°C in September in years between 2007 and 2011 (POET 2011). Most seabirds that breed on Ascension forage north of the island (Hughes 1994) in a tongue of cold water (Stonehouse 1962a). Historical records of seabirds breeding in vast numbers on the island (Stonehouse 1960, Hart-Davis 1972) would suggest that the environment on Ascension is conducive for breeding seabirds. A more detailed account of the environment has been published in Ashmole and Ashmole (2000).

On Ascension there are few commercial facilities and no indigenous human population. Most of the inhabitants (approximately 900 and declining) are from St Helena or are military contractors on short-term contracts (approximately 6 months) from the UK or the USA. Until the 21st century few professional scientists visited Ascension (Pienkowski 2010) and amateur naturalists from the UK or the USA are not on the island for sufficient time to monitor changes in the environment (Pienkowski 2010). However, the island came to prominence in 1982 during the Falklands War when many service personnel including some of the ≈ 500 members of the services' ornithological societies staged through the island on their way to war (McQueen 2005).

1.4. Services' ornithological societies

The influx of British service personnel to the South Atlantic in the 1980s was quickly followed by ornithological reports in the grey literature from military amateur ornithologists. Surgeon Lieutenant Commander D.G. Bruce from the hospital ship H.M.S. Hecla reported on seabird foraging ranges in *Sea Swallow*, the Royal Navy Birdwatching Society's (RNBWS') journal (Bruce 1982). Major P.J. Hubert, reconnaissance officer for the task force, visited Ascension in February 1982 and published a report on Ascension seabirds in *The Adjutant*, the Journal of the Army Bird Watching Society (ABWS) (Hubert 1982). It was later renamed the Army Ornithological Society (AOS). Squadron Leader M.J. Blair led a Royal Air Force Ornithological Society (RAFOS) expedition to Ascension in 1987 and completed a census of all birds on the island, publishing a report in their journal (Blair 1989). In 1990 under the direction of Field Marshall Sir John Chapple (AOS President from 1990 to 2012), the AOS began to mount ornithological expeditions to Ascension. My first field season on Ascension with the AOS coincided with the field season of Drs Philip and Myrtle Ashmole, and Ken Simmons (see Appendix 1). All had extensive knowledge of the Ascension avifauna from previous visits to the island (Ashmole *et al*. 1994). The AOS received guidance on seabird monitoring techniques from these ornithologists and since then the AOS has continued regular monitoring on the island. During the field season I discovered that my skills in topographical surveying were needed to census large colonies of seabirds and it was from this that I maintained regular censuses of the breeding population of sooty terns. Since then AOS members have overcome financial constraints by self-funding and have continued regular monitoring of sooty terns to the present day. To date, the total expenditure on monitoring and data collection has been £380,000 with time in the field amounting to 1,328 person-days. The eighteenth AOS expedition to the island took place in December 2012 and the nineteenth is scheduled for August 2013.

1.5. Historical research

Many earlier visitors commented on the large number of seabirds found breeding on Ascension (see reports from the 18th century in Hart-Davis 1972, Ashmole & Ashmole 2000). Although the island has been visited by scientific expeditions including The Beagle in 1838 (Darwin 1844), only five have remained long enough to make detailed studies of the avifauna (Ashmole & Ashmole 2000): (1) During World War II, while advising the United States army on the removal of sooty terns from the site selected for an airfield, Chapin (1946, 1954) and Chapin and Wing (1959) produced comprehensive accounts of the sub-annual breeding cycle of the sooty tern; (2) The British Ornithologists' Union (BOU) mounted an expedition to Ascension from October 1967 to May 1969 to study the breeding cycles and breeding seasons of resident seabirds (Stonehouse 1962a). They found that non-native predators (i.e. domestic cats *Felis silvestris*; Driscoll *et al.* 2007 and black rats *Rattus rattus* [hereafter referred to as 'rats']) had largely restricted seabird breeding to predator-free offshore islets (Allan 1962, Dorward 1962, 1963). These studies remained the definitive ones of seabirds on Ascension and provided a useful baseline for measuring changes in seabird populations over the following half century. (3) Ken Simmons was a resident on Ascension between 1962 and 1964 when he studied brown boobies *Sula leucogaster* on two offshore stacks (Simmons 1967). (4) Independent of my study, a seabird restoration programme managed by the Royal Society for the Protection of Birds (RSPB) targeted feral cats and commenced in 2001 midway through my study period (Pickup 1999, Ratcliffe *et* *al.* 2009). (5) The Ascension Island Government (AIG) with the support of the RSPB opened a Conservation Office in 2002 with two, later rising to five, full-time staff. The office has a remit to monitor the flora and fauna of the island (Bolton *et al.* 2012).

1.6. Fauna of Ascension Island

There are no indigenous extant reptile, mammal and landbird species on Ascension (Duffey 1964). The animal species extant on the island can be divided into three groups: non-native mammals, non-native landbirds and pelagic seabirds. Four of the most widespread and devastating (for indigenous species) invasive mammals (ISSG 2011a) are found on Ascension Island: feral cats, rats, European rabbits *Oryctolagus cuniculus* and house mice *Mus musculus.* Rats and mice probably arrived in February 1701 when H.M.S. Roebuck foundered close to the shore near Georgetown (Anon 2001, Fig. 1.1). The crew safely abandoned the ship as probably did the ship's complement of rats and mice. The rodent population flourished and W. Davies who visited Ascension in 1798 recorded rats in "amazing numbers" (Hart-Davis 1972). Cats arrived with the marine garrison in 1815 to control rat numbers and in 1820 rabbits were also deliberately introduced (Packer 1983). Further major changes to the environment occurred when Mexican thorn *Prosopis juliflora* was deliberately introduced in 1990. Cats were the dominant invasive species in the early part of my study period while rats dominated the latter period (NISIC 2011). Feral cats were eradicated between 2002 and 2004. Common mynas *Acridotheres tristis* (hereafter referred to as 'mynas'), that are also classed among the world's top most invasive species (ISSG 2011b), were introduced between 1879 and 1892 (Duffey 1964) in an attempt to reduce crop damage from black grubs of another non-native species of the noctuid moth *Agrotis obliviosa*

(Royal Botanic Gardens, Kew 1877). The non-invasive red-necked francolin *Francolinus afer* was introduced in 1851 as a gamebird (McCulloch 2004). Of the numerous other species of landbird introduced to the island (Hart-Davis 1972), common waxbills *Estrilda astrild* and yellow canaries *Serinus flaviventris* are the only species to have survived (Table 1.1). Except for some rocks, Ascension is the only place in 1 million km² of ocean where pelagic seabirds can nest. Seabirds traditionally nested on the coastal plain of Ascension (Fig. 1.2) where plant species' diversity is low (i.e. < 11 species per 2.6 km²; Duffey 1964). Between 1958 and the present day the main island of Ascension, together with Boatswainbird Islet (BBI) and 14 small stacks supported populations of 11 species of pelagic seabirds (Table 1.2). All but two of the seabird species (i.e. sooty tern and brown noddy) bred primarily on BBI with the islet having a surface area of 0.05 km² and lying 300 m off the shoreline of Ascension's mainland (Fig. 1.1). Breeding colonies of boobies and terns are marked on historical maps of the island (Bedford 1838). Signs of old seabird colonies are still clearly visible on the ground (see Bourne *et al.* 2003b and image on Google Earth™ 2013). The old colonies covered much of

Table 1.1. Estimates of population sizes of non-native avian species on Ascension Island in 1958, 1987, 1988 and from most recent estimates. Estimates of bird numbers (individuals) differ widely in reliability and include an indeterminate number of breeders.

Species	**1958**[a]	**1987**[b]	**1988**[c]	**Most recent**
Red-necked francolin	Very small	80-250	100	75[d]
Common myna	400	>1,000	No estimate	1200[e]
Common waxbill	300–400	800	>400	550[d]
Yellow canary	100–200	800	>200	1,100[d]

Sources of data: [a]Stonehouse 1962a; [b]Blair 1989; [c]Nash and Osborn 1988; [d]Varley and Dickey 1994; and [e]Saavedra 2009 (prior to cull of mynas)

Figure 1.2. View of Ascension Island coastal plain and the sooty tern colony at Waterside (Photo: D. Thomas).

the western coastal plain and extended to some 5 km² (Bourne *et al.* 2003b). Today, these large colonies have reduced in size to an area of 0.10–0.15 km² in the south-west corner of the island (Fig. 1.1) occupied by sooty terns (Fig. 1.3).

Figure 1.3. A breeding adult sooty tern on Ascension Island in the South Atlantic. (Photo: D. Osborn).

Table 1.2. Estimates of population sizes of native avian species on Ascension Island, Boatswainbird Islet (BBI) and the offshore stacks in 1958, 1987, 1988 and from the most recent work. Estimates of bird numbers (individuals) differ widely in reliability and include an indeterminate number of breeders.

Common name of species	**1958[a,b]**	**1987[c]**	**1988[d]**	**Most recent**
Madeiran storm petrel	3,000	2,000	No estimate	No estimate
Red-billed tropicbird	1,000	50	100	1,100[e]
White-tailed tropicbird	2,000	250	400–600	2,200[e]
Masked booby	9,000	8000	10,000–20,000	4,666[f]
Brown booby	2,000	< 2000	1,500–2,000	2,000[f]
Red-footed booby	30	> 15	> 20	50[g]
Ascension frigatebird	9,000–12,000	> 1100	> 2,500	15,700[h]
Sooty tern	750,000	≈ 100,000	No estimate	351,000[i]
Brown noddy	1,000	200	100+	900[g]
Black noddy	75,000	6,500	10,000	20,000[e]
White tern	2,000	5,300	1,000	1,300–1,400[j]

Sources of information: [a]Stonehouse 1962a; [b]Ashmole 1963a; [c]Blair 1989; [d]Nash and Osborn 1988; [e]Ashmole and Ashmole 2000; [f]White *et al.* 2002; [g]BJH unpubl. data; [h]Ratcliffe *et al.* 2008; [i]Hughes *et al.* 2008; and [j]Easterbrook 2004.

1.7. Sooty terns

The sooty tern (Fig. 1.3) is a seabird species of tropical oceans that nests in large dense colonies on islands throughout the equatorial zone. Eight subspecies are currently recognized but their taxonomical status is uncertain (del Hoyo *et al.* 1996). Sooty terns are sexually monomorphic in plumage traits but there is slight sexual body size dimorphism, typically with males being 2–5% larger than females (Reynolds *et al.* 2008). Sooty terns begin to breed at four years of age (Harrington 1974) and their lifespan can exceed 34 years (Schreiber *et al.* 2002). Over much of their range they show marked fidelity to their natal colony. Sooty terns may remain continuously airborne for years and we think that they can sleep as well as feed ‘on the wing’ (Ashmole 1963a). Very occasionally they settle on water (Bourne & Simmons 2001) but their plumage has poor waterproofing and they rapidly become waterlogged (Johnston 1979). Before they reach sexual maturity and breed for the first time, we think that they remain at sea foraging above deep water (Schreiber *et al.* 2002). However, there is uncertainty as first year sooty terns from the Dry Tortugas, Florida, USA are known to forage closer to land in the Gulf of Guinea (Robertson 1969). Outside the breeding season, adult birds are truly pelagic (Ashmole 1963a). They rely solely on the ocean for foraging and are known to associate with top-predator fish species to locate ‘patches’ of small fish (Au and Pitman 1986). Sooty terns are commensal with tuna *Thunnus* spp*.* The bird is of considerable use to Pacific Ocean (Burger 1988) and Indian Ocean (Jaquemet *et al.* 2007) fishermen who follow their feeding flocks to locate schools of tuna (Montevechi 1993). They have an important religious significance to Easter Islanders in the Pacific Ocean (Luke 1954) and are a major food source in The Seychelles in the Indian Ocean (Feare 1976) where they are known as the "egg bird".

1.8. Current knowledge

The global population estimate of sooty terns is 21 million birds and the species status is of 'Least Concern' (BirdLife International 2012a). However, the global population trend is unknown and this is of concern because of the large discrepancy between population estimates. Just 10 years ago, Schreiber *et al.* (2002) estimated that the global population size was 36 to 46 million birds. Feare *et al.* (2007) completed an inventory of sooty terns in the western Indian Ocean but most of the estimates of sooty tern population size in the Pacific Ocean are based on old counts and estimates of population size in many Atlantic Ocean colonies are lacking (Schreiber *et al.* 2002). On Ascension Ashmole (1963a) guessed that size of the sooty tern population in 1958 was 750,000 birds and that the population of sooty terns between 1815 and 1990 has declined in size (Ashmole *et al.* 1994). Censuses of the Ascension population are fundamental if such a decline is to be quantified.

Sooty terns have an extremely large range (BirdLife International 2012b) despite having been extirpated from many breeding islands due to egg collection (Cott 1954), habitat alteration (Feare *et al.* 2007) and the introduction of predators, especially cats and rats (Taylor 1979, Moors & Atkinson 1984, Russell & Le Corre 2009). Sooty terns provide a valuable model for investigating the causes of population change as they are numerous (Birdlife International 2012b), are tolerant of human presence (Feare 1976), nest in dense colonies (Schreiber *et al.* 2002) and are relatively easy to census compared with other avian species

(Bolton *et al.* 2012). Sooty terns can fly long distances and population size can fluctuate between seasons from immigration and emigration. However, Ascension Island has the advantage of being isolated and possibly has less migrants than in other colonies thus simplifying the investigation of causes of population change.

Non-native predators that may have caused the decline in size of some sooty tern populations have been controlled or eradicated on some islands (e.g. rats on Bird Island in The Seychelles; Feare 1999). Yet, the impacts of the eradication of apex predators (Taylor 1979) on sooty terns and on some other avian species (Cook's petrel *Pterodroma cookii;* Rayner *et al.* 2007) are relatively poorly studied. Ascension is an ideal site for studies of predator-prey interactions.

The breeding ecology of sooty terns is well-studied (Ashmole 1963a, Harrington 1974, Feare 1976, Schreiber *et al.* 2002) but there are some important gaps in knowledge that can only be bridged with findings from long-term studies (e.g. Schreiber *et al.* 2002, Schreiber & Burger 2002). Sooty terns have great plasticity in their breeding cycle (Ashmole 1965). Most avian populations have a strict annual breeding cycle with timing of breeding varying by region and with annual weather conditions. Timing of breeding may shift by 1–3 months annually but still generally begin in the same timeframe each year (Newton 1989, Welty & Baptista 1990). On Ascension the sooty tern population was reported to return to breed every 9–10 months (Chapin 1954, Chapin and Wing 1959, Ashmole 1963a) but the breeding periodicity of individual sooty terns is not known.

1.9. Aims of the thesis

The general aim of my thesis is to bridge some of the knowledge gaps that exist in the breeding ecology of sooty terns. Data are sparse on the breeding periodicity of seabirds (Dawson 2008). In particular, the suggestion that some birds may have a regular sub-annual breeding cycle is not supported by a large body of scientific empirical evidence because breeding cycles that are less than annual (i.e. sub-annual) are frequently linked to stochastic climatic events (Schreiber & Burger 2002). Determining the breeding cycles of the sooty terns at both the individual and population levels is one of the aims of my thesis. Croxall *et al.* (2012) identified seabird population size as a priority for research and Schreiber *et al.* (2002) called for field research to determine population size and trend of historically known colonies of sooty terns. Ascension Island has two colonies where such censuses are needed and documenting long-term censuses of the breeding population was another aim of this research. Causes of seabird population changes are poorly understood (Newton 1998, Perrins *et al.* 1991), and Croxall *et al.* (2012) called for studied of the population biology and life-history traits of seabirds. I also aimed to determine factors that regulate the population size of sooty terns and to quantify the intrinsic capacity for the population to increase. Feral cats have recently been eradicated on Ascension but the loss of the top (or apex) predator may have unforeseen consequences, especially through the process of mesopredator release (Courchamp *et al.* 1999, Courchamp *et al.* 2003, Bonnaud *et al.* 2010). Therefore, studying predator numbers, investigating whether mesopredator release occurred and examining sooty tern population responses to it are also aims of my study. Food shortages during, and outside of, the breeding season are known to limit avian population size (Newton 1998, Oro *et al.* 2004, Weimerskirch 2007), and my final aim is to determine if fluctuations in the size of the sooty tern population on Ascension were related to the availability of food.

1.10. Thesis structure

In **Chapter 2** I investigate the sub-annual breeding cycle of Ascension sooty terns. I hypothesised that (1) the breeding periodicity of the population is consistently less than 12 months, (2) the breeding periodicity of most individuals in the breeding population is consistently less than 12 months, and (3) the interval between hatching dates is longer for individuals whose egg in the first season gave rise to a chick that was reared successfully than those that were unsuccessful. I predicted that (1) the breeding periodicity of the population was sub-annual, (2) the breeding periodicity of most individuals was sub-annual, and (3) the breeding periodicity of successful breeders is close to 12 months.

In **Chapter 3** I determine the size of Ascension sooty tern population from field censuses and from an analysis of secondary data from historic breeding colonies of the species, resulting in a population trend. I argue that the species' current IUCN Red List category of 'Least Concern' should be reviewed.

In **Chapter 4** I examine immigration, emigration, the age of first breeding, longevity and the intrinsic capacity for Ascension sooty terns to reproduce with the aim of determining potential causes of population decline on the island.

In **Chapter 5** I investigate breeding success by (1) calculating breeding success at egg and nestling (i.e. brooded chick in scrape) stages as well as overall breeding success, (2) quantifying breeding failure attributed to desertion and predation, (3) quantifying lethal interactions of mynas, (4) evaluating frigatebird predation, and (5) establishing if loss of eggs, nestlings and chicks (i.e. free-ranging, pre-fledging chicks frequently found in crèches) were major factors limiting the size of the breeding population.

In **Chapter 6** I investigate the possibility that the eradication of cats from Ascension could disadvantage sooty terns as a result of mesopredator release. I hypothesised that (1) cat eradication has resulted in a ‘release’ of rats, predicting that rat abundance would increase, and (2) the impact of potential increased rat predation on the size of the sooty tern population would be greater than that from both rat and cat predation. I predicted that the potential benefits of apex predator loss for the sooty tern population would be out-weighed by the increased threat from rat predation as a result of mesopredator release.

In **Chapter 7** I determine trends in the population sizes of cats, mynas, rats, and humans on Ascension Island, in the tuna population in the Atlantic Ocean, and in the quantity of squid consumed by sooty tern chicks. I investigated the various influences of such factors on the size of the sooty tern population and projected my findings into the next decade.

Finally, in **Chapter 8**, I summarise my results and place them in a more general context. I answer the question: Why did sooty terns survive on Ascension when other seabird species were extirpated? I provide directions for future research.

Chapter 2

BREEDING PERIODICITY OF SOOTY TERNS ON ASCENSION ISLAND

2.1. ABSTRACT

Most birds have a breeding periodicity that is annual. On islands the breeding periodicity of seabirds may vary with temporal variations in productivity in the marine environment. The breeding periodicity of a population of tropical seabirds in the South Atlantic is 9.6 months. I used a dataset spanning 19 breeding seasons between 1990 and 2012 (inclusive) containing first chick hatching dates and captures and/or re-captures of individuals from the colony of sooty terns on Ascension Island to confirm previous reports of sub-annual breeding of both the population and its individuals. I show that the sooty tern population breeds sub-annually with a periodicity of 288.9 ± 8.7 days and individual birds from the population, many but not all of which were unsuccessful breeders, have a periodicity of 289.1 ± 1.4 days. Nesting is not continuous and the population migrates for 125 days. From a review of the literature and my own data, the breeding cycle has apparently been consistent over the last 140 years. Breeding periodicity was either 342.0 ± 2.8 days or 282.8 ± 3.1 days based upon whether individuals were successful or unsuccessful, respectively, in the previous breeding attempts. The timing of breeding seasons is predictable and is not significantly influenced by El Niño–Southern Oscillation events that have altered the periodicity of seabirds in the Pacific Ocean. My findings indicate that some seabird populations such as those of sooty terns have adopted a life-history strategy of sub-annual breeding as a viable alternative to seasonal breeding.

2.2. INTRODUCTION

Most avian species reproduce annually but the breeding periodicity (defined as the interval between first hatching dates in consecutive breeding seasons) can vary considerably between and within some species.

2.2.1. Patterns of seasonal breeding in animals

Animals that are seasonal breeders only breed during certain times of the year when they can nurture offspring during periods of reduced thermal stress and high food availability. Animals that breed aseasonally are not constrained by annual peaks in food availability or by seasonal weather patterns but instead they breed year-round or occasionally in populations that have breeding cycles longer or shorter than annual. I have found only one report by Higgins (1993) of an aseasonal breeding cycle longer than 12 months and this was 17.6 months in Australian sealions *Neophoca cinerea.* Sub-annual cycles (defined here as less than 12 months) can be found in mammals such as muntjac *Muntiacus reevesi micrurus* (Pei *et al*. 1995), in invertebrates such as ants *Camponotus gigas* (Pfeiffer & Linsenmair1997), in terrestrial birds such as bat hawks *Machaeramphus alcinus* (Hartley & Hustler 1993) and in seabirds.

2.2.2. Patterns in the breeding cycle of birds

Approximately 75% of all avian species have a breeding cycle that is annual and this may be underpinned by predictability of annually occurring breeding resources (Nelson 1980). The majority of the remaining 25% of species have either a biennial cycle, arising because of their extended breeding season and then having to wait for the predictable occurrence of resources in a second season after they have successfully bred (Chastel 1995), or are opportunistic breeders (typically biennial), taking advantage of unpredictable peaks in breeding resources (e.g. food) whenever they may occur (Welty & Baptista 1990, Newton 2008). Species that breed biennially, such as the albatrosses *Diomedea* spp. (Jouventin & Dobson 2002) and frigatebirds *Fregata* spp. (Harrison 1990, Ratcliffe *et al*. 2008) tend to be physically large seabirds and *K*-selected. Populations of opportunistic breeders such as the red-billed queleas *Quelea quelea* in Africa (Cheke *et al*. 2007), antbirds *Hylophylax naevioides* in Panama (Wikelski *et al*. 2000) and zebra finches *Taeniopygia guttata* in Australia (Zann 1996) that respond to rain, tend to be physically small terrestrial birds and *r*-selected.

In temperate zones the seasonal cycle of birds is made up of a sequence of life-history stages including breeding, moult and wintering (Dawson *et al.* 2001). Timing of the stages is not rigidly fixed (Dawson 2008, Senapathi *et al*. 2011). For example, some free-living birds may breed late in one season and early in the next (Perrins 1969), resulting in a breeding periodicity of less than 365 days. In captive common starlings *Sturnus vulgaris* with access to *ad libitum* food the breeding and moult cycles occur with an approximately 9 month periodicity (Dawson 2006). This suggests that purely in terms of their physiology the minimum breeding periodicity of birds is probably less than 12 months and could be closer to 9 months. If the availability of food required for the growth and development of chicks does not fluctuate on an annual cycle, there is no particular advantage to breeding annually, and under such circumstances we might envisage that non-annual breeding strategies may have evolved (Lack 1968, Perrins 1969).

2.2.3. Patterns of periodicity in seabirds on tropical islands

Sub-annual breeding is an exception to the general rule that birds are seasonal breeders (Landsborough Thomson 1950). The topic is not considered in seabird seminal works by Nelson (1980), Furness and Monaghan (1987), Burger (1988) and Mulder *et al.* (2011) but is mentioned by Newton (2008) and Schreiber and Burger (2002) who have argued that data are not sufficiently reliable to make strong assertions about the generality of aseasonal breeding. However, there are some sparse and inconclusive reports of sub-annual breeding in seabirds on tropical islands (Ashmole 1963a,b,c*,* Snow 1965, Diamond 1976, Brooke 1995). Some of these studies were conducted during breeding seasons when strong stochastic climatic events occurred. These events are known to alter the availability of food and to change the periodicity of seabirds that breed annually (Schreiber & Burger 2002). Reports of sub-annual breeding are predominantly for colonially nesting seabirds on tropical islands. These include white terns *Gygis alba* on Christmas Island in the central equatorial Pacific (01º51'N, 157º25'W) with an estimated breeding periodicity of 8–10 months (Ashmole 1968), bridled terns *Sterna anaethetus* on Cousin Island in The Seychelles (04º20'S, 55º40'E) breeding every 7.5 months (Diamond 1976), Christmas shearwaters *Puffinus nativitatis* on Ducie Atoll in the Pitcairn Islands (24º40'S, 124º45'W) breeding every 9–10 months (Brooke 1995), and Audubon's shearwaters *Puffinus lherminieri* breeding every 9 months (Snow 1965) and swallow-tailed gulls *Creagrus furcatus* every 9–10 months (Snow & Snow 1965, Harris 1970) on South Plaza Island in The Galapagos Islands (00º35'S, 90º10'W).

On tropical islands, climatic conditions tend to be more stable than at high latitudes (Schreiber & Burger 2002). Breeding seasons often last longer in the tropics than in temperate zones (Ricklefs 1966), and this occurs partly because tropical waters are less productive which can result in a more patchy distribution of food resources (Weimerskirch 2007). The breeding cycles of seabird populations are probably controlled by temporal variations in productivity in the marine environment (Ashmole 1965, Jaquemet *et al.* 2007, Wolf *et al.* 2009, Naylor 2010). On tropical islands some proximate cues that control the reproductive cycle may not be as pronounced as in temperate zones. For example, photoperiod in temperate zones triggers gonadal maturation and breeding in many bird species while closer to the equator it is less important as a timing cue (Dawson *et al.* 2001). With less pronounced annual climatic variation and more patchy distribution of food, some tropical seabird populations contain birds that breed year-round. For instance, on Johnston Atoll (169º30'W, 16º42'N) in the central Pacific Ocean red-footed boobies, white terns and red-billed tropicbirds *Phaethon aethereus* lay eggs in most months of the year (Schreiber & Burger 2002). Similarly, on Ascension Island red-billed tropicbirds and white-tailed tropicbirds *Phaethon lepturus* do the same (Stonehouse 1962b).

Ashmole (1963a) and Le Corre (2001) have identified annual changes in SST as the proximate cue for breeding in some seabirds (e.g. sooty terns breed in areas where SST is above 23°C for only part of the year with breeding occurring during this period; Ashmole 1963a). In the tropical Atlantic Ocean an annual signal is prominent in both wind temperature and in SST. In response to surface wind, warmed while passing over the landmass of the African continent, the maximum SST is attained in March and April (Li & Philander 1997). In the marine environment stochastic climatic events are reported to impact severely the breeding success of seabirds (Gaston 2004) and they may influence breeding periodicity. The El Niño-Southern Oscillation (ENSO) is one such event that historically has caused exceptionally high seabird mortality (Schreiber & Burger 2002). The ENSO is a global coupled ocean-atmosphere phenomenon centred in surface waters of the tropical eastern Pacific Ocean. It happens at irregular intervals of between two and seven years and causes extreme weather in many regions of the world (Enfield 2003). Changes in wind patterns and water temperature that occur during ENSO result in changes to upwellings (the movement of cooler waters rich in nutrients to the surface) in the ocean. Zooplankton abundance is concentrated at upwellings and a reduction in zooplankton abundance can cause the disappearance of food for seabirds and reduced breeding success. There is a consistent temporal relationship between warm episodes in the Pacific and the tropical Atlantic Oceans (Nicholson 1997). However, the effects of the ENSO in the Atlantic Ocean are much less vigorous and lag behind those in the Pacific (Latif & Grötzner 2000). In waters around Ascension Island internal Atlantic dynamics including the North Atlantic Oscillation (NAO) and ENSO phenomena cause aperiodic warming (Enfield 2003, Stenseth *et al.* 2003) and patterns of marine productivity are unlikely to follow a pronounced annual pattern (Naylor 2010).

2.2.4. Patterns of periodicity at population and individual level

Visser *et al.* (2010) suggested that studies of the timing of breeding of individuals will improve our understanding of how inter-season variation in the timing of breeding of populations occurs. The breeding regime of some seabird species is different between individual birds and population-level attributes. For example, the periodicity of individuals and populations of white terns (Ashmole 1968), Christmas shearwaters (Brooke 1995), Audubon's shearwaters (Snow 1965) and swallow-tailed gulls (Snow & Snow 1965) are reported to breed sub-annually and throughout the year, respectively.

Chapin (1954) and Chapin and Wing (1959) have shown that the cycle of laying dates within the population of sooty terns on Ascension Island has an average periodicity of 292.6 days with a range of 268 to 307 days. Breeding in the whole population was loosely synchronised with an egg-laying period that lasted approximately 10 weeks. Breeding in the population lasted approximately 6 months (Ashmole 1963a), but within sub-colonies breeding is much more synchronised with an egg-laying period of approximately 4 weeks (BJH pers. obs.) and egg-laying and chick-rearing lasting for just 4 months (Ashmole 1963a, BJH pers. obs.). The length of the breeding season for individuals was 2 months shorter than that of the whole population. This raises the question of whether breeding periodicity of the Ascension population and of individuals in the population are different?

2.2.5. Periodicity of study species

Most populations of sooty terns breed with annual intervals (Schreiber *et al.* 2002). There is flexibility in the start date of breeding which can be monitored through first return dates (a reliable proxy for the start of the breeding season). On the Dry Tortugas in Florida (24º24'N, 82º24'W), sooty terns have undergone a 3-month phenological shift with first return dates advancing from mid-April in the 1950s to late January in 2008 (Colchero 2008). Different populations have breeding periodicities that can vary between 6 and 12 months (Ashmole 1965). On Christmas Island sooty terns sometimes breed with 6-month intervals

(Ashmole 1965) and *O. f. serrata* on Michaelmas Cay in Queensland, Australia (16º36’S, 145º59’W) (King *et al.* 1992) and *O. f. nubilosa* on Lys Island in the western Indian Ocean (11º31’S, 47º22’E) (Quartly *et al.* 2008) are reported to breed at intervals of approximately 10 months. Reports of sub-annual breeding by sooty terns on Ascension Island date from the 1830s. Egg collectors observed that their breeding season was irregular, occurring three times in two years (Brandreth 1835, Power 1835). More recent estimates of laying periodicity were 268–307 days (Chapin 1954), ≈ 290 days (Chapin & Wing 1959) and 296 days (Ashmole 1963a). In 1958 Ashmole ringed several hundred sooty terns of which 63 were re-captured during the following breeding period (Ashmole 1963a). The interval between ringing and re-capture ranged from 41 to 51 weeks and there was a suspicion that birds which raised a chick (98% did not in Ashmole’s study site during the 1958–1959 breeding season) may not return to breed until late in the following breeding period so as to avoid breeding and moulting at the same time. Sooty terns that raised a chick may defer the start of their moult cycle thus prolonging the breeding periodicity. The sample of birds reported by Ashmole (1963a) across two breeding cycles was small and a strong ENSO event occurred in 1958 (Bureau of Meteorology 2011) which cast doubt (Schreiber & Burger 2002) on the likelihood of the sub-annual breeding observations being a regular feature of the breeding behaviour of these birds or whether it was a result of a perturbation in food availability precipitated by the ENSO event.

Given the conjecture regarding the regular occurrence of sub-annual breeding in populations and individuals within the population, a detailed study of the breeding phenology of sooty terns on Ascension Island is important because they are one of only a few cases in birds of long-term evidence of sub-annual breeding.

2.2.6. Sub-annual breeding hypotheses

Here, I test four hypotheses concerning the reported sub-annual breeding periodicity of the sooty tern population on Ascension Island. I use a 22-year dataset of first hatching dates and a ringing–re-capture dataset of > 24,000 birds to shed light on the breeding periodicity at both individual and population levels. First, I hypothesised that the breeding periodicity of the population is consistently less than annual (i.e. 12 months). In waters around Ascension no annual peak in food availability that would favour breeding in a particular season has been identified. Birds are physically capable of breeding at less than annual intervals and may choose to do so to improve lifetime reproductive success. Secondly, sooty terns are not restricted to food availability close to their colony, as they are known to forage over very long distances, I hypothesised that breeding periodicity of sooty terns in years with ENSO events is not significantly different from years without ENSO events. Thirdly, as breeding in the whole population is loosely synchronised I hypothesised that the periodicity of most individuals in the breeding population is consistently less than annual. Finally, I hypothesised that the interval between hatching dates is longer for individuals whose egg in the first season gave rise to a chick that was reared successfully than those that were unsuccessful. I predicted that the breeding periodicity of successful breeders is close to 12 months (i.e. 365 days). I contrasted patterns in the breeding cycle of sooty terns on Ascension Island with populations of annually breeding conspecifics on other islands.

2.3. MATERIALS AND METHODS

I replicated methods used by previous studies addressing breeding periodicity (e.g. Chapin 1954, Chapin & Wing 1959, Ashmole 1963a). The breeding distribution of sooty terns on Ascension Island is now entirely restricted to the coastal plain at two sites, Mars Bay and Waterside, in the south-west corner of the island (Fig. 1.1). The species nests in ≈ 15 sub-colonies that range in number from a few hundred to ≈ 50,000 pairs (BJH pers. obs.). Some inter-seasonal changes in their distribution do occur and birds do not return to the same nest site in successive seasons (BJH pers. obs.).

2.3.1. Breeding periodicity of the population

To test the hypothesis whether breeding periodicity of the population differed significantly from 12 months, I monitored the interval (approximately ten months) between first hatching dates across consecutive breeding cycles. Each season the sub-colony that was occupied first was identified by observing pre-laying, incubation and brooding behaviour in the various sub-colonies. Breeding was synchronised (i.e. date ± 14 days) in each sub-colony and a single date when eggs hatched (i.e. date ± 14 days) in the first sub-colony was recorded. Observations were collected when field seasons on Ascension Island coincided with the start of the sooty tern breeding cycle. Ascension meteorological staff (early in the study period), AIG Conservation Office reports (latterly), personal communications (with contract workers on Ascension) and a literature search provided additional information on first arrival and departure dates and extended the dataset of first hatching dates at Waterside and Mars Bay. Individual nests were not sampled for first hatching dates but all sub-colonies were surveyed and description sheets with details of the stage of breeding (i.e. pre-laying, incubation, brooding and feeding chicks) were completed. Field observations including the occurrence of desertion (freshly deserted eggs are indicative of recently laid eggs), evidence of predation and incidents of broken eggs (where the embryo could be seen) were used to ascertain the age of eggs within the sub-colony. More deserted and predated eggs were found in sub-colonies where eggs were close to hatching and terns were seen to protect their nests more fiercely (BJH pers. obs.). Differences in hatching dates of birds at Waterside and Mars Bay were recorded.

2.3.2. Breeding periodicity in ENSO years

To test the hypothesis that breeding periodicity of sooty terns on Ascension Island in years with ENSO events is not significantly different from years without ENSO events, I compared the breeding periodicity of the sooty tern population on Ascension in years with and without ENSO events in the Atlantic Ocean. Dates of ENSO events in the Atlantic were extrapolated from ENSO dates in the Pacific Ocean (Bureau of Meteorology 2011) that were obtained from a monthly Southern Oscillation Index (SOI). ENSO lagged effects and strength of pressure differences were not considered. Kozlenko *et al.* (2009) estimated that ENSO events in the tropical Atlantic Ocean last about 3 months and lagged behind those in the Pacific Ocean by approximately 2 months. Latif and Grötzner (2000) estimated that ENSO events lagged behind by approximately 6 months. To identify ENSO years (± 6 months) in the tropical Atlantic, it was sufficient to add an average of 4 months to the dates of ENSO Pacific Ocean peaks.

2.3.3. Breeding periodicity of individuals

Incubating adults of unknown age were captured with long-handled nets by members of the AOS and ringed by C. Wearn (under a British Trust for Ornithology [BTO] ringing licence number A4318) using uniquely numbered metal BTO rings. To minimise disruption in a particular area of the colony, birds were generally ringed in groups of 100 (Fig. 2.1). Searches for ringed incubating birds involved teams of two to four people who attempted to catch all that were detected. Searches were undertaken during the incubation period when sooty terns were reluctant to leave their nests. Occasionally, ringed sooty terns flying over the colony or loafing were re-captured and these potential non-breeders were recorded separately. To determine the breeding periodicity of individual birds, ringed sooty terns were re-captured during incubation across multiple

Figure 2.1. A team from the Army Ornithological Society ringing sooty terns in 2004 on Ascension Island in the South Atlantic. (Photo: D. Foley).

breeding cycles. The mean interval and its standard deviation between capture dates of incubating birds during two consecutive incubation periods were determined. The incubation period of sooty terns is 29 days (Ashmole 1963a) and birds were captured during 25 days of the incubation period. Birds were not re-captured while incubating pipping eggs or during the first three days of the incubation period when they were prone to desert their eggs when disturbed. Multiple breeding intervals from the same bird were not independent records and were excluded from subsequent analysis.

2.3.4. Factors underlying sub-annual breeding

2.3.4.1. Breeding periodicity in relation to breeding success. To establish if individuals that successfully bred in one season returned significantly later in the following breeding season, a sample of adults was caught that were successful breeders as they were feeding chicks that were close to fledging. Birds that were regurgitating food (or were apparently on the point of feeding) large chicks that were at least 1-month old were given green colour rings. Catching them required approximately 90 minutes of effort per bird but it was the most effective way to study birds that had successfully bred. Late-breeding sooty terns in a given season that were incubating more than 2 months after the first eggs of the season were laid, were assumed to be unsuccessful breeders as there was insufficient time for them to raise a chick before the colony was vacated. Late-breeding sooty terns are known to abandon eggs (Ashmole 1963a) when the majority of breeding colony migrates. Therefore, a cohort of sooty terns incubating late in the season was also ringed. Searches for successful and unsuccessful breeders were made during the following breeding season and the interval between their egg-laying dates in successive seasons was determined.

2.3.4.2. Circannual patterns in the breeding cycle. Duration of each stage (i.e. courtship, incubation, chick-rearing and migration) of the breeding cycle was compared between sub-annually breeding sooty terns on Ascension Island and annually breeding conspecifics on other islands. Typically, the courtship period of sooty terns lasts 1–4 months and involves aerial swarming and groundfall at night (Schreiber *et al*. 2002). A literature search was undertaken to establish the duration of breeding stages of non-Ascension sooty tern populations. Incubation, courtship and chick-rearing periods of sub-annually breeding sooty terns were obtained from Ashmole (1963a). The migration period of the sub-annually breeding sooty terns was calculated from the formula:

$$\text{Migration period (days)} = d1 - d2 - i - c + s \qquad \text{(Eqn 2.1)}$$

where $d1$ is the date when the first chick of the season hatches, $d2$ is the date when the last terns departed the previous season, i is the mean incubation period (i.e. 29 days; Ashmole 1963a), c is the mean courtship period (i.e. 58 days; Ashmole 1963a) and is defined as the interval between the first sooty tern to return and the first egg laid, and s is the mean interval (obtained from the sub-colony description sheets; see section 2.3.1) between the commencement of laying in the first sub-colony and that in the last sub-colony occupied during the same breeding period.

2.3.5. Statistical analyses

I carried out analysis of breeding periodicity in the population of sooty terns across 19 seasons and of 2,700 individuals that were re-captured out of an overall total of 16,000 sooty terns that were ringed between 1996 and 2012. Laying dates were back-calculated from hatching dates by subtracting 29 days knowing that the incubation period for the species on Ascension Island ranges between 28.25 to 30.25 days ($n = 33$) (Ashmole 1963a). I used an unpaired *t*-test to compare the breeding periodicity of sooty terns with and without ENSO events. I compared the length of the stages constituting the breeding phases of sooty terns on Ascension (i.e. sub-annual breeders) with conspecifics elsewhere (i.e. annual breeders). Throughout this thesis, unless otherwise stated, mean values are presented with ± 95% CL and the alpha level is 0.05.

2.4. RESULTS

2.4.1. Breeding periodicity of the population

Each season all sub colonies (typically approximately 10) were sampled and the sub-colony where chicks first hatched identified. The intervals between first chicks hatched in two consecutive breeding periods were recorded between January 1996 and June 1998, and January 2000 and December 2012 (Table 2.1). The mean interval between hatch dates, from observations in the colony, at Waterside was 288.9 ± 8.7 days (range: 262–317 days, $n = 19$) and at Mars Bay was 289.4 ± 10.1 days (range: 257–317 days, $n = 17$). The mean breeding periodicity of sooty terns on Ascension Island was shorter than that of annual breeders by 76 days with the former confirmed as breeding sub-annually with a periodicity of 9.6 months (Fig. 2.2).

Table 2.1. Breeding periodicity (in days) of population and dates of first hatching across 29 breeding seasons of sooty terns at Waterside and Mars Bay colonies on Ascension Island in the South Atlantic between March 1990 and December 2012. Dates in bold were recorded in the field. Unbolded dates are anecdotal and were not used to determine the mean breeding periodicity of population.

Season	**Waterside**		**Mars Bay**	
	Date of first chick hatched	**Breeding periodicity**	**Date of first chick hatched**	**Breeding periodicity**
1	**12/03/1990**	-	**20/03/1990**	-
2	31/01/1991	325	-	-
3	24/12/1991	327	-	-
4	09/09/1992	260	17/10/1992	-
5	15/08/1993	340	09/09/1993	327
6	**15/05/1994**	273	**25/05/1994**	258
7	20/03/1995	309	-	-
8	**23/01/1996**	309	**03/02/1996**	-
9	**28/10/1996**	**279**	**10/11/1996**	**281**
10*	**07/09/1997**	**314**	**19/09/1997**	**313**
11*	**01/06/1998**	**267**	**03/06/1998**	**257**
12	07/04/1999	310	-	-
13	**19/01/2000**	287	-	-
14	**19/11/2000**	**305**	-	-
15	**23/08/2001**	**277**	**06/09/2001**	-
16	**12/06/2002**	**293**	**19/06/2002**	**286**
17*	**27/03/2003**	**288**	**25/04/2003**	**310**
18	**07/02/2004**	**317**	**26/02/2004**	**307**
19	**05/12/2004**	**302**	**13/12/2004**	**291**
20*	**10/09/2005**	**279**	**20/09/2005**	**281**
21	**08/06/2006**	**271**	**18/06/2006**	**271**
22*	**02/04/2007**	**298**	**26/04/2007**	**312**
23	**02/02/2008**	**306**	**10/02/2008**	**290**
24	**27/11/2008**	**299**	**02/12/2008**	**296**
25	**16/08/2009**	**262**	**24/08/2009**	**265**
26*	**14/05/2010**	**271**	**19/05/2010**	**268**
27	**25/03/2011**	**315**	**01/04/2011**	**317**
28	**01/01/2012**	**282**	**04/02/2012**	**309**
29	**21/09/2012**	**264**	**27/10/2012**	**266**

NOTE: *Atlantic Ocean ENSO years

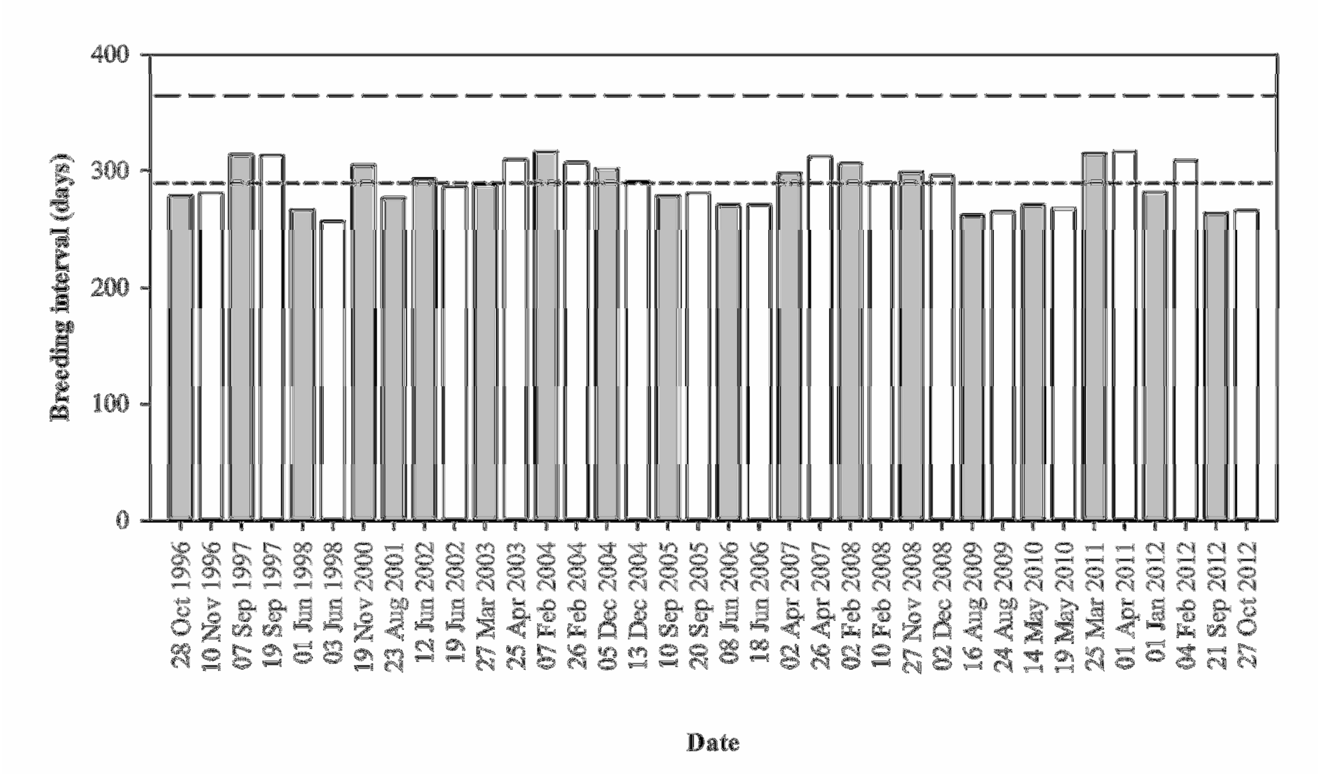

Figure 2.2. The breeding periodicity of sooty terns at Waterside (grey bars) and Mars Bay (open bars) on Ascension Island during breeding seasons from October 1996 to October 2012. The mean breeding periodicity (289 days) is indicated by the short dash-line and annual breeding periodicity (365 days) by the long dash-line.

2.4.2. Breeding periodicity in ENSO years

The sooty tern breeding periodicity was 286.2 ± 18.6 days during ENSO years (range: 267–314 days, *n* = 6) and did not differ significantly from that of non-ENSO years when it was 293.6 ± 12.5 days (range: 262–317 days, *n* = 11) (independent sample *t*-test: *t* = 0.80, *df* = 15, *P* = 0.44).

2.4.3. Breeding periodicity of individuals

A total of 16,276 sooty terns that were incubating eggs, were captured and ringed between 1996 and 2012 (Table 2.2). During breeding periods between 2002 and 2010 (i.e. over 10 breeding cycles), 1,978 (or 12%) of ringed birds were re-

Table 2.2. Details of ringers and summary of adult and juvenile sooty terns ringed and re-captured on Ascension Island in the South Atlantic in 1975 and between 1996 and 2012.

Month & Year	Cumulative total of ringed:		Cumulative total of re-captures	Ringer(s)
	adults	**pulli**		
Nov 1975	0	200	0	Gale
Oct 1996	149	225	0	Wearn
Jun 1998	331	535	0	Wearn
Nov 2000	881	535	0	Wearn
Oct 2001	1,084	552	2	RSPB
Jun 2002	2,464	602	9	Wearn & RSPB
Apr 2003	2,864	852	52	Wearn & RSPB
Feb 2004	4,864	852	215	Wearn & Carr
Nov 2004	5,364	852	379	Wearn
Oct 2005	5,750	2,466	495	Wearn
Aug 2006	6,150	3,066	699	Wearn
May 2007	9,050	4,166	960	Wearn & Dickey
Feb 2008	11,050	4,166	1,356	Wearn & Dickey
Dec 2008	13,200	4,166	1,932	Wearn, Dickey & Conservation Office
Oct 2009	13,200	5,200	2,048	Wearn, Dickey & Conservation Office
Jul 2010	13,250	5,200	2,072	Conservation Office
Apr 2011	15,776	5,200	2,454	Wearn, Dickey & Conservation Office
Jan 2012	16,276	5,200	2,721	Wearn, Reynolds & Dickey

captured while incubating. Efforts to re-capture individual sooty terns were focussed on periods when the majority of the population was known to be incubating (period identified from migration departure and return dates). Intervals between capture dates showed a well-defined peak at regular intervals of approximately 290 days across the breeding cycles (Fig. 2.3). The interval between dates of incubation for individual birds in two consecutive seasons was

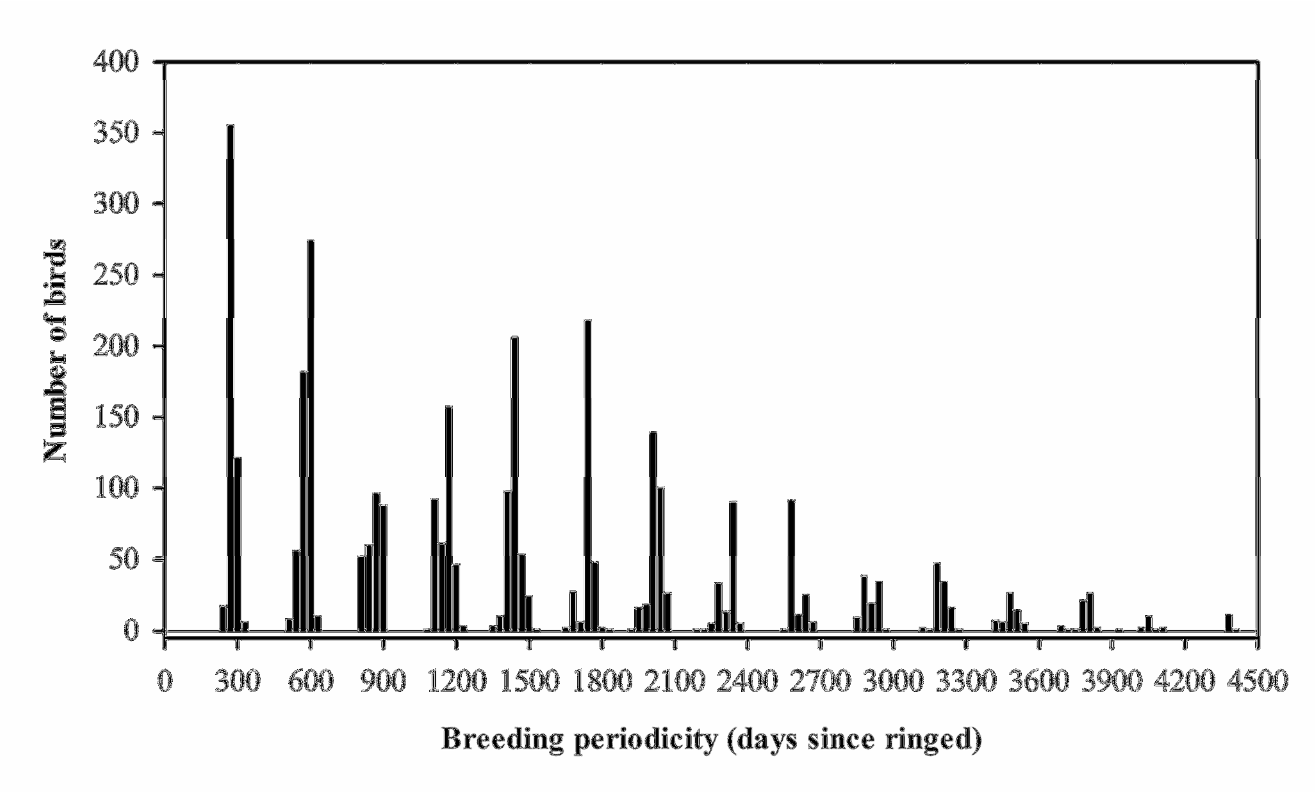

Figure 2.3. The frequency distribution of breeding periodicities (bar widths of 30 days) of sooty terns based upon their re-capture during incubation since they were first ringed as incubating adults on Ascension Island in the South Atlantic.

289.1 ± 1.4 days (range: 241–338 days, *n* = 393). An indication that sooty terns do not defer breeding was provided by three incubating birds captured in four consecutive breeding seasons (Table 2.3).

Table 2.3. Dates of initial ringing and re-captures, and breeding intervals of three incubating sooty terns in four consecutive breeding seasons on Ascension Island in the South Atlantic.

Ring number	**Date of ringing**	**Date of re-capture:**			**Breeding interval (days):**		
		1	**2**	**3**	**1**	**2**	**3**
DD37599	09-05-07	20-02-08	10-12-08	10-08-09	287	294	243
DD95684	15-05-07	20-02-08	09-12-08	09-10-09	281	293	304
DD81583	14-08-06	20-05-07	11-02-08	06-12-08	279	267	299

2.4.4. Factors underlying sub-annual breeding

2.4.4.1. Breeding periodicity in relation to breeding success. Of 64 sooty terns that bred successfully, five were re-captured and of 386 birds that were unsuccessful breeders, nine were re-captured. Successful birds were first captured between 31 October and 2 November 2005 while feeding chicks of ≈ 54 days of age and then re-captured ≈ 280 days later between 7 and 14 August 2006 while incubating eggs that were ≈ 22 days old (Table 2.4). Successful breeders had a breeding periodicity of 342.0 ± 2.8 days (range: 341–346 days, $n = 5$) and was significantly different from that of unsuccessful breeders 282.8 ± 3.1 days (range: 277–289 days, $n = 9$) (independent sample *t*-test: $t = 29$, $df = 12$, $P < 0.01$). The difference between these breeding periodicities and that of the majority of individuals that had most probably failed to breed successfully (i.e. 289.1 ± 1.4 days) was 53 days longer and 6 days shorter, respectively.

Table 2.4. Dates of ringing and re-captures, and breeding intervals calculated from estimates of egg-laying dates for sooty terns that bred successfully on Ascension Island in 2005 and were re-captured while incubating in 2006.

Ring number	Date ringed	Date of egg laying in 2005	Date re-captured	Date of egg laying in 2006	Breeding interval (days)
DD66612	31/10/2005	09/08/2005	07/08/2006	16/07/2006	341
DD66620	01/11/2005	10/08/2005	08/08/2006	17/07/2006	341
DD66624	01/11/2005	10/08/2005	08/08/2006	17/07/2006	341
DD66705	02/11/2005	11/08/2005	09/08/2006	18/07/2006	341
DD66709	02/11/2005	11/08/2005	14/08/2006	17/07/2006	346

2.4.4.2. Circannual patterns in the breeding cycle. The mean number of days between the commencement of laying in the first sub-colony and last sub-colony occupied was 58.8 ± 14.4 days (range: 37–112 days, *n* = 13). The mean period away from the colony was 124.7 ± 15.6 days (range: 97–146 days, *n* = 10). Comparing between sub-annually breeding birds (i.e. those on Ascension) and annually breeding birds elsewhere, there was little difference in the durations of incubation (1 day or 2%), chick-rearing (6 days or 8%) and migration (15 days or 11%) (Table 2.5). There was, however, a difference in the lengths of the courtship period between the 128 days of annual breeders (range: 90–165 days, *n* = 4) and the 59 days of sub-annual breeders (range: 56–62 days, *n* = 2). This difference of 70 days was close to the 76-day difference in their breeding periodicity. On Ascension laying peaked in the middle of the laying period 40–60 days after the first egg was laid (Ashmole 1963a, BJH pers. obs.). In annual breeding

Table 2.5. The duration of courtship, incubation, chick-rearing and migration (see text for definitions) and the percentage difference for each between annually and sub-annually breeding sooty terns. The sources of information are also provided.

Location	**Length (in days) of:**				**Reference**
	courtship	**incubation**	**chick rearing**	**migration**	
Annual breeders					
Europa Island	165	28	77	97	Le Corre 2001
Dry Tortugas	≈ 90	29	65-70	≈ 180	Colchero 2008, Florida Fish and Wildlife Conservation Commission 2003
Johnston Atoll	≈ 120	29	66	≈ 150	Harrington 1974
Seychelles	≈ 135	28	77	≈ 135	Feare 1976, Feare & Gill 1997
Mean	**128**	**28.5**	**72**	**140**	
Sub-annual breeders					
Ascension Island	59 (55%)	29 (2%)	66 (8%)	125 (11%)*	Ashmole 1963a *This study

populations of sooty terns egg laying is more synchronised with 85% and 90% of eggs laid in 28 days on Europa Island (Le Corre 2001) and Johnson Atoll (Harrington 1974), respectively, 75% of eggs laid in 9 days on The Seychelles (Feare 1976), and on the Dry Tortugas all eggs were laid in 21 days (Colchero 2008).

2.5. DISCUSSION

It is not known how or why sub-annual breeding arises as a life-history strategy but it may be due to a combination of intrinsic factors (e.g. birds are physically capable of breeding at intervals of less than 12 months) and extrinsic factors (e.g. populations that are reported to breed sub-annually breed on tropical islands with little seasonality). However, my results provide strong evidence of sub-annual breeding at both the level of the Ascension population and that of individuals. They may dispel some doubts over the validity of previous studies. The terns bred twice in 2000, 2004, 2008 and 2012 and sub-annual breeding periodicity translated into breeding peaks in different months of the year over the course of many years (Table 2.1). Start dates of breeding provide strong evidence of sub-annual breeding which is independently supported by ringing and re-capture data. The breeding periodicity of individuals in two conservative breeding periods was 289.1 ± 1.4 days. Failed breeders returned after 282.8 ± 3.1 days and the breeding periodicity of successful breeders was considerably longer at 342.0 ± 2.8 days.

2.5.1. Breeding periodicity of the population

For more than 140 years the periodicity of the sooty tern population on Ascension Island appears to have remained constant. The mean periodicity between 1942 and 1958 was 291 days (Chapin & Wing 1959) and was near identical to the mean I obtained between 1996 and 2012 (Table 2.6). I have been able to establish from historical records that the periodicity in the 1870s (Table 2.6) was between 8 and 10 months. Sooty terns departed Ascension Island in May 1875 and returned in August 1875 (Penrose 1879). The H.M.S. Challenger Expedition collected eggs and chicks on 3 April 1876 (Saunders 1881) while Gill (1878) reported that the start of the breeding season was approximately 1 November

Table 2.6. Means and ranges of breeding periodicities of the sooty tern population from a number of studies on Ascension Island in the South Atlantic between 1875 and 2011. Also provided are years in which ENSO events took place (Enfield 2003) and sources of information.

Years of study	Periodicity (days)	Range (days)	Number of breeding periods	ENSO years during study period	Source
1875–1877	240-300		2	1876	Gill 1878, Penrose 1879, Saunders 1881
1942–1952	292.6	268–307	14	1941,1946 & 1952	Chapin 1954
1953–1958	≈290		6	1953 & 1957	Chapin & Wing 1959
1958	296		1	1957	Ashmole 1963a
1962–1963	300		2	1963	K.E.L. Simmons pers. comm.
1996–2012	288.9 ± 8.7	262–317	19	1998, 2003, 2005, 2007 & 2009	This study

1877. These dates suggest that the start of the breeding seasons was August in 1875, March in 1876, early in 1877 and again in November of the same year. In the 1960s K.E.L. Simmons recorded first egg date at Waterside on 29 January 1962, 17 November 1962 and 21 September 1963 (K.E.L. Simmons pers. comm.), representing periods of 292 and 308 days, respectively (Table 2.6).

2.5.2. Periodicity during the ENSO years

Ocean climate variability is known to influence the timing of reproduction of birds (Wolf *et al.* 2009). In the Pacific Ocean ENSO events have a profound impact on reproductive timing of sooty terns (Schreiber & Schreiber 1984) but in the Atlantic Ocean the influence of ENSO is less pronounced (Latif & Grötzner 2000). ENSO events do not appear to have influenced reproductive timing of terns at Europa Island in the southern Mozambique Channel (Le Corre 2001) and I could find no correlation between dates of ENSO events and the breeding periodicity of sooty terns on Ascension Island.

2.5.3. Breeding periodicity of individuals

Ashmole (1963a) was able to show that the interval between producing a fertile egg in two successive breeding seasons for individual sooty terns was less than 12 months. My study provides evidence that 393 individual sooty terns were incubating eggs in two consecutive seasons at a mean interval of 289.1 ± 1.4 days. The interval was consistent over 10 breeding seasons (Fig. 2.2). The meagre data collected on birds re-captured in more than two consecutive seasons (Table 2.3) suggest that sub-annually breeding sooty terns do not defer attempts to breed but additional evidence is required to reinforce this statement.

On Ascension Island egg production per pair is one per sub-annual season or 1.22 eggs per annum (this study). On islands where sooty terns breed annually clutch size is just one (Schreiber *et al.* 2002). However, the increased annual egg production of sub-annually breeding birds appears to be mitigated by fewer re-laying attempts. Thus, if an egg is lost on Ascension Island, only 15% of birds lay again (Ashmole 1963a) while in The Seychelles as many as 90% of birds lay again (Feare 1976). This may result in similar or even lower reproductive output on Ascension (measured in terms of fledged chicks per year) compared with birds in The Seychelles.

2.5.4. Breeding periodicity in relation to breeding success

Stonehouse (1962b) and Dorward (1962) found that in tropicbirds *Phaethon* spp. and boobies *Sula* spp. the interval between laying periods was longer in birds that had bred successfully in the first breeding season. Ashmole (1963a) found that the majority of sooty terns returned after 294 days but one female whose chick fledged returned after 357 days. I found that five successful and nine unsuccessful breeders in one season were re-captured in the following breeding season and the interval between start dates of incubation was 342 ± 2.8 days in the former and 282.8 ± 3.1 days in the latter. Individual birds that successfully fledge chicks returned 53 days later and those that were unsuccessful returned 6 days earlier than the mean for the whole population. The interval between laying of eggs by successful breeders in my very small sample was close to one full year and suggests that the driver for sub-annual breeding is failure to fledge a chick.

2.5.5. Circannual patterns in the breeding cycle

There appears to be little flexibility in the time available for sooty terns to moult, incubate, rear chicks and migrate (Table 2.5). Only in the courtship phase (i.e. aerial swarming and landing at night) of the breeding cycle is circannual variation apparent. Ascension Island sooty terns appear to be able to maintain a sub-annual breeding cycle by reducing the length of time allocated to the courtship period which is 70 days shorter on Ascension than for conspecifics elsewhere in their range (Table 2.5). Seventy days closely approximates to the difference in periodicities (i.e. 76 days) of annual and sub-annual cycles. Ashmole (1963a) has shown that during the courtship phase sooty terns visit the colony each night in small numbers (≈ 5,000 compared with the total population of ≈ 750,000). Harrington (1974) caught birds during the courtship phase but only 5% of those caught (n = 756) had active brood patches. These data suggest that during courtship many birds were not ready to lay. It is possible that pairs landed to copulate but then departed for their feeding grounds and returned to the colony 2 or 3 weeks later when the egg was ready to be oviposited. This return to feeding grounds may provide additional time to gain weight and improve body condition before the start of incubation.

2.5.6. Potential bias in fieldwork

The breeding success of some sooty terns may have been incorrectly classified as I was unable to follow birds across their entire breeding attempt. The circannual pattern of ringing and re-capture activity took place over a period of ≈ 20 days in the field at intervals of ≈ 290 days. During the analysis it was realised that a potential bias in the periodicity of individuals would occur by focusing re-capture activity on a narrow 20-day period in the breeding cycle (A. Dawson pers. comm.). Clearly, if searches for ringed birds only occurred at intervals of ≈ 290 days the data would contain a major bias. Fortunately, the target dates (40–60 days after the first egg was laid) were missed on occasions and the re-capture period was significantly extended. Ashmole (1963a) estimated that the peak of the breeding cycle occurred 40–60 days after the first egg of the cycle was laid. Individual sooty terns incubate their eggs for 29 days (Ashmole 1963a) but the incubation period of the population lasted approximately 100 days (Fig. 2.4). The

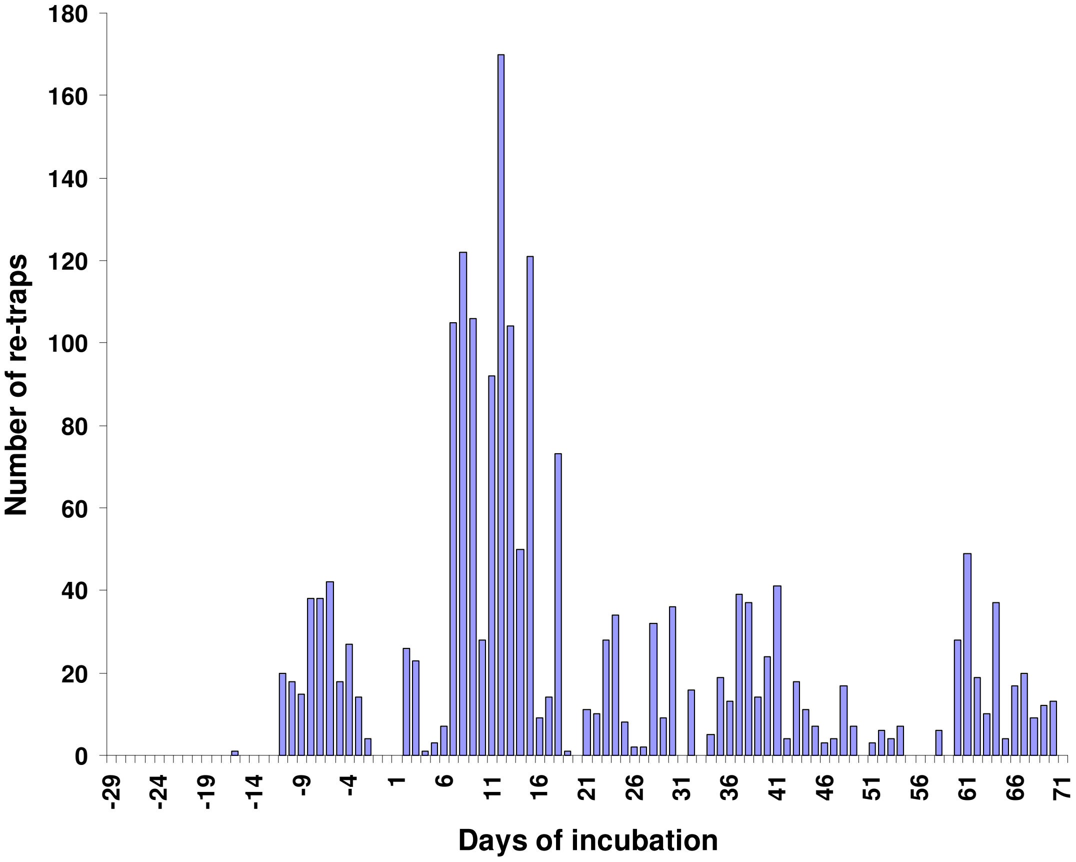

Figure 2.4. Frequency distribution of numbers of re-captured incubating sooty terns on Ascension Island across 100 days of the incubation period of the population. Day 1 was when the first chick hatched in the colony.

circannual range of days of the incubation period on which birds were re-captured was from -11 to +70 days (Fig. 2.3). Sooty terns were re-captured during 81% of the total incubation period, reducing potential bias.

Based on a sample of just five birds, I have reported that the average breeding periodicity of successful breeders was 342 days (i.e. close to an annual cycle). The periodicity of successful breeders is a crucial factor in the life history of sooty terns and further work with a larger sample size of successful breeders is needed to confirm this finding.

2.5.7. Wider application of findings

Sooty terns on Ascension may have responded to unpredictable food supply and low breeding success (Ashmole 1963a) by adopting a sub-annual breeding strategy so as to maximise their lifetime reproductive success. Strong evidence that some free-living birds have a regular sub-annual breeding cycle is scarce and my findings will be of interest to reproductive biologists working across many taxa. The food availability hypothesis (Lack 1954, Perrins 1969) suggests that availability of food determines when animals breed. In temperate latitudes where seasonal timings are currently changing, some annually breeding species (e.g. great tit *Parus major*; Charmantier *et al.* 2008) appear to be adjusting their timing of breeding to coincide with variable seasonal peaks in food availability. Some species and/or populations are not able to adjust the timing of their breeding attempts, and some may not detect seasonal peaks in food availability because of the latter's unpredictability (Visser *et al.* 2010). In such cases sub-annual breeding could increase the probability of encountering favourable feeding conditions and the gamble of sub-annual breeding for some individuals might become essential for survival. Further research is needed to confirm that the cycle of sub-annual breeding in reports from other species is consistent, predictable and enduring. More work is needed to identify other species with sub-annual breeding cycles. Sooty terns on Ascension Island may have fine-tuned their breeding behaviour to lunar rhythms associated with the marine environment (Chapin & Wing 1959, Naylor 2010). The bird’s regular and distinct breeding periodicity of 290 days warrants further investigation to gain more insights into this unusual breeding phenomenon.

2.5.8. Conclusions

I have provided evidence that the population of sooty terns on Ascension Island are sub-annual breeders with a periodicity of 289 days and individual birds also have periodicity of 289 days. The cycle is consistent, predictable, has been maintained for more than 140 years, and is not significantly affected by ENSO events. My data suggest that those birds which raise a chick successfully in one breeding period, albeit a small fraction of the overall breeding population, may not start breeding until later in the following breeding season. The sub-annual breeding periodicity of the sooty tern population on Ascension Island may have profoundly affected demography and population-limiting factors of sooty terns on Ascension Island.

In the next chapter I will examine population size and trends in the numbers of breeding sooty terns.

(Note: The publication status of Chapter 2 as of December 2013 is that it is in review).

Chapter 3

THE SIZE OF THE SOOTY TERN BREEDING POPULATION ON ASCENSION ISLAND FROM 1877 TO THE PRESENT DAY

3.1. ABSTRACT

Worldwide, wild animal population size has declined by approximately 33% in the last 20 years. Similar rates of decline are reported in abundance estimates of mammals, fish and birds in the UKOTs. On Ascension Island most large seabird colonies have been extirpated from the main island with only sooty terns having persisted. Censuses of sooty terns are identified as a priority for research. I completed censuses of the sooty tern breeding population on Ascension Island between 1990 and 2012 as part of an investigation of their demographics. The population varied in size between 138,000 and 535,000 birds with a mean of 351,000 (± 34,000 birds, $n = 22$ breeding seasons). Rigorous fieldwork to obtain such census data did not occur prior to 1990 but analysis of secondary data revealed that the breeding population in 1877, 1942 and 1958 numbered 2.72, 2.79 and 2.95 million birds, respectively. A decline of > 80% in the size of the sooty tern breeding population occurred between 1958 and 1990 on Ascension and similar precipitous declines have occurred in the second half of the 20th century on other islands elsewhere in their range. I argue that the species' current IUCN Red List category of 'Least Concern' should be reviewed. The cause of the decline needs further investigation in order to make conservation efforts more informed and, therefore, more effective.

3.2. INTRODUCTION

The human population increased in size by more than 80% from 3.7 to 6.7 billion between 1970 and 2008 (United States Census Bureau 2012) and at the same time the population sizes of mammals, fish and birds fell by one third (WWF 2012). Of the 9,934 extant bird species (Birdlife International 2012a), 1,313 (or approximately 13%) are threatened with extinction (Birdlife International 2012a). The UKOTs hold some of the world's largest seabird colonies but are also among some of the world's major centres for extinctions (e.g. a sandpiper *Prosobinia,* a pigeon *Ducula* and a ground-dove *Gallicolumba leonpascoi* on Henderson Island in the Pitcairn Islands; Hilton & Cuthbert 2010). On the UKOT of Ascension Island populations of breeding seabirds (e.g. frigatebirds, red-footed boobies, etc.) are threatened with extinction (Ashmole *et al.* 1994). However, censuses used to identify changes in population size (Bibby *et al*. 2000) have only been used on the island to characterise the trend of the frigatebird population (Ratcliffe *et al.* 2008).

3.2.1. Population size and trends

Reliable population size estimates are essential for the effective management and conservation of avian species (Newton 1998). Population size is defined as the number of mature individuals (IUCN 2009) and a count of nests at the peak of their incubation activity is a common way of censusing mature seabirds (Mitchell *et al.* 2004). A change in the number of occupied nests over a period of years provides a measure of population trend (Baillie *et al.* 2010). However, monitoring programmes of short duration may not provide an accurate picture of the environmental changes that occur throughout the life of a long-lived species and prolonged observational measurements are required to investigate the ecological influences on population change (Collins 2001). A long series of nest counts will reveal trends in numbers but it will not necessarily indicate when fluctuations in population size started (Green 1994). Population limitation may be implicated if a change in the direction of a population trendline is related to a change in an ecological variable (e.g. food availability, disease, predation pressure). Of course, manipulation of such a variable may be impossible and often such relationships remain correlative rather than causative (Green 1994).

Seabird colonies are amongst the best surveyed of all avian taxa and census methodologies are relatively well developed (Mitchell *et al.* 2004). However, the practical and theoretical problems of measuring immigration and emigration rates have hampered attempts to determine population size for some species (e.g. yellow-legged gull *Larus michahellis*; Oro 2003) except for some island endemics (e.g. Nihoa millerbird *Acrocephalus familiaris*; Conant *et al.* 1981). Many seabirds (e.g. albatrosses *Diomedea* spp.*,* terns of the Sternidae) do not attempt to breed every season (Schreiber & Burger 2002), and, as a result, nest counts can often markedly under-estimate the size of the population for several successive years. This could, for example, indicate a population decline based upon such estimates when in reality many population members have simply deferred breeding during the census period (e.g. European shags *Phalacrocorax aristotelis* on the Isle of May; Mitchell *et al.* 2004). On the other hand nest estimates that indicate a stable population can sometimes conceal a decline in population size. When increased mortality occurs in breeding seabirds (e.g. Votier *et al.* 2005), the decline in the overall population size can be buffered by increased recruitment of immatures (e.g. Votier *et al.* 2008a) at the breeding colony.

Sooty terns are an archetypal seabird in that they are long lived and colonially nesting, have a low rate of reproduction, defer breeding and migrate (Ashmole 1963a, Schreiber *et al.* 2002). Adult sooty terns return to Ascension at intervals of 9.6 months (Chapter 2) where they nest on the ground in dense easily accessible colonies. The birds are prey to non-native mammals; the population has declined and remedial conservation actions to restore the population have been initiated (Ashmole *et al.* 1994, Ratcliffe *et al.* 2009). Seabird populations such as the sooty tern are often slow to recover when threats to their survival are removed (Newton 1998) and repeat population censuses are essential for evaluating the effectiveness of remedial conservation actions (Mitchell *et al.* 2004). The sooty tern population on Ascension Island is well suited to census work using conventional methods (Bibby *et al.* 2000), but no censuses were conducted prior to this study.

Despite inherent difficulties associated with censusing of bird species (Bibby *et al.* 2000), population estimates and trends in population size are the 'bedrock' of species' threat categories (e.g. IUCN 2009). Declining population trends have been identified in two of the three most abundant, tropical colony-nesting seabird species (namely wedge-tailed shearwater *Puffinus pacificus* and guanay cormorant *Phalacrocorax bougainvillii*), but the trend in the global population size of the most abundant species, the sooty tern, is listed in the species' fact sheet of Birdlife International (2012b) as 'Unknown'.

3.2.2. Global population of sooty terns

The global population of sooty terns was estimated to be more than 25 million pairs in the 1990s (del Hoyo *et al.* 1996), 18–23 million pairs in the early 2000s

(Schreiber *et al.* 2002) and, more recently, 10.5–11 million pairs (Birdlife International 2012b). The trend in the population is not believed to be declining sufficiently rapidly (i.e. > 30% decline over three generations; IUCN 2009) to be of major concern and the species' current IUCN Red List category is of 'Least Concern' (Birdlife International 2012b). However, in some parts of the species' range (e.g. New South Wales, Australia) the sooty tern is listed nationally as a 'Vulnerable' species (NSW National Parks & Wildlife Services 1995). Colonies of sooty terns that frequently breed on small remote islands (e.g. Tinhosas, Sâo Tomé; del Hoyo *et al.* 1996), are poorly monitored (Schreiber & Burger 2002). Priority for future research on the species is for censuses of historically known colonies (Schreiber *et al.* 2002). Ascension Island has two such colonies where the population trend has not been studied and described.

3.2.3. Ascension population of sooty terns

Sub-fossil evidence and distribution of guano deposits indicate that large colonies of seabirds once nested on Ascension (Stonehouse 1962a, Olson 1977, Ashmole & Ashmole 2000). Sooty terns were reported to breed in vast numbers when the first settlers arrived on Ascension in 1815 (Bedford 1838, Penrose 1879). Informed guesses of the size of the sooty tern population in the 20th century vary between 1 and 2 million birds. Simmons (1927) estimated the breeding population as "millions" on the island in 1925. Colonel Tomlinson, British Government Representative on Ascension from 1942 to 1946, was unable to decide if the tern colony consisted of 1 or 2 million birds (Chapin 1954), while both Chapin (1954) and (Harford 1958) estimated the breeding population size to be 1 million birds in 1942 and 1957, respectively. Ashmole (1963a) estimated its size in 1958 to be

750,000 birds. In the latter part of the 20th century the breeding distribution of sooty terns contracted and by 1987 colonies was entirely restricted to the coastal plain at two sites, Mars Bay and Waterside, in the south-west corner of the island (Blair 1989; Fig.1.1). Sooty terns remain by far the most common bird species on Ascension (Ashmole & Ashmole 2000) and as prey are crucial to ecosystem functioning (Krebs 2001).

3.2.4. Historical and secondary data

Secondary data (defined here as data that is publicly available) concerning the size of the sooty tern population are available for Ascension Island. For example, secondary data are available from breeding colonies that were marked on maps of the island during the 19th century (Bedford 1838, Penrose 1879). The species was an important natural resource to the first settlers and there are records of egg harvesting and reports from visiting naturalists (Hart-Davies 1972). There are distinct benefits of using secondary data to study population trends of sooty terns on the island. For example, they can provide historical measurements (i.e. area of colony) that can be used to determine population size, and if collected during the study period, they can confirm or refute primary census data. This is not the first time that secondary data collection has been used to augment primary data in a study of avian demographics. Retrospective investigation of population trends has been used to study songbirds (Gooch *et al.* 1991) and lesser snow geese *Anser caerulescens caerulescens* (Cooch *et al.* 2001). Nevertheless, it is difficult to estimate the size of breeding colonies of seabirds that were lost in the early stages of human occupation of islands (Hilton & Cuthbert 2010). On Henderson Island an estimate of historical population size has been obtained by backward extrapolation from current rates of decline (Brooke *et al.* 2010). An alternative approach recommended by Igl and Johnson (2005) is to collect current data and contrast them with data collected earlier. This is the approach I have adopted.

3.2.5. Population trend of sooty terns on Ascension Island

Population monitoring plays a critical role in conservation biology by providing the information necessary to identify conservation problems and to suggest possible solutions (Goldsmith 1991). Prior to this study there had not been any systematic censuses of seabirds on Ascension Island except for frigatebirds (Ratcliffe *et al.* 2008). The population trend of sooty terns breeding on Ascension Island is required (Ashmole *et al.* 1994, Ratcliffe *et al.* 1999) to assess progress in the management of the species, to discriminate among competing hypotheses on the causes of this population's historical decline (e.g. predation, ENSO events and food shortages) and to enhance our understanding of factors which may limit its future growth. Furthermore, a population trend is required to quantify the outcomes of a restoration project that removed feral cats from the island between 2002 and 2004 (Bell 2005, Hughes *et al.* 2008, Ratcliffe *et al.* 2009). When determining the population trend of avian species the numbers of birds attempting to breed each year, based upon a regular annual breeding cycle, are commonly used. However, here, I have used the sub-annual breeding periodicity of 9.6 months (see Chapter 2) as the time period between censuses. Ratcliffe *et al.* (1999) calculated that surveys in 10 or more seasons are required to obtain an accurate measure of sooty tern population trends on Ascension.

In this study I have used secondary data to describe the population trend of breeding sooty terns on the island between 1877 and 1958. I have also used primary data from field censuses to examine the population trend between 1990 and 2012.

3.3. MATERIALS AND METHODS

3.3.1. Study site

Sooty terns were censused in the AOS study areas at Mars Bay (approximately 70 ha) and Waterside (approximately 300 ha) (AOS 2012). Please see full details of the study site that are provided in section 2.3. During each field season the coastal plain (see Fig. 1.1) was searched but no sooty terns were ever found breeding outside the study areas at Mars Bay and Waterside. The only other colony of sooty terns on Ascension is a very small one (approximately 50 pairs) on Boatswainbird Islet (see Fig.1.1; Ashmole 1963a).

3.3.2. Field research

The total population of sooty terns on Ascension Island is so large that the censuses estimated mean Apparently Occupied Nest (AoN) density in sample quadrats and extrapolated these to the estimated area of the colony (Bibby *et al.* 2000). Population estimates were based upon the assumption that all AoNs were available to survey (Mitchell *et al.* 2004). The area of the colony was determined by mapping of the perimeter of the breeding colonies. Census data were collected during 19 expeditions mounted by the AOS that visited the island between 1990 and 2012, inclusive. Fieldwork lasted approximately 10 days and the mean field research effort was 79 human-days (range: 21–150 human-days; *n* = 19) and mean field team size was seven members (range: 3–12 members; *n* = 19).

3.3.2.1. Peak of breeding. Sooty terns breed relatively synchronously every 289 days but there is a spread of ≈ 59 days in the timing of laying within a breeding season (section 2.4.4.2). Timing of the surveys is crucial if the total number of nesting birds is to be estimated accurately (Mitchell *et al.* 2004). If the census is too early many birds will not have laid and if it is too late then chicks will have formed crèches (BJH unpubl. data), resulting in an under-estimation of the area of the breeding colony and of AoN density. Ashmole (1963a) estimated that the peak of the breeding season occurred between 40 and 60 days after the first egg of the season is laid. Field season dates were planned to coincide with the peak of the sooty tern breeding season but peaks were sometimes missed especially during the early years of fieldwork when the regularity of the sub-annual breeding cycle was not appreciated. The duration of fieldwork (≈ 10 days) provided some flexibility when the census work was completed. For example, if the field team arrived before the peak, the census work was completed at the end of the period in the field. The AIG provided additional census data post-fieldwork. Please see section 2.3.1 for full details of how first egg data and the peak of the breeding season were determined.

3.3.2.2. AoN density from field surveys. During each field season AoN density was determined from > 100 randomly placed 10 m^2 circular 'quadrats'. Transects were placed at random through the colony at Waterside and Mars Bay. At every 10 paces along a transect, a pole on which a 1.784 m length of string was attached was used to describe a circle of area 10 m^2. The number of clutches within each circle was counted by two observers. Clutches (rarely more than one egg) were used in the estimate of AoNs. Transects were not placed in sub-colonies where eggs had already started hatching. The mean AoN density of adjacent sub-colonies was used to calculate the population in the sub-colonies where eggs were hatching.

3.3.2.3. Colony area from field surveys. During each census, the potential breeding area was searched systematically for sub-colonies. Sooty terns nest in spatially separate sub-colonies with typically approximately 10 occupied by breeding birds that are at different stages in the breeding cycle; some sub-colonies contained chicks while in others birds were still laying (BJH unpubl. data). Typically, sub-colonies ranged in size between 0.1 and 6 ha. Sub-colonies occupied different parts of the potential breeding area between breeding seasons. The area of the breeding colony was determined using conventional field survey techniques (Curtin & Lane 1961, Lisle *et al*. 2011). Sooty terns nest in dense colonies and the perimeter of the colony is well defined (Fig. 3.1). If sub-colonies were observed to have expanded during the period of fieldwork, the sub-colony was re-surveyed at the latest opportunity before departing the island. The area of each sub-colony was surveyed in 1990, 1996 and 1998 using compass and tape ring-traverses (Curtin & Lane 1961). In 2000 and 2001 the sub-colonies were surveyed twice with the first using compass and tape ring-traverses and then by walking the boundary and taking GPS readings (Lisle *et al*. 2011) at regular intervals (approximately every 20 m) and at all turning points. The area of the breeding colony obtained from the compass and tape survey method was similar to that from the GPS survey in 2000 and 2001. Only GPS surveys were used from 2002 onwards. Co-ordinates around the perimeter of each sub-colony at intervals

Figure 3.1. A sooty tern sub-colony at Waterside on Ascension Island in the South Atlantic. The photograph shows the edge of the sub-colony and the terrain occupied in 2011. (Photo: A. Giles).

of approximately 20 m were plotted on 1-mm square graph paper at a scale of 1:1000. The total area of the sub-colony was deduced by counting the number of 1 mm squares in each sub-colony plot. Towards the end of the study period these hand-drawn plots were scanned into a Geographical Information System (GIS) and the area and perimeter re-calculated. Both methods yielded similar results with the difference in area ranging from 0.00 to 0.57 ha with the mean difference of 0.06 (± 0.10 ha; *n* = 12).

3.3.3. Secondary data

A literature search was conducted for maps, nest density records and photographs of the sooty tern colonies on Ascension Island. An outline of the colony boundary and a scale were sufficient to determine the area of the breeding colonies from such sources. Photographs of nesting terns provided evidence of nest density. Records of sooty tern colonies prior to and during the study period were collected from various sources. These included written descriptions of the colonies (Chapin 1954, Ashmole 1963a), informed estimates of colony sizes (Simmons 1927, Chapin 1954, Ashmole 1963a), photographs (Porthcurno 1910-1930, Simmons 1927, Chapin 1954, Stonehouse 1960) from which nest density could be determined, counts of nests in measured quadrats (Chapin 1954, Ashmole 1963a) and boundary surveys (Penrose 1879, Chapin 1954, Ashmole 1963a, R. Prytherch pers. comm.) of the colonies. Most of the colonies in these surveys no longer exist such as the “first fair” described by Ashmole (1963a) and the large colony that was destroyed during the building of the airfield (Chapin 1954).

3.3.3.1. Peak of breeding from secondary data. Maps by Gill in (Penrose 1879), Chapin (1954) and Ashmole (1963a) who worked on Ascension Island for 26, 6 and 78 weeks, respectively, may not have been drawn at the peak of the breeding season of sooty terns but since these professional ornithologists were present on the island in part to study the biology of the birds, I have assumed that they were composed during or close to the peak of breeding activity. Chapin (1946) surveyed the colony from the air and the ground, and Ashmole (1963a) observed the colony for two seasons.

3.3.3.2. AoN density from secondary data. AoN density from secondary data was determined from records of egg counts in areas of known size and from photographic evidence. Where AoN density could be calculated from secondary data, records of one egg were assumed to represent one AoN. Imperial measurements were converted to metric to provide density in AoNs per m². Photographs were scrutinised and a visual comparison was made of photographic nest density and contemporary AoN density by two field researchers with recent experience of measuring AoN density in the sooty tern colonies on Ascension (Fig. 3.2). Each researcher compiled an independent series of comparative index

Figure 3.2. Sooty terns nesting on Ascension Island circa 1910. In 1942 Wideawake airfield was built on this site.
(© Cable and Wireless Communications 2014, by kind permission of Porthcurno Telegraph Museum)

values (I). The value of I = 1.0 was assigned to a photograph where AoN density appeared to be similar to contemporary AoN density. If twice as many terns were nesting I = 2.0 and if the density on the image was half that observed in the field I = 0.50. AoN density from historical photographs was calculated from the formula:

$$\text{Historical AoN density} = \text{mean AoN density from field surveys} \times I \qquad \text{(Eqn 3.1)}$$

3.3.3.3. Colony area from secondary data. Historical scaled drawings that delineated the boundary of the colonies were used to determine the breeding colony areas. Copies of the original documents were scanned in GIS as 300 dpi jpeg images using a TruScan® Vidar Scanner. These files where then rectified using Erdas Imagine 9.2 (Leica 2008) to give the dumb images a true location on the ground. This was achieved by either using known GPS coordinates on the vertices of the original sketches or by referencing the original map/sketch to existing re-projected imagery/mapping. Once the files had been given a projection, the areas could then be digitised as Shapefiles using ESRI's ArcMap 9.2 (ESRI 2009). This GIS software located at the MOD Joint Aeronautical and Geospatial Organisation and managed by A.D. Giles enables the areas of these colonies to be calculated.

3.3.4. Statistical analyses

AoN densities were calculated by dividing the number of AoNs counted in each quadrat by its area in m^2. AoN densities differed between sub-colonies but were grouped together at Mars Bay and at Waterside to obtain a mean from a bigger sample at the colony level. The mean nest density and 95% confidence limits were then calculated. Spearman Rank Correlations were used to test for trends in the sooty tern mean AoN density at Mars Bay and at Waterside from 1996 and 2012. Wilcoxon's test for matched pairs was used to test for differences in median nest density at Mars Bay and at Waterside. In most seasons where the census was determined from field surveys, the population size was obtained from the mean AoN densities at Mars Bay and Waterside applied to the area of the breeding colonies and summed to give a total population estimate with 95% confidence limits. In seasons where the colony area was determined from secondary data, the population size was calculated from a single mean AoN density applied to the total area occupied by the population of sooty terns. Spearman Rank Correlation was used to test for a relationship between nest density and population size between 1990 and 2012.

3.4. RESULTS

3.4.1. Primary data

Sixteen of 19 censuses on Ascension Island coincided approximately with the peak of breeding. However, censuses in 1992, 1994 and January 2012 were conducted before any chicks had hatched and thus probably missed the peak. The AIG provided additional data for the January 2012 census but censuses in 1992 and 1994 were not included in further analysis. The mean date of the census was 3 ± 7 days before the population peaked with censuses ranging between 29 days *before* and 21 days *after* the peak in breeding (*n* = 16).

3.4.1.1 AoN density from field surveys. AoN density was calculated from counts of 83,070 AoNs in 4,707 quadrats in the sooty tern colonies at Mars Bay and Waterside between 1996 and 2012 (Table 3.1). Between 1996 and 2012 nest density at Waterside varied between 2.52 and 1.41 AoNs per m^2 and declined significantly ($r_s = -0.53$, $n = 16$, $P = 0.04$), while over the same period at Mars Bay it varied between 2.02 and 0.96 AoNs per m^2, also a significant decline ($r_s = -0.54$, $n = 15$, $P = 0.04$; Fig. 3.3). Median AoN density of 1.91 per m^2 at Waterside was

Table 3.1. Variation in Apparently Occupied Nest (AoN) density, the number of 10 m^2 quadrats measured and the number of sub-colonies of sooty terns on Ascension Island among the Mars Bay and Waterside breeding colonies between 1996 and 2012.

Breeding season	**Mars Bay**			**Waterside**		
	Number of sub-colonies	**Number of quadrats**	**AoN density (per m^2)**	**Number of sub-colonies**	**Number of quadrats**	**AoN density (per m^2)**
Oct 1996	2	118	1.93	1	219	2.52
Jun 1998	2	70	1.73	2	209	2.12
Nov 2000		No colony		1	155	1.90
Aug 2001	3	100	2.00	6	239	2.23
Jun 2002	1	157	2.02	6	229	1.86
Mar 2003	3	153	1.40	10	226	1.94
Feb 2004	3	77	1.26	6	287	2.06
Nov 2004	3	91	1.46	10	108	1.98
Oct 2005	2	225	1.48	7	231	1.74
Aug 2006	3	50	0.96	4	56	1.41
May 2007	2	204	1.28	8	184	1.70
Feb 2008	11	165	1.14	13	245	1.79
Dec 2008	3	156	1.36	7	130	1.46
Oct 2009	5	119	1.09	3	No quadrats surveyed	
May 2010		No quadrats surveyed			No quadrats surveyed	
Apr 2011	8	65	1.32	8	195	2.05
Jan 2012		No quadrats surveyed		5	81	1.95
Dec 2012	4	136	1.75	8	28	1.82

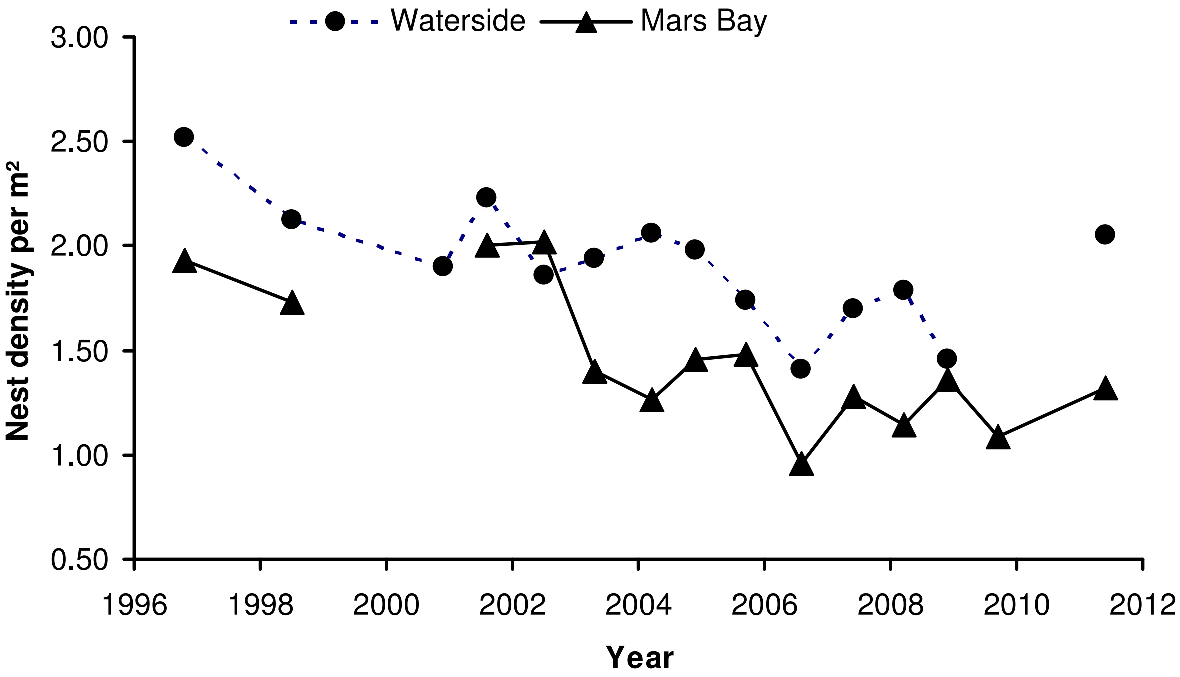

Figure 3.3. The Apparently Occupied Nest (AoN) density (see text for details) at Waterside and Mars Bay breeding colonies of sooty terns on Ascension Island showing a significant decline between 1996 and 2011. Only survey data from successive breeding seasons are joined by lines in each colony.

significantly higher than that of 1.48 per m^2 at Mars Bay (Wilcoxon's test for matched pairs, $T = 3$, $n = 14$, $P < 0.01$).

3.4.1.2. Colony area from field surveys. The decline in nest density was offset by a significant increase in the area of the breeding colonies ($r_s = 0.65$, $n = 16$, $P = 0.01$) which varied significantly from 15.68 ha in 2006 to 3.63 ha in 2000 (mean area of breeding colonies: 10.55 ± 1.65 ha, $n = 16$). In contrast to an increase in the overall area occupied by breeding sooty terns, there was a decline in the area occupied at Waterside offset by a corresponding significant increase in the area occupied by breeding birds at Mars Bay between 1996 and 2012 ($r_s = 0.79$, $n =$

16, $P = 0.002$). Traditionally, two thirds of the Ascension population bred at Waterside and one third at Mars Bay. Why the area of the breeding colonies increased with declining nest density was not established.

3.4.2. Secondary data

3.4.2.1. AoN density from secondary data. Chapin (1946) counted the number of sooty tern eggs in 1942 in two rectangular quadrats of 1,000 square feet which yielded nest densities of 1.58 and 1.63 AoNs per m^2, assuming one egg represented one AoN. Ashmole (1963a) counted the number of eggs at the height of the breeding season (42 days after the first egg was laid) in 223 grid squares at the Waterside colony in January 1958 and in 24 grid squares during the next breeding season in August 1958. The nest density in January and August 1958 was 2.33 and 2.40 AoNs per m^2, respectively, and the average was 2.36 AoNs per m^2. Fifteen photographs (e.g. Fig. 3.2) dating from 1899 to 1942 provided a source of information from which two researchers calculated I, a comparative index. I ranged from 0.8 to 1.3 with a mean of 1.15 ± 0.04 ($n = 30$). Nest density from photographs provided a mean of 1.85 ± 0.15 AoNs per m^2 ($n = 15$; Table 3.2). Mean nest density from secondary data varied between 1.60 and 2.36 AoNs per m^2 with a mean density of 1.94 ± 0.96 AoNs per m^2 ($n = 3$).

3.4.2.2. Colony area from secondary data. Searches of secondary data that would provide colony area revealed eight maps/sketches, one area survey (Ratcliffe *et al.* 1999) and GPS surveys (AIG pers. comm., S. Riddick pers. comm.). Sketches by Olson (1977) and Bourne (pers. comm.) were imprecise and provided only a rough estimate of the area of breeding colonies. The areas of breeding colonies

Table 3.2. Details of historical photographs of the sooty tern breeding colonies on Ascension Island in the South Atlantic taken between 1899 and 1959. Shown are the date of each photograph (with italicised text indicating date estimates), estimates of nest densities from two independent researchers, the mean nest density and the source of photographs (see text for further details).

Photograph:		**Estimate of nest density (AoNs per m^2) for researcher:**		**Mean nest density (AoNs per m^2)**	**Source**
number	**date**	**1**	**2**		
1	*1910*	1.60	1.92	1.76	Porthcurno 1910-30
2	*1930*	1.44	1.76	1.60	Porthcurno 1910-30
3	*1930*	1.92	2.24	2.08	Porthcurno 1910-30
4	*1910*	1.92	2.08	2.00	Porthcurno 1910-30
5	*1910*	2.08	2.72	2.40	Porthcurno 1910-30
6	1899	1.76	1.60	1.68	Jenner 1899
7	1959	1.60	1.92	1.76	Stonehouse 1962a
8	1959	1.76	2.40	2.08	Stonehouse 1960
9	1925	1.92	2.56	2.24	Simmons 1927
10	1910	1.28	1.60	1.44	Hart-Davis 1972
11	1942	1.76	1.44	1.60	Clarke 1944
12	1942	1.92	2.08	2.00	Chapin 1946
13	1942	1.44	1.60	1.52	Chapin 1954
14	1942	1.60	2.08	1.84	Chapin 1954
15	1942	1.60	1.76	1.68	Chapin 1954

occupied by sooty terns on Ascension in 1877, 1942, 1958, 1971and 1984 were estimated to be 72, 73, 77, > 100 and ≈ 56 ha, respectively (Table 3.3, Fig. 3.4a, b & c).

3.4.2.3. Accuracy of secondary data colony area. A check on the accuracy of the colony area from secondary data was obtained from secondary data surveys completed during contemporary times. The colony area from secondary data varied between 9.12 and 16.34 ha from 1993 to 2010 with a mean nest area of

Table 3.3. Details of surveys of the breeding colonies of sooty terns on Ascension Island between 1877 and 1984 including the surveyor's name, the date of the survey, the number of sub-colonies surveyed, the scale of the ground survey and the area as calculated by GIS.

Surveyor	Date of survey	Number of sub-colonies	Survey scale	Area (ha)
D. Gill	Dec 1877	3	1:123,700	71.56
J.P. Chapin	Oct 1942	14	1:63,360	73.30
N.P. Ashmole	1958-1959	12	1:31,680	77.23
S.L. Olson	1970-1971	2	1:120,000	> 100
W.R.P. Bourne	Oct 1984	10	1:31,680	≈ 56

12.30 ± 3.40 ha (*n* = 5; Table 3.3) and was ≈2 ha (17%) larger than that from primary data (mean area = 10.55 ± 1.65 ha, *n* = 16).

3.4.4. Historical patterns in population size between 1877 and 1958

Population size was compiled using a nest density of 1.94 AoNs m^2 and areas from scaled drawings of 1877 (Gill 1878 cited in Penrose 1879), 1942 (Chapin 1954) and 1958 (Ashmole 1963a) (Table 3.3). Between 1877 and 1958 the breeding population varied in size between 2.78 and 3.00 million birds with a mean of 2.87 ± 1.21 million birds (*n* = 3). From the map of Olson (1977), I estimated the population to be > 3.9 million birds while Bourne (pers. comm.) revised a map of Ashmole (1963a) to provide an estimate of ≈ 2.2 million birds, thereby providing general support for an estimate of 2.9 million birds.

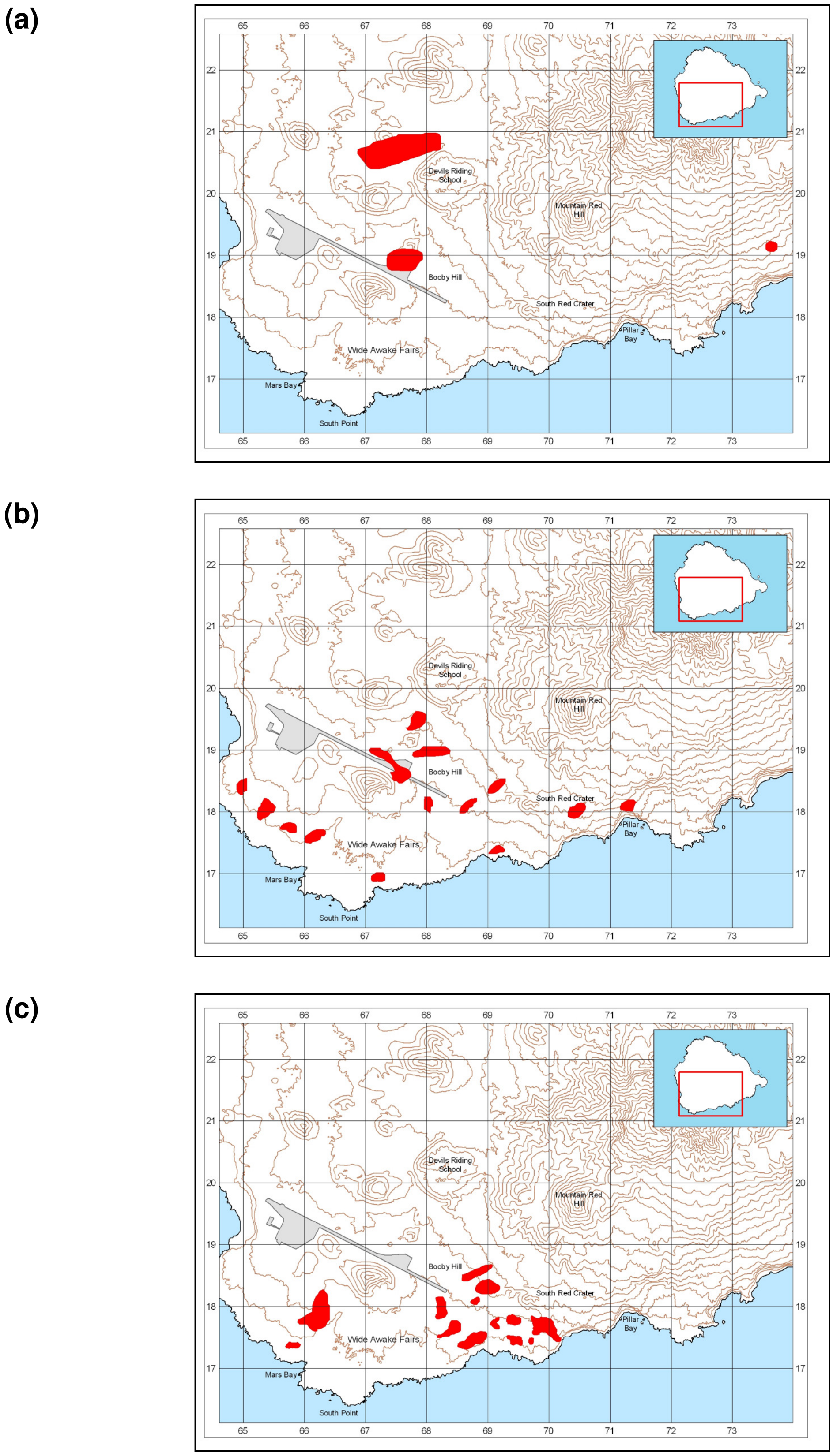

Figure 3.4. GIS re-scaled historical maps showing (in red) the size and location of the breeding colonies of sooty terns on Ascension Island surveyed in (a) 1877 (after Gill 1878), (b) 1942 (after Chapin 1954) and (c) 1958 (after Ashmole 1963a).

3.4.5. Contemporary patterns in population size between 1990 and 2012

In 2000 many sooty terns deferred breeding as in 2001 the breeding population showed a season-on-season increase of 116%. Similarly, in 2004 terns deferred breeding as in 2005 when a season-on-season increase of 49% occurred. The breeding population within the 1990 to 2012 study period varied between 138,000 and 535,000 birds with a mean of 351,000 ± 34,000 birds (*n* = 22) (Fig. 3.5). No

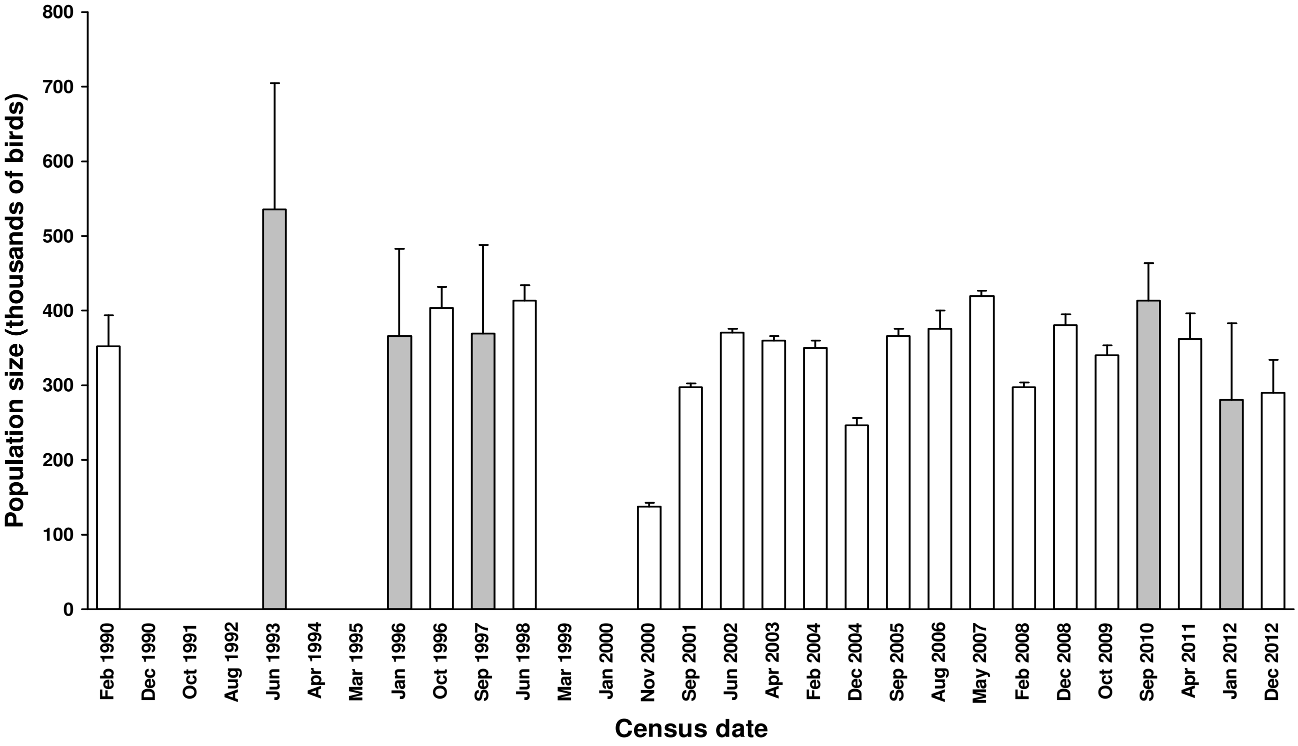

Figure 3.5. Estimated size of the sooty tern breeding population (mean + 95% confidence limit) on Ascension Island between 1990 and 2012, inclusive. Some are based on primary (field) data (open bars) while others are based on secondary data (grey bars) (see text for details). Note that the sub-annual breeding cycle results in birds breeding twice in 1996, 2004, 2008 and 2012.

significant trend across this recent period was detected (r_s = -0.25, *n* = 22, *P* = 0.25). Note that the sub- annual breeding cycle results in birds breeding twice in

1996, 2004, 2008 and 2012. Secondary data derived for September 1997 (Ratcliffe *et al.* 1999), and surveys in 1993, 1996 and 1997 (R. Prytherch pers. comm.), in 2010 (Hughes *et al.* 2012) and January 2012 were also included to construct the trend.

3.4.6. Long-term population trend

A precipitous decline of 2 million birds occurred between 1965 and 1985 (Fig. 3.6).

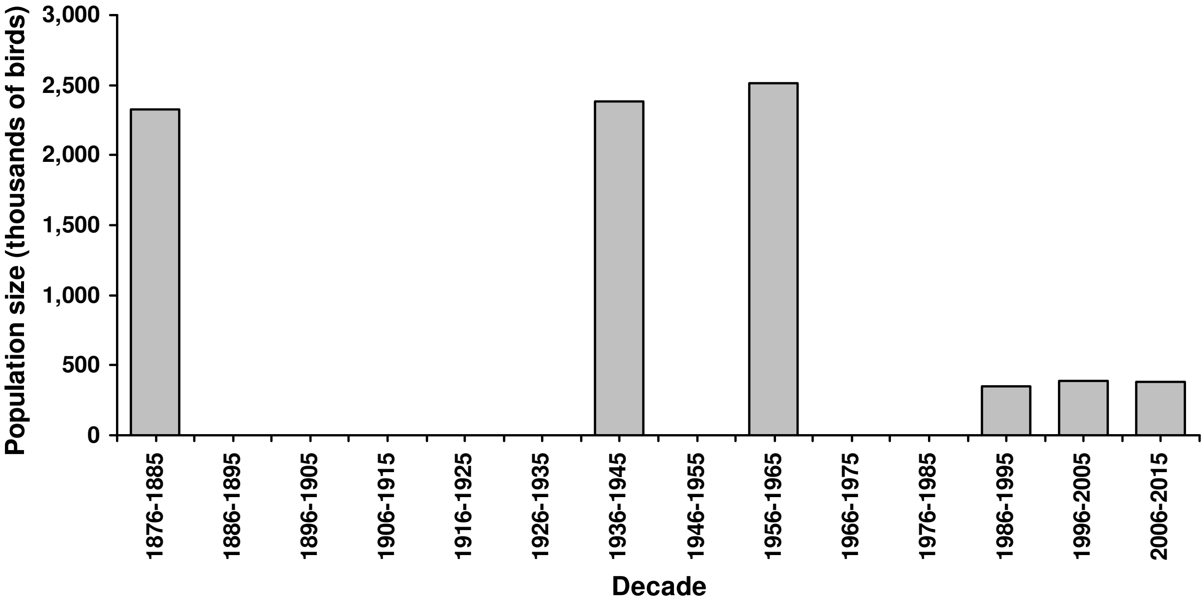

Figure 3.6. Mean size of the sooty tern breeding population on Ascension Island by decades for which data are available from 26 censuses between 1877 and 2012.

The decline was derived from 26 censuses between 1877 and 2012 (Table 3.4).

3.5. DISCUSSION

Population censuses of historically known sooty tern colonies are a priority for research (Schreiber *et al.* 2002). My census studies bridge this gap for the historical colonies of sooty terns on Ascension Island. More than 2 million sooty terns bred each season on Ascension Island between 1877 and 1958, but less than 500,000 birds bred from 1990 to the present day. A precipitous decline

Table 3.4. Areas of sooty tern colonies on Ascension Island as determined from independent surveys, nest density (AoNs per m^2) and estimated population size (mean ± 95% confidence limits) across breeding seasons. AoN densities within each breeding season are pooled for all colonies. Population sizes between 1877 and 2012 are rounded to the nearest 10,000 birds. Bold text is calculated from secondary data.

Breeding season	**Surveyor**	**Area of colony (ha)**	**Mean nest density (AoNs per m^2)**	**Population size (birds; mean ± 95% CI)**
Dec 1877	D. Gill	**71.56**	**1.94**	2,780,000 ± 1,030,000
1942–1946	J. P. Chapin	**73.30**	**1.94**	2,840,000 ± 1,040,000
1958	N. P. Ashmole	**77.23**	**1.94**	3,000,000 ± 1,110,000
1970–1971	S. L. Olson	**> 100**	**1.94**	> 3,880.000*
Oct 1984	W. R. P. Bourne	**≈ 56**	**1.94**	≈ 2,170,000*
Mar 1990	B. J. Hughes	14.38	1.85	350,000 ± 42,000
Oct 1993	R. Prytherch	**16.34**	1.64	540,000 ± 170,000
Jan 1996	R. Prytherch	**11.18**	1.64	370,000 ± 117,000
Oct 1996	B. J. Hughes	9.67	1.93	400,000 ± 28,000
Sep 1997	N. Ratcliffe	**9.12**	**1.61**	300,000 ± 16,000
Oct 1997	R. Prytherch	**11.37**	1.64	370,000 ± 118,000
Jun 1998	B. J. Hughes	10.43	1.85	410,000 ± 20,000
Nov 2000	RA survey team A	3.63	1.90	140,000 ± 5,000
Sep 2001	B. J. Hughes	6.90	2.16	300,000 ± 4,000
Jul 2002	RA survey team B	9.62	1.93	370,000 ± 5,000
Apr 2003	B. J. Hughes	10.46	1.72	360,000 ± 6,000
Feb 2004	B. J. Hughes	9.25	1.89	350,000 ± 10,000
Dec 2004	B. J. Hughes	7.07	1.74	250,000 ± 10,000
Oct 2005	B. J. Hughes	11.36	1.61	370,000 ± 10,000
Aug 2006	B. J. Hughes	15.68	1.20	380,000 ± 24,000
May 2007	B. J. Hughes	14.19	1.48	420,000 ± 7,000
Feb 2008	A. D. Giles	9.72	1.53	300,000 ± 7,000
Dec 2008	B. J. Hughes	13.58	1.40	380,000 ± 15,000
Oct 2009	A. D. Giles	12.21	1.09	340,000 ± 14,000
May 2010	AIG & S. Riddick	**13.49**	1.64	410,000 ± 50,000
Apr 2011	A. D. Giles	10.69	1.69	360,000 ± 34,000
Jan 2012	B. J. Hughes	**≈ 7**	1.95	280,000 ± 103,000

Dec 2012	A. D. Giles	8.13	1.79	302,000 ± 44,000

Note: * Census based upon rough estimate.

occurred between 1877–1958 and 1990 onwards (Fig. 3.6). Twenty-six surveys provided breeding population estimates and population trends of sooty terns on Ascension Island between 1877 and 2012 (Table 3.4). Eleven different surveyors have produced maps of the colony. Nest density was obtained from 4,707 quadrats and from a variety of secondary data sources. Although there is much inter-breeding season variability in breeding population size, there has been no significant change between 1990 and 2012 (Fig. 3.5).

3.5.1. Censuses of seabirds

For the overwhelming majority of species, long-term quantitative data on populations are lacking (Krebs 2001, IUCN 2009). Some published population sizes are just informed guesses determined by field biologists during their first visits to study sites while others may be misleading because of temporal bias in species' occurrence (e.g. deferred breeding or migration; Boakes *et al.* 2010). Seabirds are under threat (from for example commercial fishing; Waugh *et al.* 2008) and it is essential that their status is monitored to protect populations at risk (Mitchell *et al.* 2004). Given the slow intrinsic rates of population growth typical of seabirds (Croxall & Rothery 1991), historical, as well as current, population data are required to track changes in seabird populations. Population sizes of UK birds are some of the best surveyed in the world (Newton 1998) and seabirds are no exception with three censuses of the 25 seabird species having been completed – Operation Seafarer (1969–1970), Seabird Colony Register (1985–1988) and Seabird 2000 (1998–2002). More than 1,000 surveyors contributed to the Seabird

2000 census (Mitchell *et al.* 2004). In marked contrast, there are few seabird censuses in the UKOTs (Hilton & Cuthbert 2010, Pienkowski 2010). On Ascension Island informed guesses in 1958–1959 were used to establish baseline population estimates of the 11 seabird species (Stonehouse 1962a) and for some species such as red-billed and white-tailed tropicbirds (Sanders 2006) these remain the only estimates of population size that are available.

3.5.2. Population decline elsewhere in the sooty tern range

Catastrophic declines occurred in the second half of the 20th century in the sooty tern breeding colony of > 10 million birds on Christmas Island in the Pacific where > 90% of the adult population was lost possibly as a result of the 1982–1983 El Niňo event (Schreiber *et al.* 2002). Large declines also occurred in sooty tern colonies in the Atlantic Ocean. On the Culebra Archipelago in Puerto Rico the population declined by 82% between 1970–1971 and 1980–1982 (Furniss 1983). At the Dry Tortugas in the Caribbean, the population declined by 80% from 380,000 in 1950 to 80,000 during 1986–1991 (Florida Fish and Wildlife Conservation Commission 2003). On St Helena Island (the nearest neighbour to Ascension) the population has declined by 89% between 1948 and 1988 (Rowlands *et al.* 1998). Such steep declines in population size of sooty tern breeding colonies beg the question whether the decline on Ascension is symptomatic of a global or an Atlantic phenomenon?

3.5.3. IUCN Red List category

Population sizes of some avian species that are threatened (i.e. on the UK red list) such as the house sparrow *Passer domesticus* are large with a UK breeding population size of 2–3 million pairs (Robinson 2005). Large populations are not immune from catastrophic decline as is evidenced from the extirpation of the passenger pigeon. In 1866 flocks in excess of 1 billion birds were recorded and just 35 years later the last wild passenger pigeon was shot (Halliday 2003). The IUCN's aim is to provide information on trends and threats to species in order to inform conservation managers and prevent losses in biodiversity (IUCN 2009). The decline in the1980s in the large guanay cormorant population which was estimated to be 21 million birds in 1954 (BirdLife International 2012a) was acknowledged by the IUCN in its re-categorisation from 'Least Concern' to 'Near Threatened' (IUCN 2009). The population data used to re-classify the species was a 30% decline over three generations (33 years in this species; BirdLife International 2012a). IUCN categories are designed for global taxon assessments (IUCN 2009) and trends in seabird populations on the isolated island of Ascension (Ashmole & Ashmole 2000) may not be representative of population trends elsewhere in their range. However, censuses of Ascension frigatebirds have resulted in the re-classification of this endemic seabird species (Collar *et al.* 1994, Ratcliffe *et al.* 2008). During the period when the guanay cormorant population declined by 30%, the Ascension population of sooty terns declined by > 80%. Maps showing the colony area in 1958 (Fig. 3.4c) and in 2009 (Fig. 3.7) illustrate the decline. I have shown that similar declines have also occurred in other sooty tern populations in the Atlantic. The rate of population growth in seabirds is typically slow (Croxall & Rothery 1991) and sooty terns defer breeding for more than 5 years (Feare & Doherty 2011). Hence, population recovery is also inevitably slow. This is especially true if it is assumed that generation length (i.e.

the average age of parents of the current cohort of new chicks; IUCN 2009) for this species is > 11 years (Schreiber *et al.* 2002). Such a decline is perhaps

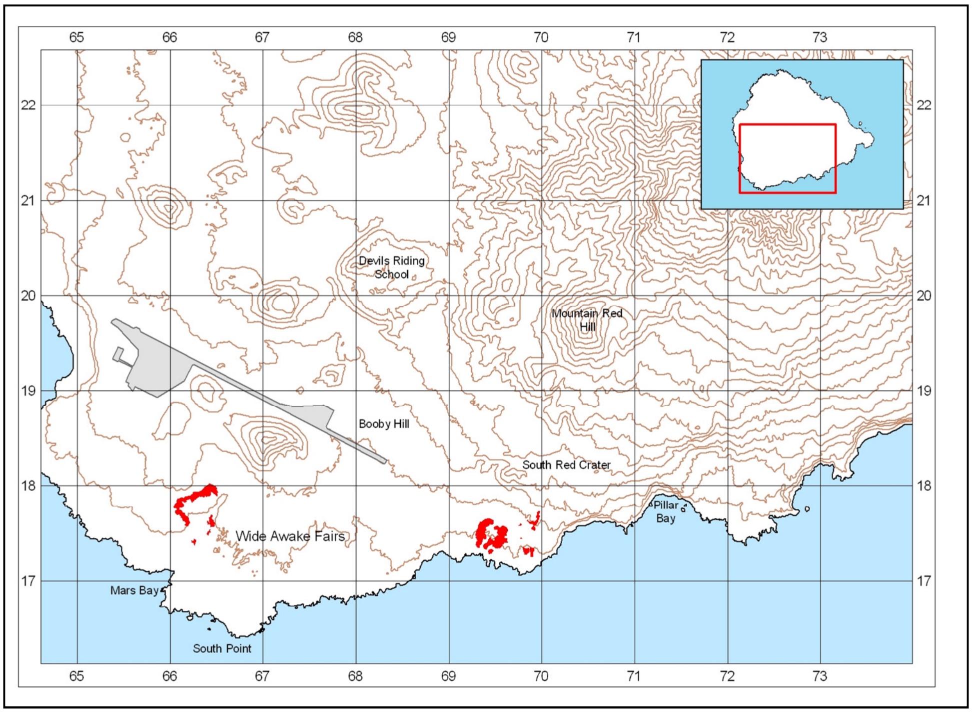

Figure 3.7. GIS map (for comparison with historical maps Fig. 3.4a, b & c) showing (in red) the size and location of the sooty tern colonies at Mars Bay and Waterside on Ascension Island in October 2009.

sufficient to be regarded as indicating that an IUCN Red List status of ‘Least Concern’ is not appropriate for sooty terns.

3.5.4. Breeding population during ENSO years

Three independent censuses of the population size of sooty terns on Ascension were completed during breeding seasons in 1997/98 when one of the largest ENSO events on record occurred (Elliott *et al.* 2001). The mean population size in 1997/98 was 3% greater than the long-term mean based on 1990–2012 data (Table 3.4). ENSO events are known to reduce the number of adults attempting to breed (Schreiber & Burger 2002) but no such reduction occurred on Ascension during the major ENSO event in 1997/98. Unlike Monticelli *et al.* (2007) who found that ENSO events in the Indian Ocean reduced breeding performance of roseate terns *Sterna dougallii*, I found that ENSO events did not affect the size of the sooty terns breeding population (Fig. 3.5) on Ascension.

3.5.5. Limitations of data

The narrow confidence intervals around the population estimates between 1990 and 2012 mean the power to detect trends is reasonably good. GIS software was used to calculate the areas of census maps that were plotted by hand on graph paper in the 1990s. The area from GIS was always larger but only by 7% compared with that obtained from hand plotting. Which method provided the most accurate measure of area has not been established. Historical nest densities were based on counts of eggs and would be < 1% higher (because of the occasional double clutch) than primary nest density data based on counts of AoNs. There is anecdotal evidence to support my findings. For example, Penrose (1879) said that "In a good mornings work, about 200 dozen eggs are collected" and Simmons (1927) described "where birds nest so thickly that walking is difficult". Such descriptions suggest higher historical nest density than in the 21st century. There is also some anecdotal evidence for when the decline in the size of the sooty tern population occurred. K.E.L. Simmons (pers. comm.) lived on Ascension at the time and stated that the population decline occurred in the early 1960s when commercial fishing began in the tropical Atlantic Ocean (ICCAT 2010).

3.5.6. Future directions

Like any monitoring programme, my aim was to monitor the sooty tern population to detect a change in the population size. To date, evidence for an increase in the population size of sooty terns is mixed. Three seasons with small breeding populations in 2008 and 2009 were preceded and followed by seasons of relatively large breeding populations (Fig. 3.5). I conclude that further censuses are imperative to characterise the population trend for this species and to detect its predicted recovery (Ratcliffe *et al.* 2009). I recognise that the logistics and finances of such exercises, especially to remote islands such as Ascension, can be prohibitive. Although in breeding seasons prior to 2010 I have managed to overcome such obstacles, it was only through cooperation and data sharing between different agencies that the censuses in 2010 and January 2012 were possible. This highlights the need for further cooperation between professional organisations and volunteer citizen scientists (Greenwood 2007) in making plans to continue the long-term population monitoring of Ascension sooty terns a reality.

3.5.7. Conclusions

This chapter demonstrates a new approach to quantifying historical population size of seabirds. Potentially, the technique I have developed to determine population size from maps of historical breeding colonies has wide application for population studies of colonially breeding animals. The size of the sooty tern breeding population on Ascension has declined by 80%. Similar precipitous declines have occurred in the second half of the 20th century on other islands elsewhere in their range so the species' current IUCN Red List category of 'Least Concern' should be reviewed. Despite conservation management interventions (e.g. cat eradication; Hughes *et al.* 2008, 2012), the sooty tern population has not increased in size between 1990 and 2012. The cause of the decline needs further investigation in order to make conservation efforts more informed and, therefore, more effective.

In the next chapter I will investigate intrinsic factors that may limit the population's capacity for such recovery.

(Note: Chapter 3 was published as part of Hughes *et al*. 2008).

Chapter 4

INSIGHTS FROM RINGING: POPULATION GROWTH RATES AND LIFE HISTORY OF SOOTY TERNS ON ASCENSION ISLAND

4.1. ABSTRACT

Determination of growth rate is key to understanding a population's ecology. The rate of population growth that can be achieved by a species depends on immigration and on the population's intrinsic capacity for increase. On Ascension Island the capture of one immigrant from a population of 9,482 sooty tern chicks ringed on other Atlantic islands and the dispersal of only two birds re-captured elsewhere from a population of 5,210 chicks ringed on the island together suggest that immigration and emigration are minimal. Ascension sooty terns show peer group-fidelity and rarely occupy the nest site used the previous season. Each breeding season 15% of the population occupy nest sites > 3 km from where they bred the previous season. I used 37 years (1975–2012) of capture/re-capture records in order to investigate intrinsic factors (e.g. age of first breeding, longevity and deferred breeding). The mean interval between fledging and recruitment to the breeding population by the youngest first-time breeders was 5.37 ± 0.30 years (*n* = 7 birds). Two adults that were 26 and 34 years old were re-captured while breeding on Ascension Island. Most successful breeders do not defer breeding and were approximately three times more likely to be re-captured in the season following successful breeding than were unsuccessful breeders. The maximum possible increase in sooty tern breeding numbers would be for the population to double after eight breeding seasons. As immigration is minimal and the capacity for sooty tern to reproduce is low, high local recruitment and adult survival rate are critical for maintaining the population size.

4.2. INTRODUCTION

With population size being determined by the balance between the four rates of birth, death, immigration and emigration, they must be quantified when attempting to determine the primary factors limiting population size (Newton 1998). The rate of increasing population growth depends on immigration and on the population's intrinsic capacity to increase (i.e. the maximum reproductive potential of the species under field conditions - Allaby 1998, Krebs 2001). In birds the intrinsic capacity for increase can be quantified from knowledge of the age of first breeding, reproductive output per breeding attempt and longevity, with these life-history parameters shaping the lifetime reproductive success of individuals (Møller 2006, Stahl & Oli 2006). Ashmole (1963a) examined some of these reproductive parameters of the Ascension population of sooty terns which could be determined over two breeding seasons. These included clutch size, incidents of laying of replacement eggs, the length of the incubation period and incubation shifts between parents. However, the precision of these parameters would benefit from studies across multiple seasons and other factors that also underpin population growth require longer term investigations. These include emigration and immigration, nest site and peer group-fidelity, age at first breeding, longevity and the length of the period of deferred breeding. It is these latter parameters that are the subject of this chapter.

4.2.1. Emigration and immigration

In any seabird colony, the breeders could include some individuals raised within the colony and others that have arrived from elsewhere (i.e. immigrants). Most young colonially nesting birds return to their natal colony to breed (Newton 2003).

However, there are a few reports of sooty terns emigrating and breeding in other colonies (Schreiber *et al.* 2002) with inter-island movements of over 1,000 km reported in the Indian Ocean (Feare & Lesperance 2002) and in the Caribbean Sea (Norton 1986). Therefore, although Ascension is geographically isolated (Fig. 4.1), emigration and immigration may occur. The island of St. Helena, the closest neighbour, lies 1,400 km to the south-east and has a population of ≈ 300 sooty terns breeding mainly on George Island (15°59'S, 05°33'W; 2 ha; Rowlands *et al.* 1998). The species is also found on: Atol das Rocas, Brazil (03°51'S, 33°49'W; 36 ha) at a distance of 2,200 km with a population of ≈ 140,000 (Neto 1998); Tinhosa Grande, São Tomé and Príncipe, Gulf of Guinea (01°21'N, 07°18'E; 21 ha) at a

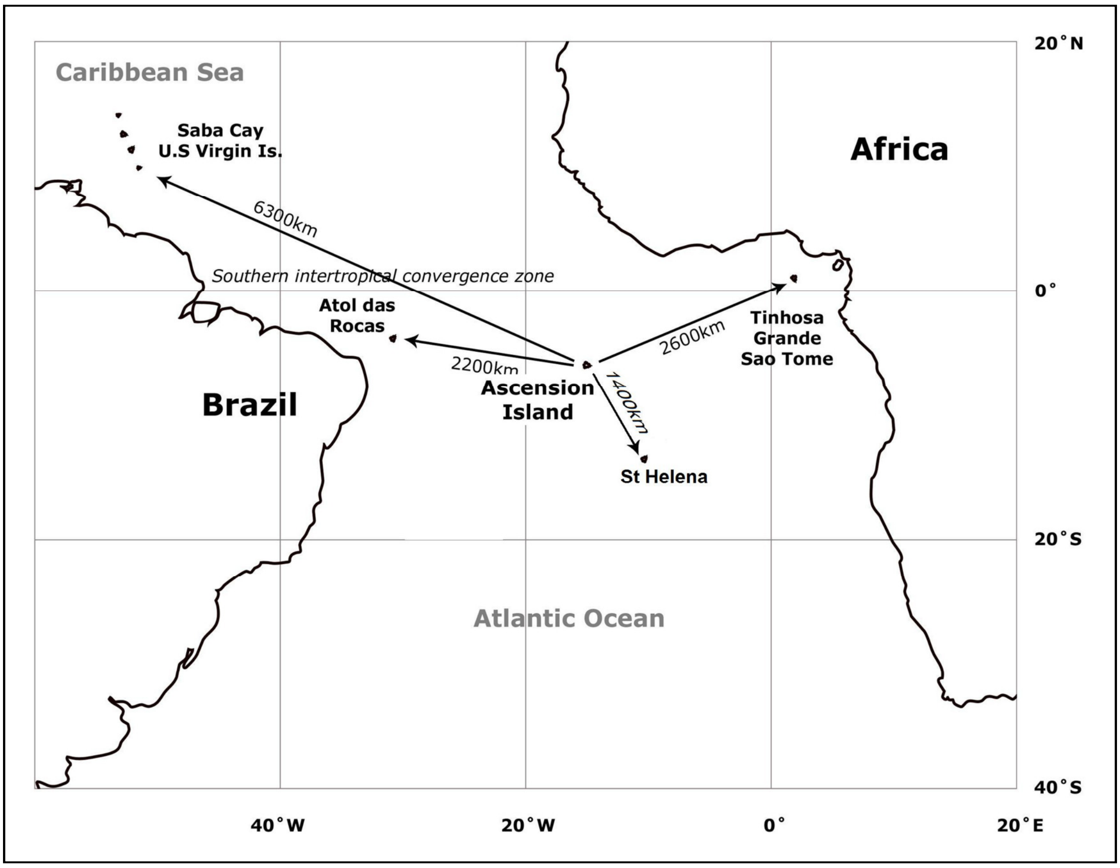

Figure 4.1. Location of Ascension Island and distances to other islands with large sooty tern colonies in the Atlantic Ocean. Scale of one degree of latitude/longitude at the equator is ≈ 100 km.

distance of 2,600 km with a population of ≈ 200,000 (Monteiro *et al.* 1997); and in the Caribbean where large colonies breed on the Dry Tortugas and on more than 50 other islands (Schreiber *et al.* 2002). The nearest Caribbean colony to Ascension is Saba Cay, St. Thomas, U.S. Virgin Islands (18°19'N, 65°00'W; 30 ha) at a distance of 6,300 km and with a population of ≈ 40,000 (Norton 1986). Juveniles on migration from the Caribbean to their nursery in the Gulf of Guinea travel 4,000 km eastwards along the southern inter-tropical convergence zone (Fig. 4.1) passing within 1,000 km of Ascension (Robertson 1969). Thus, sooty terns travel great distances and juveniles from any of these islands could be considered as providing possible recruits to the Ascension Island colonies.

A range of techniques are now available to study inter-colony movement such as the taking of blood or tissue samples from conspecifics across their range and the use of molecular markers (e.g. mitochondrial DNA) to investigate connectivity of populations (Bicknell *et al.* 2012). Dietary analyses using stable isotopes of carbon and nitrogen can distinguish between in-shore and pelagic foraging areas of seabirds (Bicknell *et al.* In press). The movement of individuals can be determined by electronic tracking devices (e.g. satellite transmitters or geolocators) attached to the seabird (Votier *et al.* 2011). Here, I have used a long-established method (i.e. capture/recapture records) to study inter-colony movements.

4.2.2. Fidelity

Once colonially nesting seabirds start breeding they show a high degree of nest site-fidelity and breeding philopatry (Greenwood & Harvey 1982, Welty & Baptista 1990, Schreiber & Burger 2002). In some seabird taxa many individuals if left undisturbed settle to breed within the same part of a colony as where they hatched. Gulls (Laridae) and terns that nest on the ground often have to move their breeding place (intra and inter-seasonally) as the site becomes flooded, accessible to mammalian predators, infested with parasites or are subject to human disturbance (Newton 2003). The main colony of sooty terns on Ascension Island originally located in the middle of the island (Bedford 1839, Penrose 1879) moved at the end of the 19th century (Daniels 1901). The colony moved 3 km south first to the site where the airfield was constructed in 1942 and then to its present location at Waterside (Ashmole 1963a; Fig. 3.4). Unsustainable egg collection may have been the initial cause of movement (Hart-Davis 1972) and the building of an airfield across the breeding grounds was clearly the driver of the subsequent relocation (Chapin 1946).

Group-fidelity rather than nest site-fidelity may provide the impetus for seabirds to congregate at natal breeding colonies. Apparently, there exists within a number of large seabird colonies associations or groups of birds that perform some acts in unison but that are not duplicated simultaneously by the remainder of the colony (Austin 1951). Such group-fidelity or group adherence (Austin 1951) is less well reported than natal or site-fidelity. Ganter and Cooke (1998) have shown that colony dynamics of lesser snow geese is influenced by group-fidelity. Acts of apparent peer group-fidelity have been observed in sooty terns on Ascension Island (BJH pers. obs.). For example, small groups were seen to desert eggs while the remainder of the colony continued incubation, week old chicks formed crèches of up to 200 until they fledged, and in areas of the colony where re-capture numbers were high re-captured birds came from cohorts that had been ringed contemporaneously. If there is a tendency for group-fidelity in sooty terns then this may indicate that the colony is an information centre (Ward & Zahavi 1973) where enhanced communication between individuals improves their foraging success (Waltz 1987).

4.2.3. Age at first breeding, clutch size and longevity

Variation in the age at first breeding, clutch size and longevity (i.e. the lifespan of an organism) are considered major factors in the regulation of populations and are critical components of demographic studies (Newton 1998). These parameters are needed to calculate lifetime reproductive success and population trends (Krebs 2001). Age at first breeding is the life-history trait that is most commonly used in quantifying the period of immaturity in birds (Bennett & Owens 2002). Seabirds generally defer breeding and this can be for as long as 11 years (i.e. southern fulmar *Fulmarus glacialoides*; Schreiber & Burger 2002). This is a considerably plastic trait in sooty terns that defer breeding across their range from 3 years on Bird Island in The Seychelles (Feare & Doherty 2011), to 5 years on the Dry Tortugas in Florida (Robertson & Robertson 1996), and to sometimes 10 years on Johnston Atoll, Hawaii (Harrington 1974) post-fledging.

Griebeler *et al.* (2010) showed that clutch size can vary with seasonality of resources, nest predation and length of breeding season. Thus, it cannot be assumed that the sub-annually breeding population of sooty terns on Ascension also have 1-egg clutches. Across their range clutch size is one egg but there are reports of 2 and 3-egg clutches (Schreiber *et al.* 2002). Ashmole (1963a) reported single egg clutches of sooty terns on Ascension in the1950s. I found a similar result with only 152 (or 0.2%) of 83,070 clutches monitored (Chapter 3) containing two eggs; these may have been laid by different females but with neighbouring eggs rolling together.

In a comprehensive meta-analysis of longevity of avian species, Wasser and Sherman (2010) identified four variables that significantly affected maximum longevity: body mass (heavier species live longer than lighter ones); diet (herbivores live significantly longer than carnivores or omnivores); sociality (social species live longer than non-social ones); and breeding insularity (species nesting on islands live longer than mainland ones). However, the application of such findings to some avian taxa does not help greatly in estimating longevity; capture/re-capture programmes of wild birds provide more reliable estimates (Clapp & Sibley 1966). The maximum ages of seabirds vary between 20 and 30 years but records of longer-lived individual birds abound (Gill 2007).

4.2.4. Skipped seasons by successful breeders

Seabirds are long-lived species and are known to avoid high investment in some years when food availability is low (Mitchell *et al.* 2004). Avian reproduction is energetically demanding with nutrient-specific foraging requiring large investments of time and energy, and nutritional deficits from previous successful breeding attempts needing to be redressed (Wooller & Coulson 1977). Some populations such as of meadow pipits *Anthus pratensis* (Hötker 1988) and Eurasian sparrowhawks *Accipiter nisus* (Newton 1985) are known to be maintained by just a few highly successful breeders. If a breeding pair fledges a chick in one season they may be more likely to defer breeding in the subsequent season (Robertson & Robertson 1996). Clearly, if successful breeders are absent in alternate breeding seasons then breeding success might only reach half of its potential and it will have an impact on the species' population size.

4.2.5. Migration and intrinsic factors – objectives

Data on immigration and emigration rates and on the intrinsic capacity for the population to increase are essential for estimating the rate of population recovery. In this chapter I have gathered information on immigration and on intrinsic factors that have the potential to limit population growth. I have used 37 years (i.e. 1975–2012) of capture/recapture records in order to: (1) establish if the Ascension Island population is isolated or whether immigration and emigration occur; (2) determine if sooty terns on Ascension Island are peer group- or nest site-faithful; (3) establish the age of birds at first breeding; (4) measure longevity; and (5) investigate if successful breeders skip breeding seasons.

4.3. MATERIALS AND METHODS

4.3.1. Study area

The study areas were the same as described in section 2.2.1.

4.3.2. Ringing/re-capture

Incubating adults and chicks (aged 19 to 60 days; Fig. 4.2) were ringed and some were re-captured (details of methods in Chapter 2). The former could not be sexed quickly in the field since sooty terns are sexually monomorphic and share incubation duties (Schreiber *et al*. 2002, Reynolds *et al.* 2008). To identify the colony where birds were ringed 300 adults and 1,000 chicks at Mars Bay were also given red colour rings and 300 adults and 1,000 chicks at Waterside were given yellow colour rings. To identify birds that were likely to be successful breeders, 63 adults feeding large chicks were given green colour rings. Cohorts of

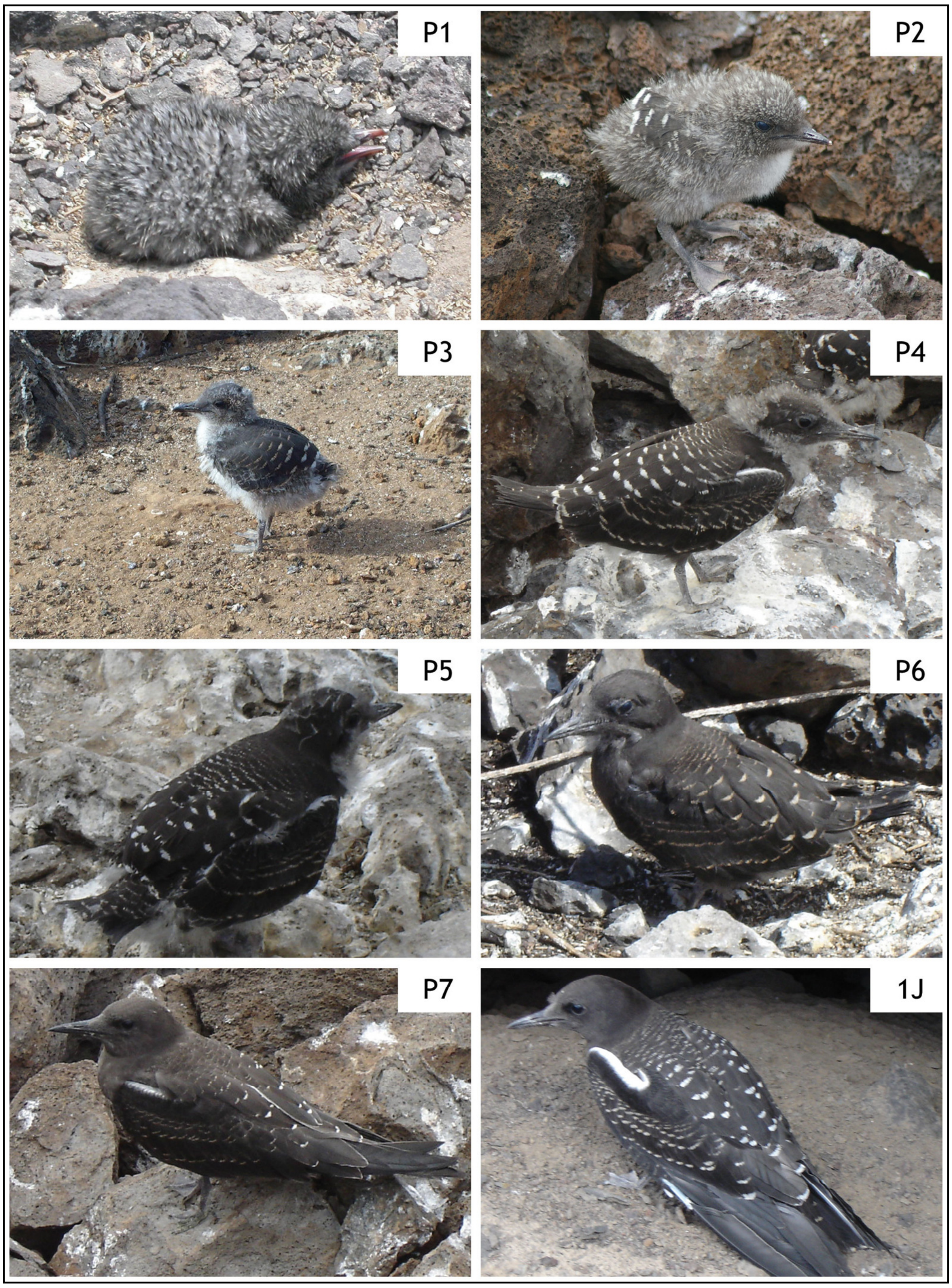

Figure 4.2. The stages of plumage of sooty terns (based on sketches by Feare 1976): (P1) *Downy* – 0-10 days and covered in down; (P2) *Small wings* – 9-20 days when scapular feathers appear; (P3) *Head moulting* – 19-29 days when feathers appear on the crown, mantle and breast; (P4) *Down on face* – 28-36 days when down restricted to face, chest and rump; (P5) *Tail cocked* – 36-43 days when tail coverts grow and tail appears; (P6) *Short tail* – 42-50 days when rectrices same length and wings < 200 mm; (P7) *Tail forked* – 50-65 days when outer rectrices considerably longer than inner ones, and wings > 200 mm; and (1J) *Fledged* – ≈ 60 days when clear white stripe on bend of wing. (Photos: M. Vincent).

adults and of well-grown chicks were ringed with numbered metal rings in 1998, 2002, 2003, 2005 and 2006. A programme of 695 hours of focussed re-capture effort took place between 2002 and 2012 to investigate natal dispersal, inter-colony movements, age at first breeding, longevity and deferred breeding.

4.3.3. Inter-island movement

In order to investigate the potential source of new recruits to the breeding population, intensive searches for ringed birds returning as adults to breed were carried out. The ring recovery programme of immigrants to Ascension Island was based on 9,482 sooty tern chicks that were ringed on three Atlantic islands on Atol das Rocas ($n = 5{,}558$) (Neto 1998), on Saba Cay ($n = 3{,}900$) (Norton 1986) and on Tinhosa Grande ($n = 24$) (Monteiro *et al.* 1997) between 1985 and 1997. Juvenile sooty terns are known to defer breeding for 5 years (Schreiber *et al.* 2002). Re-capture of recruits on Ascension took place 5–17 years after birds on other islands were ringed, and during 13 breeding seasons (2002–2012; Table 2.2). On Ascension Island 5,200 chicks were ringed between 1996 and 2009. Emigration records of birds ringed on Ascension but recovered or re-captured elsewhere were collected.

4.3.4. Fidelity

Movements of birds between the colonies at Mars Bay and Waterside were quantified during searches for sooty terns with rings. Some birds at Mars Bay that were originally given red colour rings were seen incubating in subsequent seasons at Waterside some 3 km from the nest site where they were originally ringed. Groups of terns fitted with yellow rings at Waterside were also seen at

Mars Bay. The colony and Global Positioning System (GPS) coordinates of where birds were ringed and re-captured were recorded. The ringing database was interrogated to establish the extent of inter-colony movements and group fidelity.

4.3.5. Age at first breeding

Ringing and re-capture of sooty terns began in June 1998 and April 2003, respectively, and continued until December 2012 in order to determine age at first breeding. Ten cohorts totaling 2,326 adults and 2,824 large chicks (19–60 days old) were ringed (Table 4.1). Adults that were expected to return most seasons were used to establish the likelihood of re-capture of first-time breeders. For example, if no adults were re-captured as a result of insufficient re-capture effort, we would expect to capture few or no first-time breeders. Each season the colonies were searched for ringed birds incubating eggs. To calculate age at first breeding, incubating birds were all assumed to be sitting on eggs of 14 days of age (i.e. half the incubation period of 28 days; Ashmole 1963a).

Table 4.1. The number of sooty tern adults (birds incubating) and chicks (aged between 19 and 60 days) ringed on Ascension Island during five expeditions between 1998 and 2006.

Age cohort	**Numbers of birds ringed in:**				
	Jun 1998	**Jun 2002**	**Apr 2003**	**Oct 2005**	**Aug 2006**
Adults	190	950	400	386	400
Chicks	310	50	250	1,614	600

4.3.6. Longevity

Searches for long-lived sooty terns commenced when a bird with a North American ring was re-trapped (Hughes & Wearn 2005). The Bird Banding Laboratory at Patuxent, Laurel, Maryland, USA was contacted and they provided records of ringing using US (i.e. United States Fish & Wildlife Service [USFWS]) rings on Ascension Island.

4.3.7. Skipped seasons by successful breeders

I compared the re-capture rates (i.e. number of birds re-captured/number of birds ringed) across multiple seasons of successful and unsuccessful breeders ringed in 2005. Successful breeders (fitted with green rings) were defined as birds feeding chicks close to fledging. Unsuccessful breeders were birds ringed in a sub-colony at Mars Bay that had laid at the end of the breeding season in November 2005. Sooty terns require 94 days to incubate and successfully fledge a chick (Chapter 2). The sub-colony where the unsuccessful breeders were ringed was deserted in early January 2006 (Hughes & Bray 2005) before there was sufficient time for chicks to fledge. In following seasons if successful breeders had a higher re-capture rate than unsuccessful breeders, this might indicate that the former did not skip a breeding season. Conversely, if successful breeders had a lower re-capture rate this might indicate that they had skipped breeding and were, therefore, not present on the island to be re-captured.

4.3.8. Statistical analyses

An unpaired *t*-test was used to compare the earliest age of first breeding of Ascension birds with that of birds from other islands. An unpaired *t*-test was also employed to compare the number of breeding seasons for which birds deferred breeding between Ascension Island and other island populations. A Mann-Whitney *U*-test was used to compare re-capture rates of successful and unsuccessful breeders across multiple seasons.

4.4. RESULTS

4.4.1 Immigration and emigration

4.4.1.1. Inter-island movements – immigration. Of the 74 recruits captured across 14 breeding seasons, 72 were from 5,210 chicks ringed on Ascension (Table 4.2).

Table 4.2. Re-capturing efforts of sooty terns on Ascension Island across 14 seasons (June 2002 to December 2012 [inclusive]) giving numbers of birds ringed as chicks and re-captured as incubating adults in their natal colony (i.e. philopatric birds) and as immigrants. Totals and percentages of philopatric and immigrant birds are given. (Note: Just one immigrant was re-captured in both 2003 and 2008).

Date (month & year)	**Re-capture effort (hrs)**	**Number of birds ringed as chicks and re-captured as adult birds that were:**	
		philopatric	**immigrants**
Jun 2002	10	1	0
Apr 2003	19	1	1
Feb 2004	64	4	0
Nov 2004	32	1	0
Oct 2005	18	3	0
Aug 2006	55.75	7	0
May 2007	53.25	11	0
Feb 2008	70.5	5	1
Dec 2008	52	3	0
Oct 2009	22	2	0
Jun 2010	3	1	0
Mar 2011	81.5	1	0
Jan 2012	47	7	0
Dec 2012	166.75	25	0
Totals	**694.75**	**72 (97%)**	**1 (1%)**

Of the 9,482 chicks ringed on other Atlantic islands, one immigrant was re-captured twice on Ascension Island (Table 4.2). The first evidence that mixing of populations occurs was gathered on 24 April 2003 when a sooty tern carrying a Brazilian CEMAVE (Centro de Pesquisas para a Conservação de Aves Silvestres) ring number H25617 and ringed on 31 January 1993 in Fernando de Noronha, Brazil (03°54'S, 32°54'W) was re-captured on Ascension. The same bird was re-captured for a second time six breeding seasons later on 13 February 2008. On both occasions it was re-captured while incubating at Mars Bay. The distance between the respective nest sites occupied on Ascension in 2003 and in 2008 was 0.3 km and from the natal colony it was 2,200 km.

4.4.1.2. Inter-island movements – emigration. Of the 5,210 chicks ringed on Ascension, two are known to have dispersed. An emigrant ringed with ring number DD65851 as a chick at Mars Bay on 24 October 2005 was re-captured 2,200 km away while incubating on 20 July 2011 on Viuvinha Island, Fernando de Noronha, Brazil (03°54'S, 32°54'W; Fig. 4.3). One juvenile ringed with ring number DE28402 at Mars Bay on 13 October 2009 was recovered (alive but died a few hours later) as a 10-month old bird in a salt water lagoon on 17 July 2010 in Abidjan, Ivory Coast (05°19'N, 04°34'W), a distance of 3,000 km from Ascension.

Figure 4.3. Viuvinha Island, Fernando de Noronha, Brazil where one sooty tern that had emigrated from Ascension Island was re-captured. (Photo: P. Mancini).

4.4.2. Peer group and nest site-fidelity

Re-capture data provided evidence of peer group-fidelity. From the cohort of 500 birds ringed in February 2004 at Waterside, 36 were re-captured at Mars Bay while it was just seven birds at Waterside. From the cohort of 62 birds ringed in November 2004 at Waterside, 14 were re-captured at Mars Bay while none was re-captured at Waterside. The majority of both cohorts appear to have moved *en bloc* to Mars Bay suggesting peer group-fidelity. Between April 2003 and October 2005, inclusive, 476 birds were re-captured in the two colonies of Mars Bay and Waterside on Ascension. Of the 220 birds re-captured while incubating at Waterside, 36 (or 16.4%) were first captured while incubating at Mars Bay. Of the 256 birds re-captured while incubating at Mars Bay, 43 (or 16.8%) were ringed while incubating at Waterside. Seventy nine birds (or 16% of all re-traps) had moved between the colonies (Fig. 4.4). The number of birds that moved from Waterside, the larger colony (≈ 240,000 birds), to Mars Bay, the smaller colony

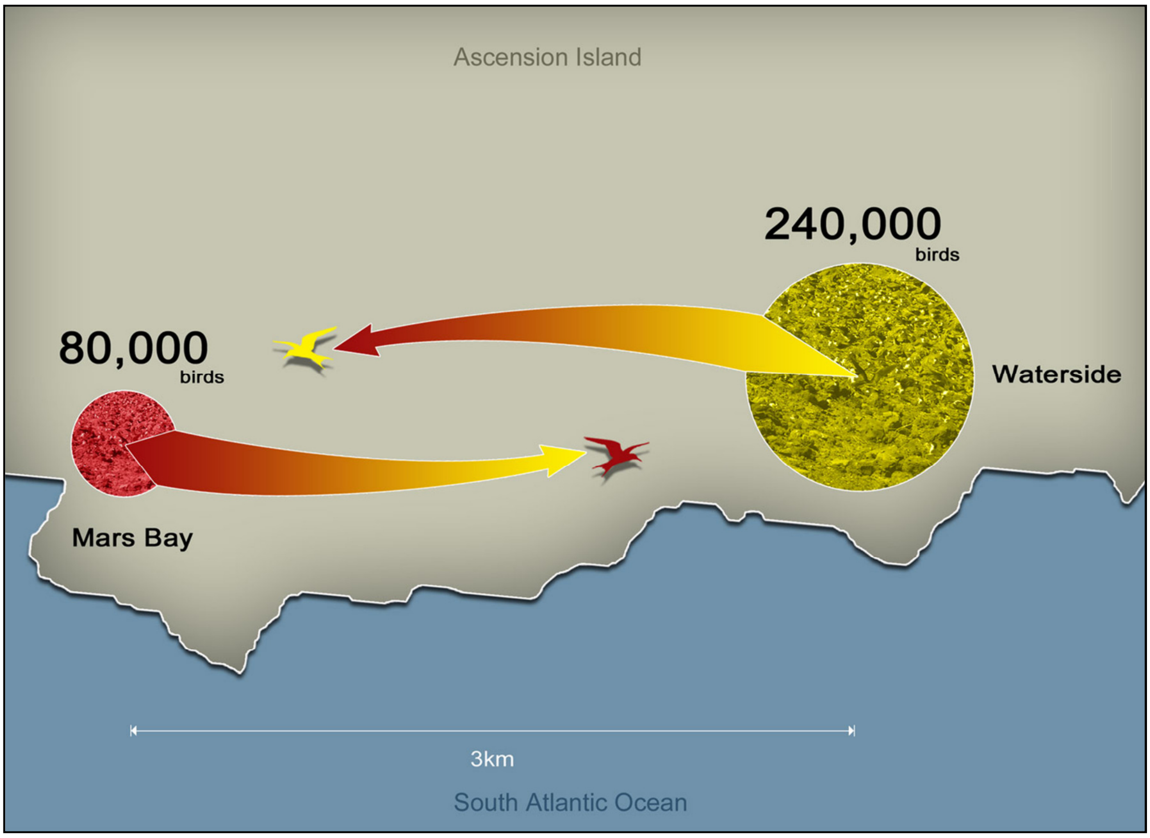

Figure 4.4. Sooty terns breeding on Ascension Island between 2003 and 2005 were not site-faithful – 16.8% of incubating birds re-captured at Mars Bay were ringed while nesting at Waterside and 16.4% of birds re-captured at Waterside had nested at Mars Bay.

(≈ 80,000 birds), between 2003 and 2005 was 27,000 greater than the number moving in the opposite direction. Inter-colony movements on Ascension rather than inter-island movements probably account for the significant increase and decrease in the population size at Mars Bay and Waterside, respectively (see Chapter 3).

4.4.3. Age at first breeding

Re-capture effort resulted in the re-capture of 443 birds (or 19.0%) of the 2,326 adults ringed and 81 birds (or 2.9%) of the 2,784 chicks ringed from matched cohorts of adults and chicks (Table 4.1). Despite intensive searches, juveniles did not return until they were 5 years old while adults from the matched cohort were re-captured each season (Table 4.3). The first three birds to breed from the 1998

Table 4.3. The re-capture history of sooty terns ringed as adults and as chicks on Ascension Island between June 1998 and August 2006. Searches for first-time breeders incubating eggs commenced four seasons after they fledged for birds ringed in June 1998. '-' refers to seasons when no re-captures took place. Searches for first-time breeders ringed as chicks in June 2002 to August 2006 commenced the season after they had fledged. (Note: Bold numbers indicate youngest age of first-time breeding; *one bird re-captured while flying (thus not confirmed breeding); **one bird re-captured in Brazil; light–yellow shaded cells denote season of low ringing effort; and dark-shaded cells denote season of first breeding.

Seasons after ringing	**Number of adults (A) and chicks (C) re-captured after ringing in:**									
	June 1998		**June 2002**		**April 2003**		**October 2005**		**August 2006**	
	A	**C**	**A**	**C**	**A**	**C**	**A**	**C**	**A**	**C**
1	-	-	1	0	34	0	15	0	11	0
2	-	-	7	0	10	0	17	0	21	0
3	-	-	1	0	8	0	21	0	16	0
4	1	0	2	0	13	0	15	0	1	0
5	1	0	2	0	20	0	2	0	1	0
6	7	0	1	0	17	0	0	**1**	11	0
7	7	**4***	3	**1**	24	**1**	14	3**	2	**1**
8	3	0	5	1	4	1	6	0	3	0
9	3	3	9	0	0	0	2	11		
10	5	8	4	0	9	1				
11	9	11	2	0	2	1				
12	6	9	13	0	17	5				
13	11	4	15	0						
14	4	1								
15	0	0								
16	1	0								
17	2	5								
18	2	9								

cohort and the first from the 2002, 2003 and 2006 cohorts started breeding seven seasons after fledging. Therefore, they appeared to have deferred breeding for the first six potential breeding seasons. One bird from the 2005 cohort started breeding six seasons after fledging and a further three recruits to the breeding population seven seasons after fledging. Only two birds were recorded breeding for the first time eight seasons after fledging. The mean interval between fledging and laying for the first time from each cohort was 1,960 ± 109 days (range: 1,699–2,042 days, $n = 7$) or seven breeding seasons. However, the interval between fledging and laying for the first time for the majority from each cohort was between nine and 12 breeding seasons (Fig. 4.5). Birds recorded as breeding for the first time at age 17 and 18 breeding seasons (Fig. 4.5) were assumed to have attempted to breed in previous breeding seasons but were not seen. The youngest age at first breeding in sooty terns on other islands has been recorded as 4 years on Johnson Atoll (Harrington 1974) and on the Dry Tortugas (Robertson & Robertson 1996), as 5 years on Saba Cay (Norton 1986) and as 3 years on The Seychelles (Feare & Doherty 2011). On Ascension the earliest age at breeding was 5.37 years ($n = 7$). The number of breeding seasons missed on

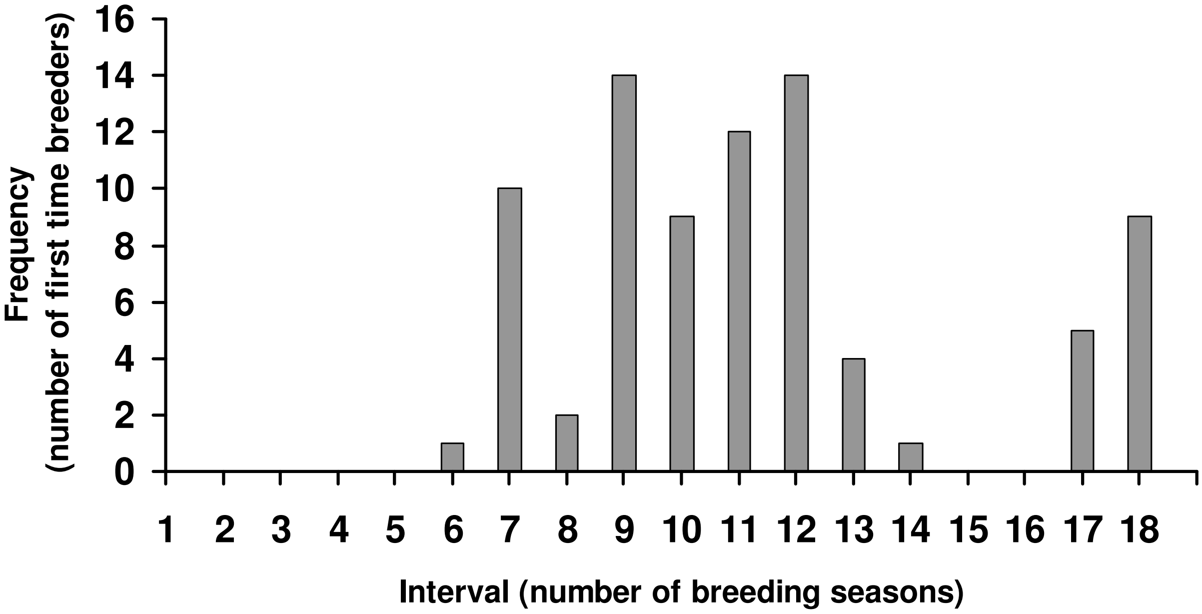

Figure 4.5. The frequency distribution of intervals (number of breeding seasons) between fledging and laying for the first time in sooty terns breeding on Ascension Island between 1998 and 2012.

Johnson Atoll, the Dry Tortugas, Saba Cay and on The Seychelles was three, four, four and two, respectively, while on Ascension it was six. This means that Ascension birds are significantly older at first breeding (unpaired *t*-test: $t = 4.05$, $df = 9$, $P = 0.003$) and defer breeding for more seasons (unpaired *t*-test: $t = 8.09$, $df = 9$, $P < 0.001$) than conspecifics elsewhere.

4.4.4. Longevity

On 25 June 2002 a bird with an American ring number 1013 13651 was re-captured while incubating on Ascension Island. The following season on 22 April 2003 another bird with ring number 1013 13584 was also re-captured on the island and re-ringed with a BTO ring (DD28149). Both birds were part of the sample ringed by Dr N.B. Gale with USFWS rings on Ascension Island during the early part of November 1975. The first tern captured was 26.5 years old and the second was 27.5 years old. The re-ringed bird was re-captured from the air for a second time on 29 March 2011 when it was 35.3 years old.

4.4.5. Skipped seasons by successful breeders

Sixty-three successful breeders and 311 unsuccessful breeders were ringed in December 2005 and some were re-captured during breeding seasons between August 2006 and January 2012. In August 2006, the first season after birds successfully bred (i.e. when skipped breeding was most likely to occur), the mean re-capture rates were 0.078 for successful birds and 0.029 for unsuccessful birds. The median re-capture rate across seven breeding seasons of sooty terns that had successfully raised a chick in 2005 was 0.047 and those that were unsuccessful was 0.027 but the difference was not significant (Mann-Whitney U-test: $U = 35$, $P = 0.21$).

4.5. DISCUSSION

The potential for avian populations to recover depends on the balance between immigration and emigration, and the intrinsic capacity (i.e. fecundity) for the population to reproduce. The central aim of my study was to quantify these vital life-history variables for the population of sooty terns on Ascension that has declined by 80% between 1958 and 1990 (Chapter 3). The above variables are essential for the analysis of population change and for predictions of population size. Here, I have shown that immigration to Ascension is minimal as only one immigrant was captured on the island. Because of this I argue that the population will be slow to recover because of the low capacity for the species to reproduce.

4.5.1. Immigration and emigration

Little is known about sooty tern migration but juveniles have been recovered > 1,000 km from their natal colonies in the Atlantic, Indian and Pacific Oceans (Schreiber *et al.* 2002). The live recovery of a 10-month old sooty tern in Abidjan indicated that Ascension Island juveniles may spend some time maturing in the Gulf of Guinea, which is where young birds from Dry Tortugas are also known to spend time (Robertson 1969). Previous reports suggested that the sooty tern population breeding on Ascension Island was totally isolated (Hughes *et al.* 2010); this no longer appears to be the case, immigration and emigration do occur but at a very low rate and immigration and emigration are not major regulators of the sooty tern population on the island.

4.5.2. Nest site and peer group-fidelity

In birds, males of many species compete over nest sites and whether individuals retain their nest site over multiple seasons is often determined by breeding success (Schreiber & Burger 2002). However, nest site fidelity does not appear to apply to sooty terns on Ascension Island. Inter-colony movements of terns on Ascension Island were initially identified from maps of the colony (Chapter 3). Most terns do not occupy the same nest sites in consecutive seasons. Mapping and census data have revealed changes in abundance at the two colonies. The population at Waterside, originally the larger of the two colonies, has declined in size as terns moved to Mars Bay. Although the colonies are more than 3 km apart, 16% of terns studied have nested at both. The Ascension population does not conform to levels of site fidelity found at other locations where sooty terns breed. Birds on Bird Island in The Seychelles tend to return to the same general area as in earlier nesting attempts but inter-annual changes in bird distribution do occur (Feare & Doherty 2011). On the Dry Tortugas Robertson and Robertson (1996) discovered that returning birds were highly site-faithful nesting each year within a 'neighbourhood' of only a few metres diameter. On Ascension, even successful breeders move between colonies and the mean distance between nest sites of successful breeders in consecutive seasons was 453 m ($n = 4$). Most sooty terns on Ascension thus re-located, albeit a few hundred metres, each breeding season (Chapter 3).

Peer group-fidelity was observed in the tern colony. Terns from the same location were ringed in groups of 50–100 (Chapter 2). When a ringed bird was subsequently re-captured, other ringed birds from that group were recorded in the vicinity, usually within a 10 m radius. The mass movement of terns ringed in 2004 from Waterside to Mars Bay in 2005 demonstrated high group-fidelity. These findings agree with those of Austin (1951) who suggested that peer group-fidelity in common terns *Sterna hirundo* is at times of more value than site tenacity in preserving populations. It appears that when colonies are forced to re-locate for a season or permanently (e.g. as a result of predation or other environmental changes such as the building of the airfield), they re-locate as a group. Hence, peer group-fidelity in the absence of nest site fidelity may well provide opportunities for information exchange and be essential to the survival of sooty terns on Ascension Island.

4.5.3. Age at first breeding

The reasons for the long period of immaturity in seabirds may be due to the time required to perfect foraging techniques, to attain physiological maturity and/or to learn to secure a mate (Schreiber & Burger 2002). However, it is more difficult to explain this variation in conspecifics breeding at different locations. The youngest first-breeding sooty terns (*n* = 7) on Ascension were 1.37 years (or 34%) older than the mean youngest age of sooty terns (*n* = 112) in The Seychelles (Feare & Doherty 2011). Twice as many birds from the 1998 cohort bred on Ascension for the first time 10–12 seasons after fledging than during the preceding four seasons (Table 4.3). Most sooty terns first bred on Johnson Atoll when 6–8 years old (Harrington (1974), in The Seychelles when 5–6 years old (Feare & Doherty 2011) and on Ascension Island when 8–10 years old (this study). The youngest first-time breeders on Ascension had two more deferred breeding seasons than sooty terns elsewhere in the world. Most first-time breeders returned to Ascension 3 years later than when most conspecifics elsewhere in their range returned. Life-history theory predicts that birds should begin breeding upon first reaching sexual maturity to maximise fitness (Newton 1998). Sooty terns are reported to reach sexual maturity at 4 years old (de Magalhaes *et al.* 2009). I have insufficient data to establish if sooty terns on Ascension are mature at 4 years or if they require more time to secure a mate than conspecifics elsewhere; it would seem unlikely. Seabirds that forage in waters of low productivity may require longer to perfect foraging techniques that will provide sufficient food for chick-rearing. The mean length of the incubation shift of individual sooty terns on Ascension is 132 hrs (n = 9; Ashmole 1963a) which is considerably longer than 24 hrs required by birds in The Seychelles and the 24-48 hrs of birds in the Dry Tortugas (Schreiber *et al.* 2002). This might suggest that Ascension birds require more time to find food and to perfect foraging skills, resulting in them deferring breeding for two or more breeding seasons beyond conspecifics breeding elsewhere.

4.5.4. Longevity

Theories of aging predict that deferred reproduction should be associated with reduced reproductive senescence and increased longevity (Kim *et al.* 2011). In common guillemots *Uria aalge* lower levels of reproductive output early in life were associated with reduced senescence later in life (Reed *et al.* 2008). In black-legged kittiwakes *Rissa tridactyla* Wooller and Coulson (1977) found that birds which started to breed at older ages had higher survival rates with each breeding attempt incurring a survival cost to the individual. This suggests that deferred breeding may, therefore, serve to increase adult survival in sooty terns. Terns are long-lived birds and the oldest sooty tern recorded is 36 years (Schreiber & Burger 2002). The oldest known breeder on The Seychelles is 34 years old, on the Dry Tortugas it is 32 years old and in the Pacific Ocean it is 26.5 years old (Schreiber *et al*. 2002). During my study two sooty terns aged 26 and 27 years were re-captured while breeding and one of these lived to more than 34 years of age. Previous such records for sooty terns on Ascension were 16.5 years in 1942 and 18 years in 1944 (Cooke 1945). The meagre evidence collected on longevity of sooty terns on Ascension suggests that lower reproductive output earlier in life is not associated with reduced senescence. Common guillemots that experienced harsh environmental conditions early in life experienced increased rates of senescence (Reed *et al.* 2008). Further research is needed to establish if harsh conditions in the Atlantic have lowered life expectancy among birds in the Ascension population of sooty terns.

4.5.5. Skipped seasons by successful breeders

Many birds that breed successfully fail to breed in the following year (Wooller & Coulson 1977). If successful breeders skip breeding, this could reduce their lifetime reproductive success if it does not result in increased longevity. Birds that fail to breed may also defer breeding. Haas (1998) found that American robins *Turdus migratorius* and brown thrashers *Toxostoma rufum* subject to nesting failure returned at a significantly lower rate than birds that nested successfully. In the Dry Tortugas 42% of males and 45% of female sooty terns that failed to breed in one year did not breed in the following year (Robertson & Robertson 1996). However, in The Seychelles sooty terns were not known to skip breeding once recruited to the breeding population (Feare & Doherty 2004). On Ascension Island successful breeders were nearly three times (or 270%) more likely to be re-captured in the season following successful breeding than unsuccessful breeders.

This provides a good indication that most sooty terns on Ascension that have bred successfully did not skip breeding in subsequent seasons.

4.5.6. Future directions

In wild bird populations on average males outnumber females by around 33% (Donald 2007). I found similar results on Ascension in a sample of 988 sooty terns that were sexed using morphometric measurements (Reynolds *et al.* 2008). Males outnumbered females by 40%. Further research is needed to establish if this sample is representative of the adult sex ratio of the population or that males were more involved than females in incubation and chick provisioning. Further searches for sooty terns elsewhere in the Atlantic would provide welcome insights into emigration from Ascension. Identifying the causes of inter-colony movements and length of the deferred breeding period of sooty terns on Ascension has the potential to indicate environmental factors limiting the size of the sooty tern population and is an exciting avenue for future research. Here, I have shown that Ascension sooty terns are slow to mature and their reproductive rate is low. Sooty terns are well known for staying airborne for years (Schreiber *et al.* 2002) so it is of considerable interest to calculate the percentage of time the birds spend on land. If sooty tern mean longevity is 26 years, mean age at first breeding is 9 years and each adult is on the ground for ≈ 40 days each breeding season, sooty terns are on the ground for just 9% of their total lifespan. Clearly their ‘life on the wing’ should be one focus of future research efforts.

4.5.7. Conclusions

My findings indicate that there are few immigrants to the sooty tern population on Ascension and the potential for the population to recover is largely dependent on intrinsic factors and local recruitment. My results provide support for studies that have found that seabird populations are slow to recover following successful remedial conservation action (Gaston 2004). Sooty terns are *k*-selected, lay a single egg every 289 days and defer breeding for a minimum of six seasons. Thus, the maximum increase in the number of breeding birds would allow the population to double after eight breeding seasons. The intrinsic capacity for increase in sooty tern population size is significantly lower than that of most *r*-selected species. For example, the maximum possible annual increase in population size of blue tits *Cyanistes caeruleus* is between 10 and 12 times the current population size (Newton 1998). As immigration is minimal and the intrinsic capacity for sooty terns to reproduce is low, productivity rates are critical for maintaining and increasing the population size.

In Chapter Five I will quantify incubation, and nestling and breeding successes of sooty terns on Ascension Island.

(Note: Chapter 4 was published as part of Hughes *et al.* 2010).

Chapter 5

BREEDING SUCCESS AND PREDATOR-PREY INTERACTIONS IN THE SOOTY TERN COLONY ON ASCENSION ISLAND

5.1. ABSTRACT

The rate at which a population increases or decreases in size depends on breeding success and survival of individuals in the population and to a lesser extent on immigration/emigration. When seabirds reach breeding age their annual survival rates are relatively stable; in contrast, breeding success is subject to greater variation. Measuring fluctuations in breeding success is one of the preliminary stages in understanding the dynamics of avian populations. To determine the most important factors controlling breeding success of sooty terns on Ascension Island in 12 breeding seasons, I subdivided the breeding period into incubation, hatching, nestling and free-ranging chick stages and measured mortality in each. Of the eggs and nestlings that failed during the 36 days when nests were occupied, a large percentage (53%) was due to desertion. The remainder was down to interactions with mynas, rats, Ascension frigatebirds, conspecifics, eggs failing to hatch and 'other' factors. Historically, mynas and rats did not predate eggs or chicks but it appears that the nature of breeding failure has changed over time. Now, each tern breeding season 800–1,200 mynas on average consume 5,824 eggs, destroy a further 10,659 eggs without consuming them and cause another 3,808 birds to desert their nests. Many eggs missing from nests were taken by rats that rolled them to food caches. Mortality from adult and juvenile frigatebirds was 2,426 ± 1,400 and 258 ± 258 chicks, respectively. Between 1998 and 2011 incubation success rates were 0.61 ± 0.15 eggs and

nestling success rates were 0.54 ± 0.20 nestlings. Both were similar to survival rates of other seabird populations on Ascension and of conspecifics elsewhere. However, breeding success was 0.31 ± 0.21 fledglings/eggs laid and was below the average of conspecifics on other islands. I discuss directions for further investigation to study the impact of predation on population dynamics of seabirds.

5.2. INTRODUCTION

Successful management of species depends critically on understanding the ecological factors that shape population dynamics (Krebs 2001). For a population to persist, breeding success and pre-breeding survival rates need to be sufficient to replace adult losses (Nelson 1980, Newton 1998). Breeding success rates of pelagic seabirds (expressed as fledglings per egg) vary from total failure to 100% success in some seasons (Schreiber & Burger 2002, Gaston 2004, Ratcliffe *et al.* 2009). To determine the most important factor(s) controlling breeding success we can subdivide the breeding period into incubation, hatching, nestling and chick stages, and measure mortality in each (Gaston 2004). Furthermore, a better understanding of the dynamics of avian reproduction can be obtained by measuring seasonal difference in egg, nestling and chick survival (Ricklefs 1969, Swennen 1989, Cresswell 2008). Here, I estimate incubation, nestling and breeding success rates across multiple breeding seasons of sooty terns on Ascension in an effort to determine the major factor(s) limiting breeding success.

Breeding success in seabirds is influenced by many factors (Nelson 1980, Schreiber & Burger 2002) including interference by conspecifics, predation, accidental loss, desertion, infertility, hatching failure, adverse climate, body condition of adults, parasitism, disease (Newton 1998, Schreiber & Burger 2002) and sub-lethal effects of predation (Cresswell 2008). Identifying *when* failure occurs is fundamental to understanding the population biology of species. Losses at the incubation stage can amount to 28–48%, 27–31% and 8–44% in the northern fulmar *Fulmarus glacialis*, the European shag and the herring gull *Larus argentatus*, respectively, with the average incubation failure rate for most seabirds being between 30 and 50% (Nelson 1980). Approximately half of post-hatching mortality of seabird chicks occurs during the first week (Nelson 1980) with many due to predators and predation commonly accounting for more than 80% of all nest failures (e.g. Newton 1998). Predation can occur as a result of direct consumption of eggs or chicks or from killing without consumption (Martin 1993, Newton 1998, Cresswell 2008). Predation can also result from conspecific consumption (e.g. cannibalism by Australian pelican *Pelecanus conspicillatus*; Smith & Munro 2008). In much of the general ornithology and ecology literature (e.g. Welty & Baptista 1990, Krebs 2001), explanations of avian prey as a source of nutrients and energy predominates in understanding predation but it does not explain why eggs and/or chicks are not always eaten (Newton 1998). Red foxes *Vulpes vulpes,* stoats *Mustela erminea* and great horned owls *Bubo virginianus* kill many more birds than they eat (Welty & Baptista 1990). Identifying the proximate causes of these lethal interactions can provide a better understanding of the causes of nest failure and inform conservation action.

5.2.1. Desertion, infertility and infanticide

Common causes of egg and chick loss are desertion, infertility and infanticide (Newton 1998). Desertion often occurs when nests are likely to fail commonly as a result of predation or food shortages (Ricklefs 1969). Furthermore, male and female sooty terns share incubation duties and care of the chick (Ashmole 1963a, Dinsmore 1972). If one of the partners is lost or there is a divorce then the other partner may desert (Choudhury 1995). Human interference and adverse weather conditions can also stimulate birds to desert their nests. On tropical islands the sudden withdrawal of food due to oceanographic changes (e.g. ENSO in the Pacific and the North Atlantic Oscillation (NAO) in the Atlantic) commonly results in wholesale desertion of eggs (Nelson 1980). Severe ENSO events affected the Humboldt Current (20 times in the last 100 years) and have resulted in marked population crashes of seabirds (Schreiber & Burger 2002). Life-history theory predicts that parents should desert a reproductive attempt if the costs of rearing the brood exceed the expected benefits (Lack 1968, Trivers 1972).

Not all incubated eggs will hatch because some will be infertile. Hatchability is defined as the proportion of eggs surviving to the end of incubation that hatch (Koenig 1982). In over 155 studies Koenig (1982) found that hatchability was on average 90.6% of all eggs. Ricklefs (1969) suggested that in seabird colonies hatching failure is one of the most prevalent factors causing eggs to fail.

Infanticide is the intentional killing of infants (Pearsall & Trumble 1996). While a parent bird broods its own young in the nest, it treats those of conspecifics with little care and often drives them away aggressively if they encroach into its nesting territory. Consequently, some lost and wandering chicks are killed by nest-defending adults. For example, infanticide of young Dominican gulls *Larus dominicanus* by adults in New Zealand was estimated to be approximately 75% of the young (Welty & Baptista 1990). On the Isle of May in Scotland 69% of all observed common guillemot chick mortality was caused by infanticide (Ashbrook *et al.* 2008). It can be readily observed by trespassing into a colonially nesting seabird colony when chicks are hatching (BJH pers. obs.).

5.2.2. Identification of predators

Causes of nestling and chick losses can be difficult to detect and in some cases, nest losses attributed to predators are based on circumstantial evidence (Prieto *et al.* 2003, Drake & Hunt 2009). Larivière (1999) provided a number of circumstances when identification of nest predators from nest remains is problematic. Eggs and chicks are lost both during the day (Libsch *et al.* 2008) and at night (Carter *et al.* 2007), and in the tropics predators of the day and the night have approximately equivalent foraging times. There is a dearth of information on predators of tropical birds (Rebegen *et al*. 1998, Libsch *et al*. 2008) and the identification of their predator species may prove fundamental to advancing our knowledge.

5.2.3. Causes of sooty tern egg, nestling and chick losses

The sooty tern breeds in large colonies to which they return each breeding season, making it relatively easy to obtain information on breeding success rates (Schreiber & Burger 2002, Gaston 2004). Sooty terns do not build a nest and, thus, their eggs and nestlings are vulnerable to predation (Schreiber *et al.* 2002, BJH pers. obs.). The nest varies from nothing (e.g. egg laid on sand, volcanic dust, rocks) to a shallow scrape. Seabirds that nest in the centre of the colony have a better chance of breeding successfully than those that nest close to the edge (Wooller & Coulson 1977). In The Seychelles sooty tern egg and chick losses are greater at the edge than in the centre of the colony (Feare 1976). The bird lays a single egg which is incubated by both parents for 29 days (Schreiber *et al.* 2002). On Ascension the incubation shift can last between 4 and 7 days (Ashmole 1963a). Chicks are semi-precocial (Fig. 5.1) and are able to walk almost immediately post-hatching (Dinsmore 1972). The nestling is closely tended by adults (Fig. 5.1) for the first 3–4 days post-hatch and they are particularly aggressive during this period (Dinsmore 1972). After the first week parental attentiveness to the nestling diminishes and chicks begin to wander from their nest sites and congregate in crèches under rocks, vegetation etc. (Dinsmore 1972). Factors limiting breeding success change when the egg hatches, and as the nestling grows and becomes more agile. For example, larger chicks are able to avoid attacks from adult conspecifics (BJH pers. obs.). Causes of sooty tern egg, nestling and chick losses on Ascension were identified but not quantified by

Figure 5.1. A sooty tern nest with a chick tended by parents on Ascension Island in the south Atlantic. (Photo: D. Osborn).

Ashmole (1963a) and included desertion, killing by adults, predation by frigatebirds and starvation. Ashmole (1963b), Dinsmore (1972) and Feare (1976) recorded non-parental adult sooty terns killing chicks but its occurrence has never been quantified so its contribution to overall breeding failure remains unknown. On Ascension, in 1958 frigatebird predation of chicks was estimated at running into the thousands but other predator species (e.g. rats and mynas) were not considered a serious threat to breeding attempts (Ashmole 1963a).

5.2.4. Avian predators on Ascension

Frigatebirds are well known for their kleptoparasitism of other seabird species and for preying on hatchling green turtles *Chelonia mydas* (Niethammer *et al.* 1992, Weimerskirch *et al.* 2004). The endemic Ascension frigatebird is also a kleptoparasite and a biannual breeder (Ratcliffe *et al.* 2008) that nests primarily in a single colony on BBI (Fig. 1.1) some 15 km around the coastline from where they predate chicks in the tern colony. Frigatebirds lay a single egg and chicks begin to fly during their sixth or seventh month (Stonehouse & Stonehouse 1963). At 8 and 9 months juveniles are able to leave the natal site for several hours at a time but they remain partially dependent on the adults for a long period possibly to attain proficiency in flying and foraging techniques (Stonehouse & Stonehouse 1963). There is relatively little information on the frequency or details of frigatebirds depredating native seabirds. Ashmole (1963b) reported significant mortality by frigatebirds on young sooty terns from the time of hatching until they are too big to swallow at perhaps 4–5 days of age; frigatebirds also harass adult sooty terns which sometimes results in them deserting their nests.

Mynas are omnivorous (Feare & Craig 1998) and their presence is known to compound the survival pressures on native avifauna through competition for resources, in particular nest sites (Peacock *et al.* 2007, Blackburn *et al.* 2009). Mynas also predate eggs and nestlings (Lever 1987, Feare & Craig 1998) and are noted for their detrimental impact on native avian communities, particularly on tropical islands (Lowe *et al.* 2000). Mynas are potent adaptors to local food sources which they can exploit with efficiency (ISSG 2011b). They are prolific scavengers (Feare & Craig 1998) and take many deserted eggs on Bird Island in The Seychelles (Schreiber *et al.* 2002). On Ascension they have been seen foraging on dead sheep *Ovis aries* and sooty terns, and on green turtle hatchlings (BJH pers. obs.). Mynas commonly nest in tree cavities and man-made structures (Feare & Craig 1998). On Ascension they were seen nesting underground at the municipal rubbish dump (BJH pers. obs.). Most mynas roost on Green Mountain (Fig. 1.1) approximately 4 km from the tern colony (BJH pers. obs.). Although accidental visitors to the island cattle egrets *Bubulcus ibis* and ruddy turnstones *Arenaria interpres* (McCulloch 2004) are known to predate sooty tern eggs on the Dry Tortugas (Parkes *et al.* 1971, Dinsmore 1972), but there are no reports of these species in the tern colony on Ascension.

5.2.5. Mammalian predators and decapods

Non-native mammalian predators are the cause of most seabird predation on islands (van Aarde 1983, Atkinson 1985, Nogales *et al.* 2004) undergoing many lethal interactions with both eggs and chicks (e.g. Atkinson 1985, Jones *et al.* 2008, Mulder *et al.* 2011). Ground-nesting seabirds on islands have suffered greatly from non-native predators because they lack appropriate responses (behavioural and otherwise) against them (Blackburn *et al.* 2009, Jones 2013, Miles *et al.* 2013). During the last 300 years three non-native predators in the form of domestic cats, black rats and mice were introduced to Ascension Island (Ashmole & Ashmole 2000). Feral populations of all three species were soon established apparently leading to a decline in the size of seabird populations (Stonehouse 1962a). Darwin visited Ascension in 1836 and referred to the cats as a “great plague” (Darwin 1844) as they took adult seabirds and large chicks. However, cats are ambush predators and are not known to be common nest predators (Gillies & Clout 2003, Medina *et al.* 2006). Feral cats were eradicated from Ascension between 2002 and 2004 which was midway through the study period. Black rats and mice are omnivorous (Meehan 1984), with the former well known predators of eggs of domestic chickens *Gallus domesticus* (Meehan 1984) and chicks of burrow-nesting seabirds (Jones *et al*. 2008, Ruffino *et al.* 2009), and are associated with the decline of many seabird populations (i.e. terns, noddies and tropicbirds; Towns *et al*. 2006). Mice also predate eggs (Cuthbert & Hilton 2004) and chicks (Wanless *et al.* 2007). On Ascension rats and mice are present in high densities (in some years in plague proportions) in areas of human habitation and on Green Mountain (Fig. 1.1) but in much lower densities on the barren coastal plain (Davies 1966).

Decapods are known to be important scavengers in tern colonies (Feare 1976) but there are few records of them predating eggs or nestlings. On Ascension native decapods in the form of landcrabs *Gecarcinus lagostoma* (Hartnoll *et al.* 2006) and the Ascension Island rock crab *Grapsus adsensionis* (H. Nash pers. comm.) have been seen predating seabirds. Both species are occasionally found foraging in the sooty tern colony but are suspected not to be major predators (Hartnoll *et al.* 2006, BJH pers. obs.).

5.2.6. Prey and predator populations

The myna population on Ascension was estimated to contain 400 birds in 1958 (Stonehouse 1962a), 800 in the 1990s (Varley & Dickey 1994), 1,200 in the early 2000s prior to a cull (Saavedra 2009) and ≈ 600 in 2010 (Fig. 5.2). In 1995 the cat population was estimated to contain 600–800 animals (Bell & Ashmole 1995). In the vicinity of the sooty tern colony cats were found at a density of 6–20 cats per km^2 (Bell & Boyle 2004). Rat abundance within the tern colony, expressed as captures per 100 corrected trap-nights (C/100TN) (Cunningham & Moors 1983),

Figure 5.2. A flock of non-native common (Indian) mynas on the periphery of the sooty tern colony at Mars Bay on Ascension Island in the South Atlantic. (Photo: D. Foley).

was 0/100TN in 1992 (Merritt *et al.* 1992), 6/100TN in 1995 (Bell & Ashmole 1995) and 34/100TN in 2005 (Hughes *et al.* 2008). The number of frigatebirds on Ascension between 2001 and 2002 was approximately 6,250 breeding females (Ratcliffe *et al.* 2008). Between 1990 and 2012 the mean population size of sooty terns was 351,000 range 138,000 to 535,000 birds (Fig. 3.5).

5.2.7. Incubation, nestling and breeding success rates – objectives

Few data are available on the incidence of egg and chick losses of tropical bird species and the relative importance of different predators (Libsch *et al.* 2008). Age-specific demographic rates and a better understanding of the level of fatal predator-prey interactions during breeding attempts of tropical seabird species will allow identification of some of the major factors limiting the size of tropical seabird populations (Croxall *et al*. 2012). Parkes and Avarua (2006) completed a feasibility study to eradicate mynas on Mangaia Island and found few studies that give reliable measures of the lethal and non-lethal effects of mynas on other bird species. The high abundance and visibility of sooty terns (Fig. 3.1) on Ascension provide a study system where assessment of the breeding failure of a colonially nesting tropical seabird species is feasible. Incubation, nestling, chick and breeding success rates will facilitate conservation management action to prevent further decline in the sooty tern population on Ascension. In this study I used 12 seasons of nest, predator and chick monitoring records in order to: (1) calculate incubation, nestling, chick and breeding success rates; (2) quantify breeding failure attributed to desertion, and predation from mynas, rats and frigatebirds; (3) quantify lethal interactions of mynas with sooty tern eggs; (4) evaluate frigatebird predation of chicks; and (5) establish if loss of eggs, nestlings and chicks were major factors limiting the size of the breeding population.

5.3. MATERIALS AND METHODS

5.3.1. Study area and time

The study areas are described in section 2.2.1. Data were collected during fieldwork conducted between 1998 and 2012. Dates of most field seasons coincided with the peak breeding season of sooty terns.

5.3.2. Identifying predation by mynas and rats

The key to quantifying egg and nestling failures was to identify reliably the source of lethal interactions (Atkinson 1985). At the start of the study period telescopes in hides were used to observe mynas in the colony. Areas where predated eggs were observed were inspected and damage to eggs noted and categorised. Scavenging was defined as the act of eating deserted eggs, predating as the act of opening a egg (assumed to be viable as incubating sooty terns were in adjacent nests) and eating some (usually < 10%) or all of the contents, puncturing as the act of pecking at an egg to inflict a single small hole in it, thereby destroying but not consuming the egg contents.

The cause of the occasional disappearance of eggs from nests between 1990 and 2003 was not diagnosed until rats were seen in the tern colony. To confirm rat predation of seabird eggs, traps were set to catch rats (see Hughes *et al*. 2008 for details), signs of rat predation were monitored and the literature was searched for reports of rats taking eggs. Rats were monitored at night in the tern colony at Mars Bay twice in 2006 when image intensifiers were used from

1900hrs to 0700hrs GMT. Sporadic searches for rat food caches in the tern colony were also conducted.

5.3.3. Egg losses

Each breeding season sooty tern incubation success was measured for approximately half of the 29-day incubation period and calculated using the Mayfield method (Johnson & Shaffer 1990). Eggs were monitored by marking nest sites with numbered plastic tags and following their fate for the duration of the field season. Each season approximately 100 nest sites were marked in this way and then checked every other day. Failed eggs were classified according to whether they were lost as a result of myna predation, rat predation, desertion or other factors. Nest sites were monitored at less than 7 m from the periphery and in the core of the colony. Nest sites were marked in sets of 10–20 nests in close proximity (< 25 m) to each other positioned randomly in two well-established and in two new sub-colonies at Mars Bay and Waterside colonies. Each breeding season I estimated the number of nest sites which were on the periphery and in the core of the sub-colonies. Incubation success was determined from the formula:

$$Inc = [(S_c \times B_c) + (S_p \times B_p)] / B_t \qquad \text{(Eqn 5.1)}$$

where Inc is incubation success rate, S_c is the pooled estimate for egg survival in the core, B_c is the number of birds breeding in the core, S_p is separate estimates for egg survival at the periphery, B_p is the number of birds breeding in the periphery and B_t is the total number of breeding birds. Eggs that had small holes were attributed to myna predation (Fig. 5.3) and eggs missing from the nest were

Figure 5.3. Sooty tern eggs on Ascension Island punctured but not eaten by common mynas. Note the puncture holes made by mynas at the blunt end of each egg. Scale bar is approximately 50 mm in length. (Photo: B.J. Hughes).

attributed to rat predation (Figs 5.4 & 5.5). Dawn and dusk watches established the times of arrival at, and departure from, the tern colony of mynas and records were kept of their occurrence. Other factors may have included eggs predated by cats (Moors & Atkinson 1984). It is likely that a few smashed eggs were wrongly categorised as they may have been recorded in an ‘Other factors’ category unless myna predation was observed in their vicinity; if the latter then the smashed eggs

Figure 5.4. A rat food cache containing > 30 predated sooty tern eggs with most containing well-developed embryos. The cache was found between rocks in the tern breeding colony at Waterside on Ascension Island in the South Atlantic in 2006. (Photo: M. Vincent).

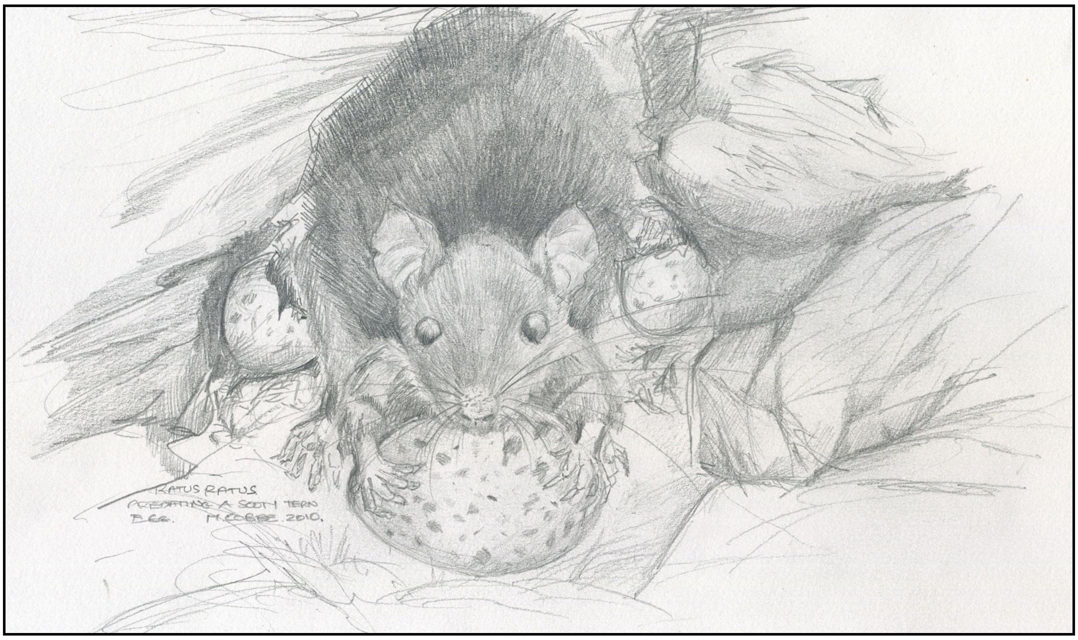

Figure 5.5. Artist's impression of a black rat rolling a sooty tern egg backwards into a food cache between rocks prior to opening the egg on Ascension Island in the South Atlantic. (Source: M. Cobbe).

indicated eggs lost to myna predation. Food shortages, predators and arthropod parasites are known to cause seabirds to desert (Feare 1974) and eggs without an adult in attendance were recorded as being lost to desertion by adults. This total seasonal incubation success rate does not take into account the fact that some birds will re-lay and fledge a chick. Fertility of sooty tern eggs was not determined in the field because of time constraints and ethical considerations but a mean hatchability rate (i.e. 0.906; Koenig 1982) was used to calculate hatching success (i.e. hatching success = incubation success × 0.906).

5.3.4. Nestling losses

Between hatching and approximately 7 days of age nestlings are lost to frigatebirds (Fig. 5.6) and also to neighbouring adult terns (Ashmole 1963a).

Figure 5.6. Five juvenile Ascension frigatebirds resting in the sooty tern colony in 2012 where they were learning foraging skills while hunting sooty tern chicks on Ascension Island in the South Atlantic. (Photo: M. Cutts).

Thereafter, chicks are larger, more agile and leave the nest to form crèches. Observers recorded the numbers of male, female and juvenile (sub-adults and immatures) frigatebirds as classified by Harrison (1983) that were hunting over the tern colony (Fig. 5.6). On occasions records of frigatebirds irrespective of age or sex were also recorded. Timed counts of the number of chicks predated and the number of hunting frigatebirds were logged sporadically during visits to the tern colony. In the evenings frigatebirds seen passing over the tern colony on their return to BBI were not counted. Records were compiled at hourly intervals covering the period of daylight. Estimates of consumption of sooty tern chicks by adult and juvenile frigatebirds were calculated using a formula developed by the US Department of Agriculture (APHIS 2007):

$$C = [(N_A \times S_A) + (N_J \times S_J)] \times D \qquad \text{(Eqn 5.2)}$$

where C is the number of sooty tern chicks predated per breeding season, N_A and N_J the average number of adult and juvenile frigatebirds, respectively, hunting during daylight hours, S_A and S_J the capture success rate (sooty tern chicks captured per hour) of adult and juvenile frigatebirds, respectively, and D is the number of days sooty tern chicks < 7 days of age are present in a breeding season.

Field records where the age of frigatebirds had not been noted provided independent data to check the above calculation. This estimate used the hourly average number of all frigatebirds, where the age of the frigatebird had not been noted, hunting and their success rates. Capture rates of chicks by adult and juvenile frigatebirds were obtained by intense observation periods of individual birds and a success rate per hour was calculated. Many captured chicks were dropped because they were too large to eat; a ratio of chicks dropped and consumed was, therefore, calculated.

Infanticide by adult sooty terns was difficult to assess because it increases enormously as a result of human presence within breeding colonies. Chicks were seen to flee when humans approached within 3 m of the nest. Fleeing chicks were savagely pecked by neighbours and in many cases failed to return to the safety of their nest when the intrusion ceased. To reduce the number of chicks being repeatedly pecked, sections of the colony containing newly hatch chicks were deliberately avoided during fieldwork. To quantify the level of mortality from infanticide, counts of newly hatched dead chicks (P1 size; Fig. 4.2) were conducted in 10 m-wide strips around the perimeter of sub-colonies. The strip width was quantified by eye and newly hatched dead chicks within the core of the colony were not counted.

Records of predation attempts by the Ascension Island rock crab and landcrabs were noted but predation by decapods was not monitored systematically.

5.3.5. Breeding success

Seasonal breeding success rates were calculated from seasonal means of egg and ready-to-fledge chick densities in quadrats (Bibby *et al.* 2000, Schreiber & Burger 2002). Mean egg density was assumed to be to be equal to AoN density as 99.9% of nests contained just one egg (Chapter 3) and was obtained from counts of AoNs in sub-colonies where sooty terns were incubating (Table 3.1). Counts of chicks were made in sub-colonies where chicks were about to fledge, most commonly at the Waterside colony. When field seasons coincided with chicks fledging, square quadrats that varied in area between 9 and 100 m^2 were marked in the sub-colony containing ready-to-fledge chicks. Each corner of the square was marked with white mine tape tied to a small rock or canes with white mine tape. The squares were set out and left undisturbed for a minimum of 2 hours before counting commenced using binoculars from a concealed elevated vantage point. The number of chicks in each quadrat was counted on two to eight occasions and the mean count used to determine breeding success.

Where ready-to-fledge chicks were found in small sub-colonies (area < 2,500 m^2), a previously unreported method of determining their density was used. The area of the sub-colony was determined using GPS. As many chicks, as could be caught in the sub-colony, were ringed and the number recorded. On the following day between 10 and 23 counts of chicks with rings and those without rings were recorded using a telescope or binoculars from a concealed elevated vantage point and the ratio of un-ringed to ringed chicks determined. Density of ready-to-fledge chicks was determined from the formula:

$$D = [R + (R \times C_2 / C_1)] / A \qquad \text{(Eqn 5.3)}$$

where D is the density of ready-to-fledge chicks per m^2, R is the number of ready-to-fledge chicks ringed in the sub-colony, C_2 is the number of un-ringed chicks counted the following day in the sub-colony, C_1 is the number of ringed chicks counted the following day in the sub-colony and A is the area of the sub-colony in m^2.

In 2005 and 2009 chick survival was determined from ringing chicks and from the recovery or re-capture of these chicks. In 2005 chick survival was determined from Capture Mark Recovery (CMR) of 596 chicks (Robinson 2010). Chicks were aged according to plumage development criteria (Feare 1976; Fig. 4.2). The chicks aged 19–36 days were ringed with red colour rings and later dead chicks with red rings were recovered. In the 2009 breeding season 50 chicks aged 9–20 days were ringed with blue colour rings. The fate of the cohort was monitored at intervals and chick survival was calculated for a period of 59 days (i.e. from leaving the nest to fledging; Table 2.5).

In 2008 the colonies were surveyed a second time during a brief visit at the end of the breeding season when following a visual inspection sub-colonies were categorised as either: (1) successful (i.e. nearly all nestlings had survived to fledge); (2) 80% successful (i.e. 80% of nestlings had survived to fledge); (3) 20% successful (i.e. 20% of nestlings had survived to fledge); or (4) complete failure. This holistic approach to determining fledging success was facilitated by the large number of sub-colonies that had completely failed.

5.3.6. Statistical analyses

A Chi-squared test with a Yates' correction (for 1 *df*) was used to determine whether more nests failed on the periphery than in the core of the breeding colony. Chick survival estimates in 2005 were calculated using 'dead recoveries Seber' with the pre-defined model in the programme MARK and in 2009 re-encounters of re-captured chicks and dead recoveries were analysed with MARK using pre-defined models – survival rate estimation with capture-recapture data in GFortran (Win32) Vers. 7.0 (Cooch & White 2007).

5.4 RESULTS

5.4.1. Identifying predation by mynas and rats

Mynas were observed interacting with sooty terns by scavenging, predating and puncturing their eggs, and harassing birds to cause them to desert eggs. Mynas puncture eggs that are attended by adult sooty terns (BJH pers. obs.). Some of the deserted eggs in the colony occurred at the same time as eggs at adjacent nest sites were predated and, therefore, it would appear that their predation by mynas causes birds in close vicinity to desert their eggs.

No evidence or sightings of rats were recorded in the tern colonies prior to 2004. Subsequently, rats were seen in the colonies at ever-increasing frequencies and were regularly trapped in the tern colonies (The increase in frequency is quantified in the following chapter). Rats appear to time their breeding season with that of sooty terns as juvenile rats and pregnant females were trapped in the tern colonies. The use of Image intensifiers in an attempt to observe rats predating eggs was unsuccessful. More than 12 rat food caches were found; one of the food caches at Waterside was exposed in 2006 and was found to contain > 30 eggs (Fig. 5.4). Caches were located under rocks and in crevices on the periphery of the colony. Six caches were examined and all contained eggs that had been opened suggesting that the caches were used as covered environments for feeding and not for food hoarding.

5.4.2. Incubation success

I monitored 1,388 nests across 12 seasons. Of the 920 nests (6,658 nest days) monitored < 7 m from the perimeter of the colony, 396 failed, and of the 468 nests (4,137 nest days) in the core of the colony, only 44 nests failed. Thus, the proportion of nest failure at the periphery of the colony during the 29 days of incubation was significantly greater than in the core of the colony (mean whole egg stage survival rate in core: 0.73 ± 0.20, $n = 11$; at periphery: 0.27 ± 0.21, $n = 11$; $\chi^2 = 92.03$, $P < 0.01$). Nests were not monitored on the periphery in 1998 and they were not monitored in the core in 2003. As so few nests were lost in the core of the sub-colonies, a single incubation success rate of 0.73 ($n = 11$ breeding seasons) was used to calculate total colony incubation success. On the periphery of the colony incubation success ranged from 0.01 to 0.85 across breeding seasons. Total colony incubation success rate between 1998 and 2011 for the whole egg stage varied between 0.21 and 0.91 (mean: 0.61 ± 0.15, $n = 12$; Fig. 5.7).

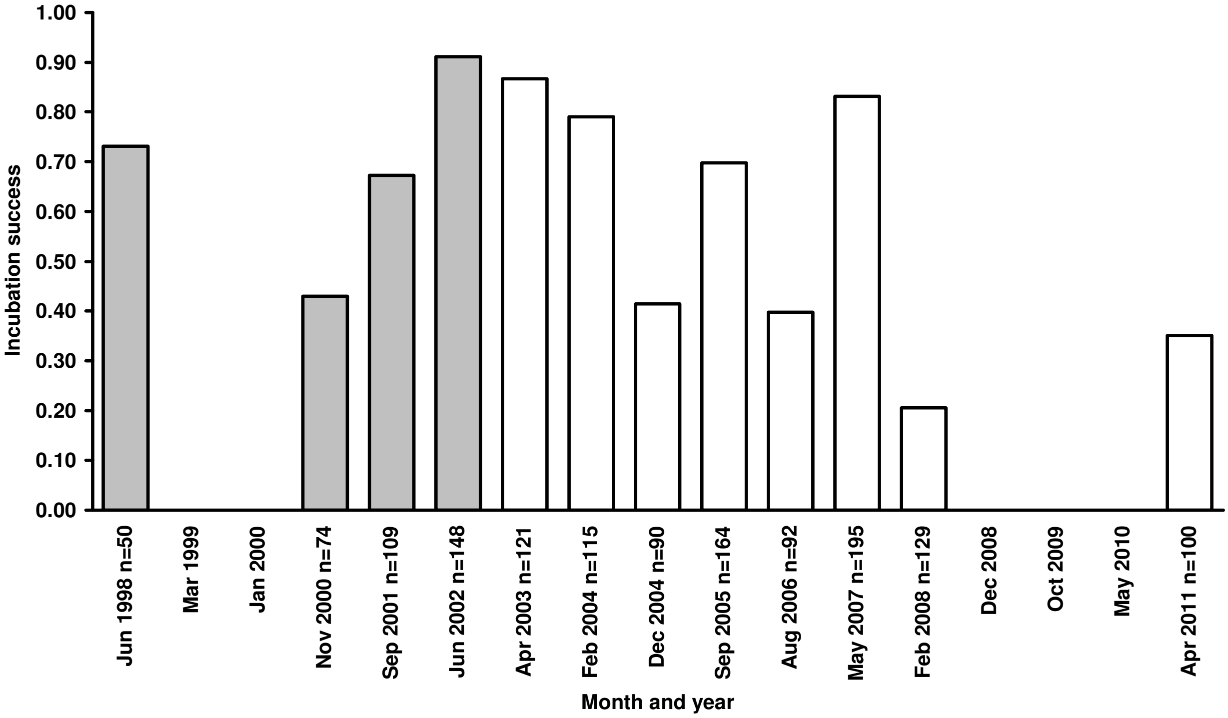

Figure 5.7. Incubation success rate of sooty terns breeding before (grey bars) and after (open bars) cats were eradicated from Ascension Island. Note that the sub-annual breeding cycle results in birds breeding twice in 2000, 2004 and 2008. The number of nests marked with plastic numbered tags (*n*) each season is placed at the base of each bar. In total, 1,388 nests were marked.

Of the 381 nests monitored in the four seasons prior to cat eradication, 118 (or 31%) failed. Of the 1,007 nests monitored in the eight seasons post-cat eradication, 322 (or 32%) failed. The mean egg survival rate pre-eradication was 0.69 ± 0.29 (*n* = 4 field seasons) while post-eradication between 2003 and 2011 it was 0.70 ± 0.20 (*n* = 8 field seasons). Thus, there was little difference in the total number of eggs lost following the eradication of cats. The mean egg failure rate due to rat predation pre-cat eradication was 0.24 ± 0.18 (*n* = 4 field seasons) and post-eradication it was 0.27 ± 0.20 (*n* = 8 field seasons); they were not significantly different (unpaired *t*-test: *t* = 0.27, *df* = 10, *P* = 0.79) . In the pool of 440 eggs that failed during the 12 breeding seasons of monitoring, I attributed 252 (or 57%) to adult desertion, 97 (or 22%) to predation by mynas, 71 (or 16%) to predation by rats and 20 (or 5%) to other factors.

5.4.3. Egg predation by mynas

Predation from mynas was not random. Sets of nests were either heavily predated or, more often, not predated at all. At any one time the maximum number of mynas seen in the sooty tern colony was 21 (mean: 4.38 ± 0.49, *n* = 72 visits). Mynas were observed in the colony on 136 (or 59%) of 229 visits made. Only 0.5% of the 800–1,200-strong myna population was found regularly in the colony at any one time. In 2004 I recorded the arrival of the first myna in the colony at 0700hrs GMT a few minutes after dawn and mynas were still in the colony at 1900hrs GMT with dusk being at 1945hrs GMT. The mean egg stage failure rate from myna predation in the core was 0.02 ± 0.02 nests (*n* = 10 field seasons) and at the periphery it was 0.30 ± 0.06 nests (*n* = 10 field seasons). The number of eggs destroyed per season varied between 2,443 and 35,970 (mean: 16,483 ± 3,366 eggs, *n* = 10 field seasons), while the mean failure rate of eggs from myna predation was 0.094 ± 0.019 (n = 10 field seasons). Monitoring of myna predation in the tern colony was suspended in 2011 following a myna cull (Saavedra 2009). Of the 16,483 eggs lost per season, I estimated that mynas punctured 10,659 (Fig. 5.3) and predated a further 5,824 eggs.

5.4.4. Nestling losses to frigatebirds

Adult male and female, and juvenile frigatebirds were observed taking nestlings (BJH pers. obs.). Occasionally, in small sub-colonies where predation by frigatebirds was heavy the remaining birds deserted (Ashmole 1963b, BJH pers. obs.). The mean numbers of adult, juvenile and unknown-age frigatebirds hunting per hour in the sooty tern colony are shown in Table 5.1. Numbers were obtained from 195 field observations recorded by seven different observers on 69 days during field seasons from 1996 to 2009. The time interval between the first and last sooty tern eggs to hatch was 58.8 ± 14.3 days (section 2.4.4.2). Nestlings were captured by frigatebirds for ≈ 66 days (58.8 + 7 days at which age chicks are too large to capture). Mean capture rates (chicks captured per hour) of adult (1.23 ± 0.71), juvenile (0.22 ± 0.22) and unknown age (0.58 ± 0.26) frigatebirds were obtained from 42 timed counts. Nestling mortality per breeding season from adult and juvenile frigatebirds was 2,426 ± 1,400 and 258 ± 258 nestlings, respectively. Total mortality by frigatebirds was 2,725 nestlings (Eqn 5.2) or 0.02 ± 0.01 of the nestling population per breeding season. Some data were collected that did not distinguish between age categories of hunting frigatebirds which indicated that frigatebirds consumed 2,370 ± 1,062 chicks, thus validating the results from the independent calculation of predation by adult and juvenile frigatebirds. Not all tern chicks captured by adults were swallowed by them with a third (0.35 ± 0.32 chicks

Table 5.1. Diurnal patterns of hunting of sooty tern chicks by adult (A), juvenile (J) and unknown age (U) frigatebirds on Ascension Island in the South Atlantic between 1996 and 2009. Table shows mean numbers of frigates hunting per hour, mean success rate (chicks captured per hour) and mean number of chick captured in hourly intervals during 66 days when chicks were available. UCL and LCL are upper and lower 95% confidence limits, respectively, of parameters.

Hourly intervals (hrs)	**Age**	**Birds hunting**	**Success rate**	**UCL**	**LCL**	**Chicks captured**	**UCL**	**LCL**
<0800	A	1.00	1.23	1.94	0.52	81.18	128.04	34.32
	J	0	0.22	0.44	0	0	0	0
	U	2.00	0.58	0.84	0.32	76.56	110.88	42.42
0800-0900	A	0.50	1.23	1.94	0.52	40.59	64.02	17.16
	J	0.20	0.22	0.44	0	2.90	5.81	0
	U	2.38	0.58	0.84	0.32	90.92	131.67	50.16
0900-1000	A	2.13	1.23	1.94	0.52	172.51	272.09	72.93
	J	2.00	0.22	0.44	0	29.04	58.08	0
	U	3.93	0.58	0.84	0.32	150.39	217.80	82.97
1000-1100	A	1.38	1.23	1.94	0.52	111.62	176.06	47.19
	J	0.75	0.22	0.44	0	10.89	21.78	0
	U	5.07	0.58	0.84	0.32	194.13	281.16	107.11
1100-1200	A	4.00	1.23	1.94	0.52	324.72	512.16	137.28
	J	3.73	0.22	0.44	0	54.21	108.42	0
	U	9.56	0.58	0.84	0.32	365.96	530.01	201.91
1200-1300	A	4.30	1.23	1.94	0.52	349.07	550.57	147.58
	J	2.10	0.22	0.44	0	30.49	60.98	0
	U	7.82	0.58	0.84	0.32	299.48	433.74	165.23
1300-1400	A	1.75	1.23	1.94	0.52	142.07	224.07	60.06
	J	2.00	0.22	0.44	0	29.04	58.08	0
	U	5.43	0.58	0.84	0.32	207.81	300.96	114.65
1400-1500	A	9.50	1.23	1.94	0.52	771.21	1216.38	326.04
	J	6.00	0.22	0.44	0	87.12	174.24	0
	U	10.71	0.58	0.84	0.32	410.14	594.00	226.29
1500-1600	A	2.00	1.23	1.94	0.52	162.36	256.08	68.64
	J	0	0.22	0.44	0	0	0	0
	U	4.00	0.58	0.84	0.32	153.12	221.76	84.48
1600-1700	A	2.00	1.23	1.94	0.52	162.36	256.08	68.64
	J	1.00	0.22	0.44	0	14.52	29.04	0
	U	7.00	0.58	0.84	0.32	267.96	388.08	147.84
1700-1800	A	0.33	1.23	1.94	0.52	27.06	42.68	11.44
	J	0	0.22	0.44	0	0	0	0
	U	4.00	0.58	0.84	0.32	153.12	221.76	84.48
>1800	A	1.00	1.23	1.94	0.52	81.18	128.04	34.32
	J	0	0.22	0.44	0	0	0	0
	U	0	0.58	0.84	0.32	0	0	0
Totals for:	**A**					**2,426**	**3,826**	**1,026**
	J					**258**	**516**	**0**
	U					**2,370**	**3,432**	**1,307**

from *n* = 3 timed counts) dropped to attending juveniles. Across the study period counts of frigatebirds hunting chicks were made in all months of the year and peak counts of hunting frigatebirds occurred in February. Peak counts during the day occurred between 1100 and 1500hrs GMT (Table 5.1) when both adults and juveniles were foraging in the tern colony. Few juveniles foraged before 0900hrs and after 1500hrs GMT. Twice as many frigatebirds were hunting between 1100–1500hrs GMT than in the morning or late afternoon (Table 5.1).

5.4.5. Infanticide by conspecifics and decapods

Counts of dead chicks were monitored in a strip around the perimeter of four sub-colonies in 2005. The mean count per hectare was 59.46 ± 34.02 dead chicks (*n* = 4 sub-colonies). The total area of the tern colonies was 11.36 ha (Table 3.4) and total number of chicks killed by adults was approximately 675. On Ascension where the sooty tern breeding population was > 150,000 pairs, killing by conspecific adults is a very small percentage of total mortality. During the whole of the study period decapods were seen to depredate just two chicks.

5.4.6. Nestling survival rate

Between 1998 and 2011 nestling survival rate was 0.54 ± 0.20 nestlings per egg laid and was obtained by applying a hatchability rate of 0.91 (after Koenig 1982), a survival rate from frigatebird predation of 0.98 nestlings per egg laid and a survival rate from conspecifics killing of 1.00 nestling per egg laid to the incubation success (see section 5.4.2).

5.4.7. Causes of egg and nestling failures

The causes of failure of breeding attempts during the 36 days when eggs were incubated and nestlings brooded were desertion (53%), mynas (16%), rats (12%), frigatebirds (5%), conspecifics (1%) and other factors (4%). The remaining 9% of failures were due to eggs failing to hatch.

5.4.8. Breeding success

During four breeding seasons between 2006 and 2012 the mean breeding success rate was 0.31 ± 0.21 fledglings per egg (range: 0.12–0.40 fledglings per egg, *n* = 4 seasons; Table 5.2).

Table 5.2. Breeding success rate (fledglings/eggs laid) with number of quadrats sampled and 95% confidence limits (CL) of sooty tern chicks calculated from fledgling and AON densities taken between 2006 and 2012 in Mars Bay (M) and Waterside (W) colonies on Ascension Island in the South Atlantic.

Breeding season	Colony	Fledgling density (per m^2)	AON density (per m^2)	Breeding success rate	Number of quadrats	95% CL
2006	W	0.549	1.41	0.39	7	0.19
2007	M	0.520	1.28	0.40	8	0.25
2009	M & W	0.179	1.53	0.12	5	0.06
2012	W	0.586	1.83	0.32	9	0.23

The estimate of breeding success in 2008 using a holistic approach (see section 5.3.5) was 0.31. In 2005 of the 596 chicks ringed, 133 chicks were recovered dead. In 2009 at the end of the 32 day-study period of the 50 chicks ringed, 12 were re-captured, seven were recovered (i.e. dead) and 31 were not found. The survival rate of chicks (from leaving the nest to fledging) in 2005 was 0.30 ± 0.24 and in 2009 it was 0.45 ± 0.20 fledglings per nestling. These survival probabilities should be considered as a conservative estimate due to unknown, although I suspect not negligible, numbers of chicks that were dead but not found.

5.5 DISCUSSION

The central aims of this study were to identify predator species and the causes of egg, nestling and chick losses during the breeding attempts of sooty terns. A better understanding of these factors can assist with the recovery of the sooty tern population on Ascension and of other vulnerable species such as the endangered St Helena plover *Charadrius sanctaehelenae* or ‘wirebird’ that are known to be predated by rats (McCulloch 1992) and mynas (Rowlands *et al.* 1998). I found that predation by non-native rats and mynas was three times greater than that by native species, that decapods had little impact on egg and nestling survival, that myna and rat predation have the potential to limit (i.e. reduce below its carrying capacity) the size of the breeding population and that sooty tern incubation and nestling success rates were similar to those of many other seabird species. However, many chicks failed to fledge possibly as a result of starvation or predation by rats and breeding success rates were lower than annually breeding conspecifics on other islands throughout the species’ range and of other seabirds with stable population sizes.

5.5.1. Incubation, hatching, nestling and breeding success rates

The mean incubation success rate of sooty terns was 0.61 which is equivalent to that of annually breeding sooty terns on Manana Island in the Pacific Ocean during the 1970s (i.e. 0.30–0.84) and on Bird Island in the Indian Ocean in 1973 (i.e. 0.75 for eggs in the centre of the colony and 0.10 on the periphery) (Schreiber *et al.* 2002). Incubation success of sooty terns on Ascension Island in 1958 and 1959 when cats were the apex predator was 0.79 (*n* = 43 nests; Ashmole 1963a) but I found that there was no significant difference in incubation success rate following the eradication of cats. Incubation success of common terns varied between 0.57 and 0.89 and incubation success of roseate terns *Sterna dougallii* varied between 0.36 and 0.59 (Le Croy & Collins 1972). Incubation success rate of tropical sooty terns breeding on Ascension Island was similar to these two temperate nesting tern species suggesting that there was no latitudinal difference in this life-history trait.

Hatching success rate of Ascension Island sooty terns was 0.55 and Ascension white-tailed tropicbirds, masked and brown boobies, and brown noddies that all nested on offshore islets free of non-native predators were similar, having hatching successes of 0.51, 0.51, 0.50 and 0.47, respectively (Ratcliffe *et al.* 2009). The mean hatching success rate of annually breeding sooty terns elsewhere in their range was 0.53 ± 0.25 (*n* = 6 populations) (Schreiber *et al.* 2002). Hatching success of Ascension sooty terns was similar to that of stable populations of conspecifics and other seabird species which would suggest that incubation and hatching rates were not factors limiting their population size.

Ascension frigatebirds predated 2% of sooty tern nestlings and this contributed negligibly to overall mortality rates. This rate contrasted sharply with the observations of Megyesi and Griffin (1996) on Wake Atoll in Hawaii where great frigatebirds *Fregata minor* were responsible for 64% of the predatory behaviours directed towards brown noddies. My findings suggest that Ascension frigatebirds prefer other prey species and only take tern chicks on occasions.

Breeding success rate between 2006 and 2012 was 0.31 fledglings per egg. Ashmole (1963a) was unable to calculate breeding success in 1958 and 1959 but reported that it was extremely variable. Simmons (1994, pers. comm.) estimated that in 1993 110,000 chicks fledged translating into a breeding success rate of 0.55 fledglings per egg. The mean breeding success rate of conspecifics on islands elsewhere was 0.44 ± 0.21 fledglings per egg (range: 0.06–0.95 fledglings per egg, *n* = 9 datasets; Schreiber *et al.* 2002). Sztukowski (2011) reported sooty tern breeding success was 0.06 fledglings per chick on Wake Atoll in the Pacific Ocean where a management plan was in place to eradicate black rats in an attempt to improve sooty tern breeding success. A management plan to improve the breeding success of Ascension sooty terns may also be needed.

5.5.2. Predation by mynas

The justification for including mynas in the list of the top 100 of the world's worst invaders has been attributed, in part, to their detrimental impact on native avian communities, particularly on tropical islands (Lowe *et al.* 2000). Yet, there are few reports quantifying the level of their predation. On Ascension of eggs that failed mynas caused 22% to fail, they harassed sooty terns to the point of desertion (BJH pers. obs.) and they were the second biggest cause of nest failure after desertion. Sooty terns do not appear to have developed specific defence behaviours against this 'novel' predator (Miles *et al.* 2013). Grant (1982) saw mynas harassing black noddies and white terns as they brooded chicks and this resulted in nest failure. He also noted eggs of both species that had been punctured (see Fig. 5.3). The failure rates in my study are based on conservative estimates and are strikingly similar to the 21% failure rate recorded by Byrd (1979) for nests of wedge-tailed shearwaters *Puffinis pacificus cuneatus*. The mean number of mynas sighted during my monitoring visits to the colony was four out of a myna population of approximately 1,000 while Byrd (1979) recorded an average of 12 birds visiting a colony of ≈ 5,000 wedge-tailed shearwater nests. On Ascension < 10% of the myna population preyed on sooty tern eggs. In 2009 mynas were trapped and culled in the tern colony using Myna Magnet (MM) traps commercially made in Australia (Saavedra 2009). The result of the cull on mynas visiting the tern colony was to reduce predation by mynas greatly. In 2012 none of the 61 eggs monitored was predated by mynas and little myna predation was observed in the two colonies. Prior to the cull, for every 16 sooty tern eggs that were destroyed by mynas, 10 were punctured and six were consumed. No evidence was found to suggest that the eggs destroyed by mynas were infertile and it would seem that myna predation is additive rather than compensatory. Sooty terns were observed attempting to incubate eggs that were pricked by mynas (BJH pers. obs.); for how long this persists at the end of the breeding attempt is unknown but it could prevent the pair from re-laying. My findings provide strong evidence that all forms of myna predation, and in particular the pricking of eggs, need to be considered when evaluating threats from mynas on the avian community. If my findings are applied more generally, I suggest that such levels of predation are far from trivial influences on the community ecology of the prey species. To the best of my knowledge, this is the first study to evaluate the impact of mynas on the breeding biology of a seabird species. Therefore, these findings reveal much about the ecological threats posed by non-native mynas.

5.5.3. Infanticide

Studies have revealed that infanticide occurs in many species of Laridae but the mortality rate of 0.5% that I report for Ascension sooty terns is substantially less than the 8% mortality reported by Villanueva-Gomila *et al.* (2009) for South American terns *Sterna hirundinacea*. Furthermore I could have over-estimated the mortality rate as my technique was open to bias because chicks taken by frigatebirds and dropped may have been included; results need careful interpretation. Unlike gulls, no evidence of cannibalism (Fordham 1964) by adult sooty terns on neighbouring eggs or chicks was observed. My observations support those of Ashmole (1963a) who found that pecking of neighbouring chicks was an adaption to reduce the chance of accidently adopting a genetically unrelated chick. I found no evidence to support the view of Wynne-Edwards (1962) that colony members control reproductive output more vigorously in areas of high nest density. In fact, more chicks appeared to be killed on the edge of the breeding colony where nest density was less but where there was a greater chance of disturbance from humans than can cause chicks to flee the nest.

5.5.4. Egg consumption by rats

Rats disrupted 15% of all failed breeding attempts by taking eggs at night from exposed nest sites and depositing them in caches where they were broken and eaten (Fig. 5.4). Sooty terns nest in the open (Fig. 3.5) but rats prefer to feed in covered environments (Meehan 1984). In Cape Cod, Massachusetts, USA caches of brown rats contained 25–150 seabird eggs (Austin 1948) while on Ascension Island the largest cache I found contained 30 eggs. Although the movement of eggs by rats on Ascension was not directly observed, we know that rats transport eggs (Meehan 1984). Prieto *et al.* (2003) used an experimental approach to determine if rats prey on eggs of Audouin's gulls *Larus audouinii* and concluded that rats did not have the ability to break their large eggs that were defended by adults so rat predation only marginally affected gull productivity. These results are in sharp contract to my findings and the disparity requires investigating. On Mediterranean islands black rats are approximately 100 g in body mass which is considerably lighter than Ascension rats with a mean body mass of 134 g (Bell & Ashmole 1995). Eggs of sooty terns (52 mm long × 36 mm wide) are smaller than those of Audouin's gulls (63 mm long × 44 mm wide) and may go some way to explain the different conclusions.

5.5.5. Frigatebird predation

Only a very low percentage (i.e. < 0.01%) of the total population of Ascension frigatebirds was represented by the maximum number of birds seen hunting over the tern colony at any one time. Thus, sooty tern chicks are unlikely to be a major food source for frigatebirds. Frigatebirds are a long-lived species and their productivity between 2001 and 2002 was 0.34 ± 0.07 chicks per breeding pair (Ratcliffe *et al.* 2008). Despite there being many more adults than juvenile frigatebirds on Ascension, approximately equal numbers of juveniles (42%) and adults (58%) hunted over the tern colony in the middle of the day (Table 5.1), suggesting that juveniles may be accompanied by parents during feeding forays into the colony (Fig. 5.6). Both male and female adults hunted sooty terns on

Ascension but on Wake Atoll male great frigatebirds did not predate chicks (Megyesi & Griffin 1996). On Ascension there was a marked difference in the success rate of chick captures by juveniles (0.22 chicks per hour) *versus* adults (1.23 chicks per hour), but on Wake Atoll the success rates of female and juvenile great frigatebirds were very similar at 37.0% and 37.8%, respectively. Ascension frigatebirds must hone that foraging skills in order to be successful kleptoparasites and the interaction with sooty tern chicks may provide juveniles with opportunities to practice these skills. Frigatebirds are usually solitary at sea (Harrison 1990) and, thus, how young frigatebirds learn to forage has puzzled researchers for many years (e.g. Stonehouse & Stonehouse 1963, Megyesi & Griffin 1996). Chicks are fed by both parents by regurgitation with the bulk of their food represented by flying fish *Exocoetus* spp. but Stonehouse and Stonehouse (1963) provided no evidence of sooty tern chicks in the diet of frigatebird chicks. The skills required by juveniles to forage successfully at sea probably need to be developed close to their natal colony shortly after they have fledged. Interaction between sooty terns and frigatebirds with the respective breeding colonies being 15 km apart probably provides many training opportunities for juvenile frigatebirds. Frequent observations (BJH pers. obs.) of juveniles roosting (and loafing) (Fig. 5.6) in the tern colony suggested that juveniles may not be ready for long foraging trips. When feeding frigatebirds were observed in the sooty tern colony, they swooped low and snatched a chick by extending the head and neck at a critical moment. The action is closely similar to that used by frigatebirds in scavenging off the surface of the sea. Adult and juvenile frigatebirds, in groups of two to seven, interacted while hunting. On frequent occasions adults were seen taking live chicks high into the air and dropping them for juveniles to catch. If the chick was small it was eaten by juveniles. Of six chicks taken by adults between 0930–1200hrs GMT on 19 October 2005, three large chicks were dropped and immediately caught by attendant juveniles. Once the latter had realised that they were too large to be consumed they too dropped the chicks. As many as half of the chicks taken were too large to eat and were not consumed.

Ashmole (1963a) noted particularly heavy predation from frigatebirds in February 1958. I found that predation from frigatebirds peaked in February 2004 and in February 2008. Frigatebirds breed throughout the year but lay the fewest eggs (i.e. < 2%) in February (Ratcliffe *et al.* 2008), suggesting that juvenile frigatebirds with their parents are most abundant in February than in other months of the year. These data suggest that parent frigatebirds may be accompanying offspring to the tern colony and that the ultimate factor driving the interaction with sooty terns is to teach young forage skills. Ashmole (1963a) reported that frigatebirds predated some sooty tern sub-colonies heavily and my findings concur. However, managing frigatebird predation is not appropriate as sooty terns are classified as of ‘Least Concern’ (BirdLife International 2012b) while the Ascension frigatebird is classified as ‘Vulnerable’ (BirdLife International 2012a) and has a higher conservation priority.

5.5.6. Breeding success estimation

The breeding success rate that I have calculated is probably an under-estimation as no account has been taken of the fact that some birds that have lost an egg or a nestling will re-lay and be successful breeders. Ashmole (1963a) estimated that approximately 15% of birds will re-lay but only eggs re-laid early in the season are likely to result in breeding success. In this study I have used the mean hatchability rate of Koenig (1982) in my estimation of breeding success. Hatchability rates of sooty tern eggs on Ascension may differ widely from this and fieldwork is needed to reach a species-specific estimate for this parameter. Non-lethal effects of mynas might compound the problem of myna predation. For example, mynas foraging in the tern colony may reduce the opportunity for terns to make brief visits to the ocean to drink and dip in the sea to cool off. Increased quantities of opened but uneaten eggs and deserted eggs may also impact on populations of parasites resident in the colony. Non-lethal effects of mynas need investigation.

5.5.7. Factors limiting the population size

Biologists such as Darwin (1859) and Newton (1998) have considered predation to be a process by which the weak (i.e. those unlikely to recruit) are eliminated without greatly affecting the viability of the breeding population. In my study two thirds (i.e. 69%) of breeding attempts failed and may be the “doomed surplus” (Errington 1945) that do not limit the breeding population size. However, like Valkama *et al.* (2005), I found that some of the predation, such as eggs punctured by mynas and losses to rats, may indeed have the potential to reduce the size of the breeding population below the carrying capacity. So, although predation of nestlings by frigatebirds may not affect the viability (i.e. long-term survival) of the breeding population on Ascension, other lethal interactions with non-native predators do limit population growth by taking individuals out of the pool of potential recruits. My findings do not support the hypothesis that predation events in the tropics occur predominantly during the day (Libsch *et al.* 2008). However, my findings do support the research of Jones *et al.* (2008) and Hilton and Cuthbert (2010) who found that non-native species limit seabird population size.

In The Seychelles where sooty terns breed annually adult survival was estimated to be 0.91 (Feare & Doherty 2004) and the probability of a young bird surviving to breed at age 5 was estimated to be 0.26 (Feare & Doherty 2011). Thus, for the population size to persist the breeding success rate needs to be approximately 0.69. Similar results were found on Skomer Island in Wales where the population size of common guillemots has increased by approximately 5% per year with no obvious immigration (Meade *et al.* 2013). Adult survival (0.92) and juvenile survival to breeding age (0.25) of guillemots were similar to those obtained by Feare and Doherty (2004, 2011) for sooty terns. The annual increase in population size of 5% was achieved when breeding success was > 0.72 chicks per pair. These two examples indicate that breeding success rates of ≤ 0.3 fledglings/egg laid of Ascension sooty terns during breeding seasons 2009 and 2012 were likely to result in a decline in population size.

5.5.8. Conclusions

The causes of losses of eggs, nestlings and chicks on Ascension have changed over the course of the last 50 years. Myna and rat predation were insignificant during the BOU expedition of 1958 but 50 years later mynas were responsible for 22% and rats for 16% of egg failures. The myna population size was < 10% of the frigatebird population size but they destroyed 10 times more eggs than frigatebirds predated nestlings. My results suggest that the stable trend in the population of sooty terns between 1990 and 2011 on Ascension (Chapter 3) is unlikely to change as a result of small fluctuations in incubation and nestling success rates. However, breeding success rates (2006 to 2012) were below the average of conspecifics on other islands and may have an impact on the size of the breeding population and warrant further investigation.

In Chapter 6 I will investigate how rats have impacted on the chick stage of the breeding cycle of sooty terns, thereby reducing breeding success.

(Note: The publication status of Chapter 5 as of December 2013 is that it is currently being prepared for submission).

Chapter 6

APEX PREDATOR ERADICATION AND MESOPREDATOR RELEASE: UNINTENDED CONSEQUENCES FOR SOOTY TERNS ON ASCENSION ISLAND

6.1. ABSTRACT

On islands native species can be driven to extinction by non-native species such as feral cats and rats. The response is often an eradication programme but complete extirpation of well-established apex predators can generate cascading effects and may not be the best solution for protecting native prey species. Ecological theory predicts that removal of cats in a predator community of both cats and rats may result in a rapid increase in mesopredator (i.e. rat) abundance; there is a shortage of empirical evidence to test theory. Black rats were introduced to Ascension around 1701 and cats in 1815. Records show that by the middle of the 19th century rats and cats had greatly reduced the size of seabird populations. The only sizeable population to survive was that of sooty terns. The two non-native predators then co-existed with a colony of > 400,000 sooty terns for two centuries. In the absence of other seabird populations cats may have limited the rat population during the period when sooty terns migrated as there was little alternative prey on the island. The eradication of cats in 2003 was followed by an increase in rat abundance. Rat relative abundance between 1992 and 2003 was 2 C/100TN (captures per 100 trap nights) but increased to 14 C/100TN between 2004 and 2012. Before their eradication cats were estimated to predate 5,800 adult sooty terns and 4,500 chicks per season while rats only predated eggs. When released from predation pressure, rat body mass, and head

and body length increased by 12% and 8%, respectively. The age structure of the rat population changed and the number of older rats, large enough to prey on chicks, increased by 2,700%. Following cat eradication, tern chicks became a component of the rats' diet and rat predation, estimated from counts of chick carcasses, accounted for > 19,500 chicks. The impact of mesopredators on the size of the sooty tern population was similar to the combined impact of both apex and mesopredators. These findings support the mesopredator release hypothesis to some extent but the full impacts of mesopredator release will not be appreciated unless the significant shifts in the morphology and behaviour of the 'released' predator species are accounted for.

6.2. INTRODUCTION

The invasion of islands by non-native mammal species and their dramatic effects on native avifauna are well-documented (e.g. Norris & Pain 2002, Nogales *et al.* 2004). Among such mammal species, feral cats and rats are probably the most potent predators (Croxall *et al.* 1984, Towns *et al.* 2011) with theirs impacts on some seabird colonies sometimes being catastrophic (e.g. cats – Nogales *et al.* 2004; rats – Jones *et al.* 2008). Predator eradication is frequently adopted by conservation managers to arrest decline in avian species (e.g. Moors 1985, Smith *et al.* 2010). To date, feral cat eradication programmes have been conducted on 75 islands (Rauzon 2007, Donlan & Wilcox 2008), but their effects on the target conservation species and other predators have been poorly monitored and the results may not be as predicted. Ground-nesting seabird populations responded positively to cat eradication in the Pacific (Bester *et al.* 2002, Peck *et al.* 2008) and on Baker Island sooty terns re-established themselves following the elimination of cats (Moors & Atkinson 1984). However, on Little Barrier Island in New Zealand cat eradication did not result in an increase in passerine populations (Girardet *et al.* 2001). On islands where seabirds are prey to both cats and rats, the eradication of the apex predator (i.e. cats) may result in changes to the demography (Russell *et al.* 2011) of the mesopredator (i.e. rat) population and to the body size of individuals in the population that might be highly detrimental to seabirds (Courchamp *et al.* 1999).

6.2.1. Apex predator eradication on Ascension

Black rat and feral cat predation on Ascension have apparently resulted in declines in the sizes of seabird populations (Stonehouse 1962a, Ashmole *et al.* 1994). As a consequence, the AIG and the RSPB produced a management plan to halt these declines in seabird populations. The objective as described in Pickup (1999) was “To re-establish by 2005 a breeding seabird colony on the Ascension mainland, containing amongst other species, frigatebirds and red-footed boobies and to maintain the existing colonies at their present levels”. To accomplish these objectives, it was proposed that all feral cats be eradicated from the island and that rat densities be controlled. Implementation of the Ascension Island Management Plan commenced in February 2002 and by December 2002 96% of feral cats were eradicated with the last cat eradicated in 2004 (Bell & Boyle 2004). Sporadic rat control in the tern colonies using bait boxes containing rodenticide commenced in 2004 (Bell 2005) and is ongoing. The programme of cat eradication had some immediate successes with five species of seabirds starting to breed again on the main island sites (Sanders 2007). Furthermore, in 2012 the first two pairs of frigatebirds were seen nesting on the main island (McKie 2012). However, not all seabird populations have benefitted (see section 3.4.5) and there has been little change in the size of the sooty tern population since the cat eradication.

6.2.2. Mesopredator release

The eradication of apex predators is generally associated with an increase in the abundance of smaller predators (Prugh *et al*. 2009). This trophic interaction is referred to as mesopredator release (Soulé *et al.* 1988) when predators of an intermediate body size (e.g. rodents) become more prevalent in the absence of larger predators (e.g. cats). This can result in reduced population size of prey species such as birds. Courchamp *et al.* (1999) used a three species (i.e. prey, mesopredator and apex predator) mathematical model with and without control of meso- and apex predators to show that mesopredator release can occur. However, Russell *et al.* (2009) modelled the effects of mesopredator release on islands and concluded that the negative impact of more mesopredators is outweighed by the benefit of apex predator removal, allowing recovery of the prey population. Rayner *et al.* (2007) suggested that the eradication of cats can result in an increase in net predation on seabirds but their evidence was inconclusive and they recommended that future research should involve period-specific estimates of demographic rates for several seasons. When cats and rats invade seabird islands, cats have a direct effect on the size of the breeding seabird population through predation of adults (van Aarde 1983) while rats have a less immediate and a more indirect effect through predation of eggs and chicks (Jones *et al.* 2008), thereby reducing breeding success and, after a period of deferred breeding (see section 4.4.3.), the number of recruits to the breeding population.

The direct impacts of cats on the breeding population of seabirds are readily observed (Fig. 6.1). However, the indirect effects on the breeding population are more difficult to quantify as rat predation is less easily observed and is confounded by rats scavenging on chicks that have died of starvation. While mesopredator release has only recently been elaborated in the literature (Ritchie & Johnson 2009), it is undeniable that the phenomenon is likely to have major implications for conservation managers which urgently require investigation through empirical study.

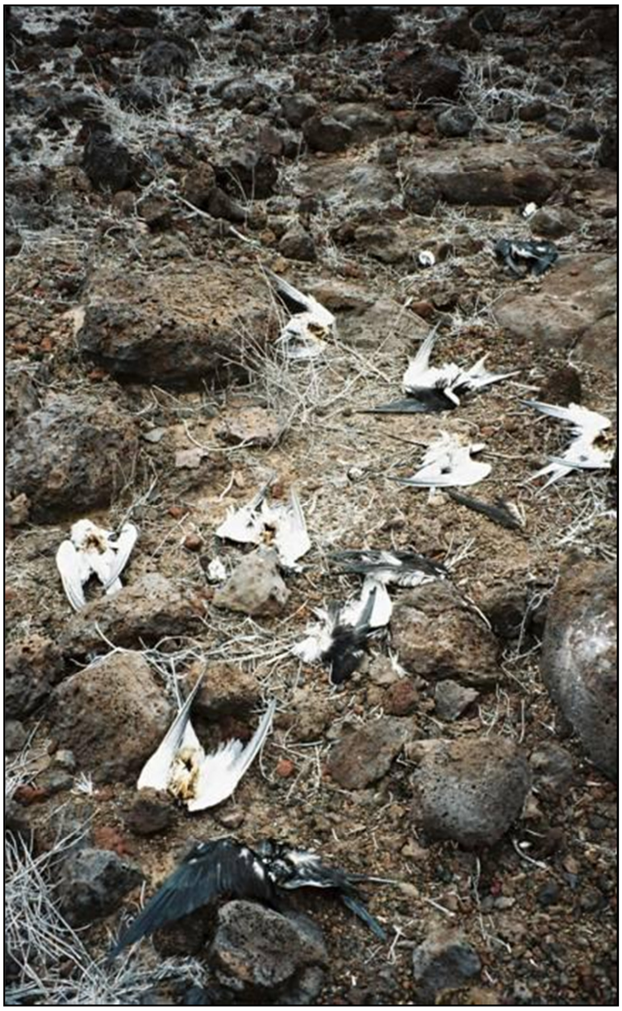

Figure 6.1. Carcasses of adult sooty terns following predation by feral cats. Carcasses were found in one of the cat larders at Mars Bay on Ascension Island in 1990. (Photo: B.J. Hughes).

6.2.3. Rats on Ascension

For 115 years (1701 to 1815) rats were the apex predator on Ascension with the rat population being sufficiently large by 1725 to put a castaway in fear of his live (Ritsema 2006). In the 19th century the Admiralty paid a substantial bounty of a halfpenny per rat in an attempt to control the rat population. The number of rats killed between 1879 and 1887 was 70,148 rats (Hart-Davis 1972) but this did little to prevent future eruptions in rat densities. In 1965 two fully-trained pest controllers were required to control the rat population around human habitation and another four were needed to control their numbers on the mountain farm (Davies 1966). Rat density increases with altitude on Ascension (Davies 1966, Lambert 2010). Duffey (1964) divided Ascension into three distinct ecological zones: (1) a dry barren coastal plain below 330 m; (2) a zone between 330 and 600 m below the cloud layer of Green Mountain; and (3) a zone of mist from 600 to 850 m. On the dry coastal plain rat density is generally low (i.e. rats were rarely seen; Stonehouse 1960, Ashmole 1963a, Merritt *et al.* 1992, Bell & Ashmole 1995) but high density pockets of rats can exist where food is available (e.g. refuse dumps, bird colonies; Bell & Boyle 2004). In zones above 330 m rats are common (Davies 1966, Bell & Ashmole 1995, Lambert 2010).

6.2.4. Rat life history and range

The life history of free-living black rats is well characterised: they are sexually mature by 109 days, producing three to five litters per year; they have a gestation period of 22 days, a litter size of four to seven viviparous young; they wean when pups are 26 days old; they have an inter-litter interval of 36 days; and they have an annual mortality of 91–97% (Meehan 1984). Rats are short-lived mammals and most die in their first year of life (Corbet & Harris 1991), but in ideal conditions (i.e. free from predators and with *ad libitum* food availability) rats live longer with captive animals living up to 4.2 years (Weigl 2005). Body mass, and head and body length of rats increase throughout their lives (Bentley & Taylor 1965) with a concomitant increase in prey size (Yabe *et al.* 2009). Home range of black rats is between 0.27 and 11.4 ha (Dowding & Murphy 1994, Pryde *et al.* 2005).

6.2.5. Mesopredator release

Understanding what drives changes in mesopredator population size when released from apex predator control allows the impacts of community-level changes on prey populations to be more reliably predicted. Counter-intuitively, the eradication of the apex predator in a twin predator regime may be more detrimental to the prey species than the situation pre-intervention (Courchamp *et al*. 1999, Courchamp *et al*. 2003). Ascension is isolated; predators and prey interact in a relatively closed environment which makes the island an ideal site to study mesopredator release. However, on Ascension apex predators and mesopredators impact on seabirds at different life stages with the size of seabird populations being more sensitive to changes in adult survival and less sensitive to changes in reproductive rates (Newton 1998). The impact of the two predators is further confounded by seabirds deferring breeding (Nelson 1980, Bonnaud *et al.* 2010) and most Ascension sooty terns defer breeding for 11 seasons (Chapter 4).

Here, I investigate the impacts of the eradication of an apex predator, the feral cat, and the release of a mesopredator, the black rat, on their prey species, the sooty tern on Ascension Island. There is strong evidence that feral cats were permanently removed from Ascension between 2002 and 2004 (Sanders 2007, Ratcliffe *et al.* 2009), and is confirmed in this study. Here, I hypothesised that: (1) apex predator eradication has resulted in release of predation pressure from cats and an increase in food availability for rats. I predicted that rat abundance, and their body mass and head and body length would increase as a result of cat eradication; and (2) the impact on prey population size of a single-predator regime would be greater than that of a dual-predator regime. Therefore, I predicted that the benefits of cat eradication for the sooty tern population would be out-weighed by a resultant increase in rat predation as a result of mesopredator release.

6.3. MATERIALS AND METHODS

6.3.1. Study period and area

I studied cat, rat and sooty tern interactions by monitoring predator and prey populations between 1990 and 2002 (i.e. pre-cat eradication), in 2003 (i.e. during cat eradication) and between 2004 and the present day (i.e. post-cat eradication). Censuses of the avian prey population were completed in the sooty tern colonies at Waterside and Mars Bay (see section 2.3 for more details). Estimates of feral cat population size were for the whole island. Rat relative abundance indices were completed in seabird colonies on the dry coastal plain (below 330 m in altitude) on the south side of the island (Fig. 1.1). Indices were completed in the tern colonies at Waterside and Mars Bay and in the masked booby colony on the Letterbox peninsula (see Hughes *et al.* 2011 for more details).

6.3.2. Confirmation of apex predator eradication

Prior to cat eradication, predation of adult sooty terns was monitored early in the breeding season by clearing the perimeter of the colony of all tern corpses and then re-visiting the colony every second day for the duration of the field season (over ≈ 2 weeks) to collect and record the number of freshly killed birds. On some islands cat larders are hidden in dense undergrowth (Bonnard *et al.* 2012) but on Ascension they were found on open ground (Fig. 6.1). The survey team circled the two colonies over a distance of ≈ 3 km and visited known cat larders searching for dead birds. The vast majority of dead birds found had been substantially eaten. The nightly average number of birds killed in the two colonies was then calculated and extrapolated across the breeding season. Evidence that cats had predated adult terns at the start of the breeding season could be seen in the colony and I assumed that loss of adult terns to cat predation at the start of the breeding season was consistent with that at the peak of the breeding season. Towards the end of the season cats began to take large chicks as well as adults (Ashmole 1963a, BJH pers. obs.) and they may also have bred. Therefore, the mortality data gathered over two weeks may sometimes under-estimate the level of predation. To compensate for this unknown level of chick predation, cats were assumed to take equal numbers of adults and chicks for 110 days (i.e. during the period when some adults were incubating and other adults were feeding chicks close to fledging). For the remaining 25 days of the breeding season cats were assumed to take just large chicks as most adults were foraging and on the ground for < 15 minutes to feed chicks (BJH pers. obs.). To confirm the success of the cat eradication programme, from 2004 numbers of any dead adult sooty terns were recorded, they were checked for signs of predation (Fig. 6.1) and then buried. Searches for adult sooty terns predated by cats continued throughout the study.

6.3.3. Change in mesopredator abundance

I measured the abundance of mesopredators pre- and post-cat eradication by constructing a simple rat relative abundance index calculated as the number of rats trapped in the study area and expressed as captures per 100 corrected trap-nights (C/100TN). Trap-night calculations were corrected for traps tripped as per the field method recommended by Cunningham and Moors (1983) and employed by Bell and Ashmole (1995). During nine field seasons 50 break-back traps baited with peanut butter and cornflakes were set out in pairs along the edge of the tern's breeding colony. Trapping occurred over two consecutive nights. Traps were set in the late afternoon, left overnight (i.e. for 14 hours) and then disabled when capture contents were removed.

To test if mesopredator release had occurred, I compared the mean of rat indices obtained from a literature search in 1992 (Merritt *et al.* 1992), 1995 (Bell & Ashmole 1995) and from my own rat index in 2003, with rat indices (i.e. a mean for 2004–2012) post-cat eradication.

6.3.4. Body mass and body length of rats

I used identical methods to those used by Bell and Ashmole (1995) to measure body mass (BM) and head and body length (HBL). BM was measured to the nearest 1 g with a Pesola spring balance and HBL was measured as the length of the head and body to the nearest 1 mm with a metal rule (after Cunningham & Moors 1983). Tail lengths were measured on occasions to confirm rodent species identification as black rats have longer tails than brown rats *Rattus norvegicus* (Meehan 1984). I used a weight curve for wild-trapped black rats between one and 20 weeks of age (Hirata & Nass 1974), a table of age-specific body measurements (Ventura & López-Fuster 2000), age estimation based on when rats reach maximum body mass (Bentley & Taylor 1965) and a classification of "median size at maturity" (after Clark 1980), to categorise rats into three age classes (i.e. sub-adult, sexually mature and seniors). Sub-adults are rats that have not reached sexual maturity, sexually mature rats have a median HBL of 152 ± 13 mm (*n* = 12) (Clark 1980) and, here, I have defined seniors as rats that were close to reaching maximum body mass and are over one year old (Table 6.1).

Table 6.1. Age class and age as defined by body mass (BM) and head and body length (HBL) of black rats trapped in sooty tern colonies on Ascension Island between 1995 and 2012.

Age class	Age (days)	BM (g)	HBL (mm)
Sub-adult	< 109	< 120	< 150
Sexually mature	109–404	120–199	150–179
Seniors	> 404	> 199	> 179

6.3.5. Impact on prey of mesopredator release

The impact of mesopredator release on sooty terns was determined from: (1) an analysis of sooty tern breeding population census data pre- and post-cat eradication; (2) an analysis of sooty tern fledging success rates on Ascension post-cat eradication with those of conspecifics on other islands; and (3) a comparison of counts of adult terns and chicks predated by cats and rats pre- and post-cat eradication.

6.3.5.1. Censuses of the breeding population size of sooty terns. Please see details in Chapter 3 of the methods used to census the tern breeding population. The impact of eradication of cats on the sooty tern breeding population was assessed through a comparison of census data pre- and post-cat eradication. The majority of sooty terns defer breeding for 11 breeding seasons (see section 4.4.3.). Adults counted in censuses pre-2011 fledged from colonies where both cats and rats predated sooty terns and post-2011 from colonies where there was no cat predation and rats were the apex predator. Breeding success and thus the number of recruits to the breeding population may vary between dual- (i.e. cats and rats) and single- (i.e. just rats) predator regimes. The impact of eradication of cats was also assessed by comparing censuses of the breeding population of terns between 1990 and 2011 with those of the breeding population in January and December 2012.

6.3.5.2. Fledging success. Please see details in Chapter 5 of the methods used to determine sooty tern breeding success (i.e. fledglings per pair). Secondary data from R. Prytherch (pers. comm.) were used to determine reproductive success rates during one breeding season prior to the eradication of cats. Data from Schreiber *et al.* (2002) were used to calculate the mean breeding success rates of annually breeding conspecifics on other islands.

6.3.5.3. Chick carcass density and indications of starvation. Mean chick carcass density was determined from counts in 2009 by two observers of carcasses in 68 randomly placed 10 m^2 circular quadrats. Chicks that were partly eaten were assumed to have been predated by rats (Towns *et al.* 2006). Rodents (e.g. Polynesian rats *Rattus exulans* – Kepler 1967; house mice – Wanless *et al.,* 2007) are known to open the backs of predated ground-nesting seabird chicks. Similarly, black rats on Ascension commonly predate sooty tern chicks (Fig. 6.2) by opening a wound in the back slightly anterior to the uropygial gland and forward to between the scapulae. Black rats are known to open the skulls of short-tailed shearwater *Puffinus tenuirostris* chicks (Norman 1970) and on Ascension the skulls of sooty tern chicks were opened in a similar manner (Fig. 6.3). Evidence from freshly predated carcasses (Fig. 6.2) suggested that rats

Figure 6.2. A sooty tern chick on Ascension Island that has been predated by a rat as evidenced by flesh removed along the spinal tract. (Photo: B.J. Hughes).

pounce on sooty tern chicks from behind. The rat may need to be of sufficient body mass to hold the chick down to avoid injury from bird's flailing legs before

Figure 6.3. Fresh predation of a sooty tern chick by a black rat; the skull of the chick has been fractured and the brain tissue accessed through the eye socket. (Photo: D. Thomas).

killing it with bites to the head, neck and/or thorax. There are doubts that rats on Ascension are responsible for losses of eggs and chicks of sooty terns; Lambert (2010) saw little evidence of rats in the tern colonies of Mars Bay and Waterside. Rats are scavengers (Towns *et al*. 2006) and it could be argued that they were feeding on chicks that were dead or dying (i.e. the 'doomed surplus' of Newton 1998). In an attempt to eliminate the possibility that starvation was the ultimate cause of chick death, muscle score and body mass of live chicks were recorded. Chicks were sampled in the same parts of the colonies as carcass surveys. The shape of the pectoral muscles was scored between 0 and 2 according to the prominence of the keel as described in Gosler (1991). A scale of 0 tells us that breast muscle profile was low and may be indicative of low body condition. Body mass to the nearest 1 g was recorded with a Pesola spring balance.

6.3.5.4. Adult:chick ratio. Cats predate adult sooty terns and rats predate chicks. The loss of one breeding adult reduces the sooty breeding population size by one but the loss of one chick is unlikely to reduce recruitment to the breeding population by one as many chicks do not survive to breeding age (Feare & Doherty 2011). To evaluate the impact of chick losses on the breeding population size a ratio of adults to chicks is required. In other words on average how many fledged chicks are needed to replace one adult in the breeding population? The ratio of adults breeding for at least the second time to chicks subsequently recruited to the breeding population as adults (i.e. first-time breeders) was calculated from ringing/re-capture data. Adults and chicks of the age commonly predated by rats (i.e. P5 and P6; Fig. 4.2) were ringed during the same breeding seasons and re-captured in subsequent seasons. Sooty terns defer breeding for a minimum of seven seasons with the majority deferring for 11 seasons (Chapter 4). Ratios were determined each breeding season by the re-capture from each cohort of adults and new recruits and a mean with a 95% CL calculated.

6.3.6. Statistical analyses

Spearman Rank Correlations were used to test for relationships between adult sooty tern mortality and years (1990 to 2012) and between relative abundance of rats and years (1992 to 2012). I used unpaired *t*-tests to compare BM and HBL of trapped rats pre- and post-cat eradication. I also used unpaired *t*-tests to compare

BM and HBL of trapped rats on Ascension with rats on other islands with and without cats (details obtained from a literature search).

6.4. RESULTS

6.4.1. Results of apex predator eradication

During the seasons 1990 to 2000, before cats were eradicated, > 4,500 bodies of sooty tern adults were collected as a result of cat kills during the pre-laying and incubation phases, and for two weeks after first chicks had hatched (i.e. 100 days in total in Fig. 6.4). Thereafter, cats were killing large chicks as well as adults. The only predators of adult sooty terns recorded in the colony were cats. Following the 2000 season the number of cat kills declined and ceased after 2002. Nightly averages of cat kills during a 2-week period immediately after hatching at Mars Bay and Waterside colonies showed similar declines from 1990 to 2002 (Fig. 6.4). Assuming that cat predation continued at the same intensity in the second half of the season as it did in the first, the overall percentage of the adult population predated by cats varied from 1.8% (or 5,800 birds) in 1990 to 0.1% (or 340 birds) in June 2002 following the knock-down phase of the cat eradication programme. Following cat eradication, predation of adult sooty terns has declined significantly from 33 birds per night in the early 1990s to no birds 2003–2012 (r_s = -0.83, *df* = 17, P = 0.03; Fig. 6.4).

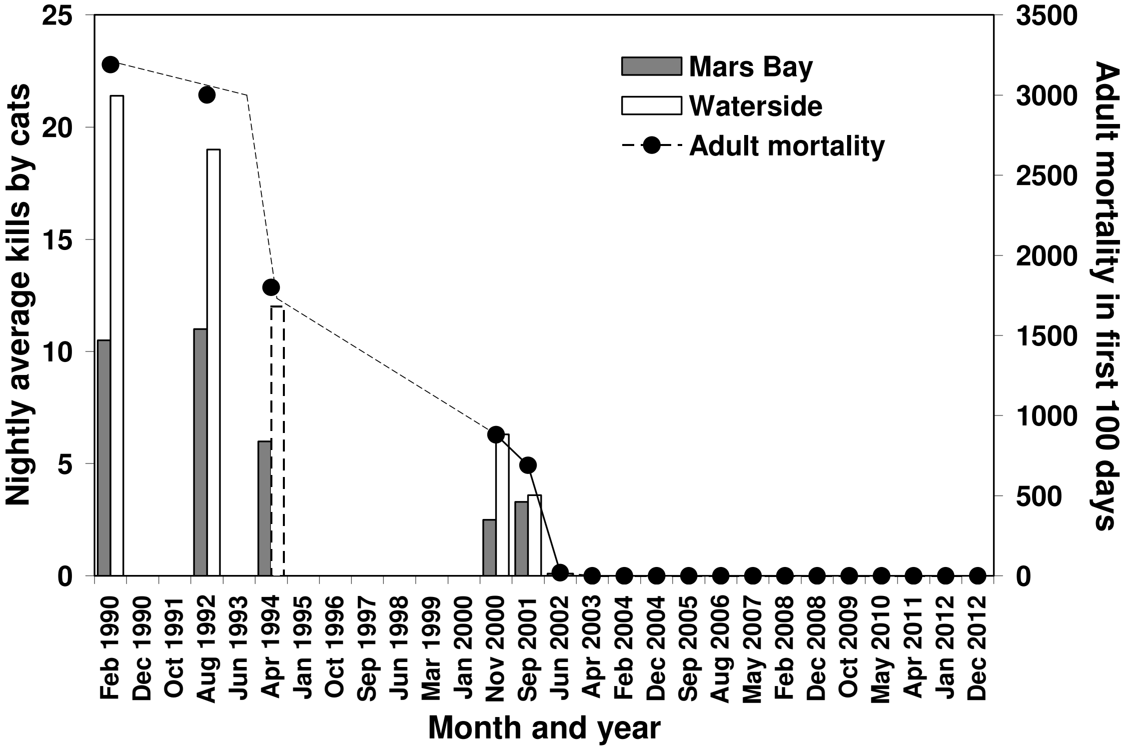

Figure 6.4. Mortality of adult breeding sooty terns attributed to cat predation on Ascension Island. The total number of birds killed during the 100-day period (61% of the full breeding season) that included pre-laying, incubation and a two-week period immediately after the first chicks hatched are shown as data points. Nightly average kills at each sub-colony are shown as bars. Note: Data for Waterside in April 1994 are estimated and the trendline between non-successive breeding seasons is dashed.

6.4.2. Mesopredator relative abundance

Between 1992 and 2003 the pre-cat eradication relative abundance of rats varied between 0.0 and 6.0 C/100TN with a mean of 1.8 ± 1.8 C/100TN (*n* = 9). Between 2004 and 2012 the post-cat eradication relative abundance of rats varied between 0.0 and 74.5 C/100TN with a mean of 13.8 ± 6.8 C/100TN (*n* = 27). The relative abundance of rats has increased significantly during the study period (r_s = 0.51, *df* = 34, *P* = 0.002; Fig. 6.5).

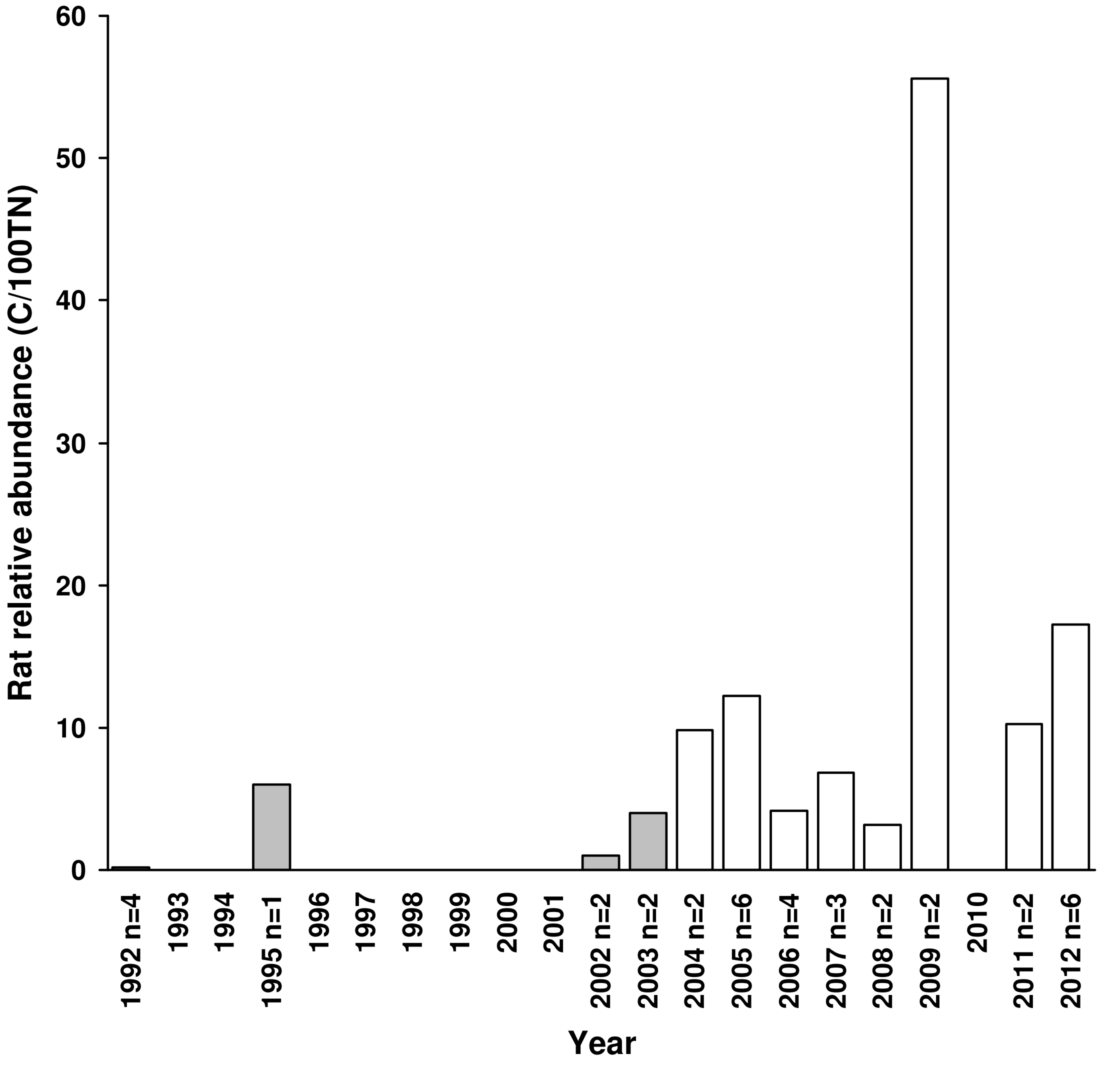

Figure 6.5. The relative abundance of rats caught in sooty tern colonies before (grey bars) and after (open bars) cat eradication on Ascension Island. The number of indices (*n*) during each year is placed at the base of each bar. In total 36 rat indices (nine before and 27 after cat eradication) were derived.

6.4.3. Mesopredator body mass and length

The mean BM of rats on Ascension Island between 2004 and 2012 post-cat eradication was heavier than that of rats pre-cat eradication (data from Bell & Ashmole 1995) (150.7 ± 12.9 g, $n = 55$ vs. 134.9 ± 5.9 g, $n = 35$ rats; unpaired *t*-test: $t = 1.88$, $df = 88$, $P = 0.06$). The mean HBL of rats was significantly longer post-cat eradication compared with pre-cat eradication (178.3 ± 3.4 mm, $n = 55$ rats vs. 164.8 ± 2.4 mm, $n = 35$ rats; $t = 5.73$, $df = 88$, $P < 0.01$).

BM and HBL of trapped rats were used to identify age class. According to my classification of longevity of rats as described in Table 6.1, this translates into longevity of rats having increased with 1.5% of rats trapped being seniors pre-cat eradication compared with 35.5% of rats trapped following cat eradication (Fig. 6.6).

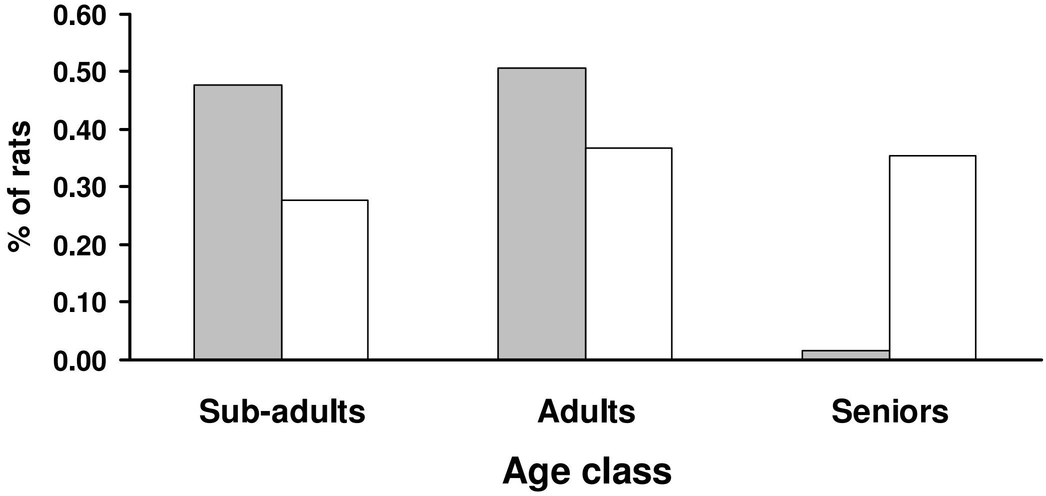

Figure 6.6. Age structure of the population of black rats trapped on the coastal plain of Ascension Island pre- (grey bars) and post- (open bars) cat eradication.

6.4.4. Rat sizes on islands

Rats on islands without cats were significantly heavier than those with cats (Table 6.2; 162.5 ± 10.8 g, $n = 19$ vs. 123.0 ± 6.3 g, $n = 24$; $t = 2.02$, $df = 41$, $P < 0.01$). They also had significantly longer bodies (185.5 ± 9.2 mm, $n = 14$ islands vs. 169.7 ± 3.6 mm, $n = 23$; $t = 2.03$, $df = 35$, $P < 0.01$).

Table 6.2. Body masses (BM) and head and body lengths (HBL) of male (M) and female (F) rats caught in different years on islands where feral cats are absent and present. Data sources are given in the right hand column. Note: ? – not known from original source; - – data are not collected.

Islands without cats	Year	Sex	*n*	BM (g)	HBL (mm)	Source
Europa, Mozambique	Summer 2007	F	11	171.0	186.0	Russell *et al.* 2011
	Winter 2007	M	31	172.0	193.0	Russell *et al.* 2011
	Winter 2007	F	26	164.0	189.0	Russell *et al.* 2011
	Summer 2008	M	15	175.0	201.0	Russell *et al.* 2011
	Summer 2008	F	12	157.0	201.0	Russell *et al.* 2011
	Winter 2008	M	23	160.0	197.0	Russell *et al.* 2011
	Winter 2008	F	11	153.0	200.0	Russell *et al.* 2011
Higashijima, Japan	Summer 2008	44	44	165.5	-	Yabe *et al.* 2009
Palmyra Atoll, Hawaii	2004	M	10	198.0	-	Thorson 2004
		F	11	174.5	-	Thorson 2004
Congreso Is., Spain	1994-1995	M	9	201.1	202.6	Ventura & López-Fuster 2000
		F	9	196.7	196.0	Ventura & López-Fuster 2000
Midriff Is., Mexico	1981-1995	?	?	172.0	-	Velarde *et al.* 2007
Goat Is., New Zealand	2005	M	12	128.0	163.0	MacKay & Russell 2005a
		F	16	123.0	160.0	MacKay & Russell 2005a
Tawhitinui Is., NZ	2005	M	23	135.0	167.0	MacKay & Russell 2005b
		F	29	137.0	164.0	MacKay & Russell 2005b
Palmyra Atoll, Hawaii	2010	M & F	300	146.1	-	Alifano *et al.* 2010

Islands with cats	Year	Sex	*n*	BM (g)	HBL (mm)	Source
Glorieuse	2008	M	11	123.0	177.0	Russell *et al.* 2011
Glorieuse	2008	F	19	123.0	172.0	Russell *et al.* 2011
Mayotte	2007	M	43	142.0	184.0	Russell *et al.* 2011
Mayotte	2007	F	57	130.0	176.0	Russell *et al.* 2011
Seychelles	1999-2000	M	199	-	167.2	Russell *et al.* 2011
Seychelles	1999-2000	F	171	-	158.0	Russell *et al.* 2011
Andringita, Madagascar	1993	M & F	10	105.7	167.0	Russell *et al.* 2011
Ranomafana, Mad.	2000	M	9	119.0	170.9	Russell *et al.* 2011
Juan de Nova	Summer 2007	M	16	133.0	165.0	Russell *et al.* 2011
Juan de Nova	Summer 2007	F	12	119.0	153.0	Russell *et al.* 2011
Juan de Nova	Winter 2007	M	7	107.0	169.0	Russell *et al.* 2011
Juan de Nova	Winter 2007	F	4	104.0	166.0	Russell *et al.* 2011
Juan de Nova	Summer 2008	M	32	113.0	176.0	Russell *et al.* 2011
Juan de Nova	Summer 2008	F	17	111.0	174.0	Russell *et al.* 2011
Juan de Nova	Winter 2008	M	13	116.0	187.0	Russell *et al.* 2011
Juan de Nova	Winter 2008	F	19	102.0	180.0	Russell *et al.* 2011
New Island, Falklands	2000-2004	M & F	306	122.8	154.4	Quillfeldt *et al.* 2007
Port-Cros, Mediterranean	2007	M & F	47	171.5	-	Bonnaud *et al.* 2008
Corsica, France	2004	M	3	139.5	-	Magnanou *et al.* 2006
Corsica, France	2004	F	4	129.1	-	Magnanou *et al.* 2006
Kahanahaiki, Oahu	2010	M	122	130.6	170	Shiels 2010
Kahanahaiki, Oahu	2010	F	99	120.2	165	Shiels 2010
Honouliuli, Oahu	2010	M	70	126.7	170	Shiels 2010
Honouliuli, Oahu	2010	F	60	111.3	163	Shiels 2010
Makaha, Oahu	2010	M	32	130.8	171	Shiels 2010
Makaha, Oahu	2010	F	16	121.4	167	Shiels 2010

6.4.5. Impact of mesopredator release on sooty terns

6.4.5.1. *Censuses of the sooty tern breeding population.* Between 1990 and 2003, prior to cat eradication, the size of the breeding population of sooty terns varied between 138,000 and 535,000 birds with a mean of 361,000 ± 71,000 birds (n = 10). Post-cat eradication between 2004 and 2011 the breeding colony varied in size between 246,000 and 420,000 birds with a mean of 355,000 ± 37,000 birds (n = 10) (Fig. 3.5). Adults counted in censuses pre-2011 fledged from colonies where both cats and rats predated sooty terns and post-2011 in colonies where there was no cat predation and rats were the apex predator. The breeding population within the 1990 to 2011 study period varied between 138,000 and 535,000 birds with a mean of 358,000 ± 36,000 birds (n = 20) (Table 3.4). The breeding population in January and December 2012 was 280,000 and 302,000 birds, respectively (Table 3.4).

6.4.5.2. *Breeding success.* Sooty tern breeding success on Ascension post-cat eradication varied between 0.12 and 0.40 fledglings per pair with a mean of 0.31 ± 0.21 fledglings per pair (n = 4 breeding seasons). Breeding success in my study was thus low compared with that reported in other sooty tern study sites in Schreiber *et al.* (2002) (e.g. 0.62 in the Dry Tortugas, Florida, USA; 0.58 at Bird Island in The Seychelles).

6.4.5.3. *Chick carcass and signs of starvation.* During 473 days of fieldwork prior to the eradication of cats no predation of sooty tern chicks by rats was observed or suspected. Some chick carcasses that were assumed to have died of starvation were seen but numbers were not recorded. Carcasses of chicks predated by rats were first observed in 2005 when of 596 ringed chicks, 131 (or 22.0%) were predated. In 2009 carcass density in quadrats varied between 0 and 0.9 per m^2 (0.16 ± 0.22, *n* = 68). The area of the colony was 12.21 ha and thus it contained an estimated 19,500 ± 27,000 carcasses. Carcass density was likely to provide an under-estimate of chick losses as decomposition of corpses was rapid and rough ground made it easy to overlook them.

The mean muscle score of live sooty tern chicks aged P5 and P6 (Fig. 3.2), that had the potential to be predated by rats, was 1.05 ± 0.31 (range 0–2, *n* = 998). In the sample 13 (or 1%) had a muscle score of 0 and were in low body condition, 79 (or 8%) had a score of 0.5, 740 (or 74%) were in moderate condition, 136 (or 14%) had a score of 1.5 and 30 (or 3%) were in high body condition. Mean body mass of chicks was 157.5 ± 29.2 g (range: 54.8–220 g, *n* = 946).

6.4.5.4. *Carcass counts.* Between 1990 and 1994 during the dual-predator regime of cats and rats, cats were estimated to predate 5,800 adult and 4,500 chicks per breeding season. From 2004 to 2012 during the single-predator regime of rats < 10 adult carcasses were found in the tern colonies while in 2009 an estimated 19,500 chick carcasses were found. I estimated that one in every 2.70 ± 1.06 chicks that fledge (range: 0.65–6.67, *n* = 16 datasets) are recruited into the breeding population. Thus, 15,660 (i.e. 5,800 × 2.70) chicks need to fledge to replace the 5,800 adult sooty terns taken by cats each breeding season. The level of predation of both adults and chicks during the dual-predator regime was the equivalent of 20,000 chicks.

6.5. DISCUSSION

One might intuitively expect that the eradication of apex non-native invasive predators on islands would be beneficial. However, on Ascension Island cat eradication has not resulted in an increase in the sooty tern breeding population size. Predation on adult sooty terns has ceased but chick predation has increased and the combined effect of predation from non-native mammals has not changed between 1990 and 2012. Apex predator eradication on Ascension has reduced bottom-up and top-down pressures on mesopredators. The eradication of feral cats between 2002 and 2004 was followed by a significant increase in black rat (relative) abundance. Rat BM and HBL also increased significantly as did suspected rat longevity, as predicted from published body dimension and age relationships for the species. Sooty tern breeding success (as estimated between 2005 and 2012) may be insufficient to maintain the population. As most sub-adults do not join the breeding population for 11 seasons, the impact of lower breeding success only becomes apparent in 2012 and further censuses are essential.

Published studies of the benefits of cat eradication are much less common than impact studies (Nogales *et al.* 2004). On islands where cats share prey with rats detailed estimates of the long-term effects of cat eradication are lacking (Towns *et al.* 2011). My research supports the findings of Crooks and Soulé (1999) and Rayner *et al.* (2007) that mesopredator release is a real ecological phenomenon and my findings will add to uncertainty about the effectiveness of eradication of apex predators as a conservation action.

6.5.1. Rat relative abundance

Changes in the abundance of apex predators can have marked effects on mesopredator abundance (Ritchie & Johnson 2009). The effect of feral cat eradication on the rat population of Ascension resulted in a seven-fold increase in rat relative abundance at sooty tern colonies at Waterside and Mars Bay. Cat eradication probably had the greatest impact on changes in rat abundance but was not the only factor. An increase in precipitation (Anon 2011), vegetation (Mexican thorn *Prosopis juliflora*; Walker 1998) and mice abundance (BJH pers. obs.) occurred during the study period. However, increases in the relative abundance of rats during the 20-year study period can be clearly ascribed to the removal of cats. Indices in near-desert locations on the coastal plain are not indicative of rat abundance across the whole island where densities are considerably larger (Davies 1966, Lambert 2010). Bell and Ashmole (1995) trapped 35 rats per 100TN on Green Mountain in 1995 and I trapped 83 rats per 100TN on the lower slopes of the mountain in 2012. Any doubts that rats are not found in the seabird colonies (Lambert 2010) can be dispelled from results of 36 rat indices spanning 20 years.

6.5.2. Rat size

I predicted that rat BM, HBL and longevity would increase as a result of cat eradication. My predictions were based on an analysis of rat size on islands with and without cats. Morphological records of rats show that there is a pattern to rat BMs and HBLs on islands (Russell *et al.* 2011). Cats may have created selective pressures limiting rat body size. Palkovacs (2003) suggested that decreased extrinsic mortality due to lowered predation pressure may increase body size and this appears to be one of the outcomes of apex predator eradication. When predation pressures on rats are removed, their body size increases and this enables them to prey on animals that previously were too large to overpower. On Ascension, following cat eradication, the mean BM of rats increased by 12% and rats began predating chicks that were closer to their body mass. When rat BM was less than the mean BM of prey no predator interactions were observed and the two species co-existed. When mean BM of rats was close to that of prey the latter were heavily predated presumably by senior rats with BMs > 199 g. Yabe *et al.* (2009) found similar results when mean BM of rats that ate birds was significantly heavier (202 g) than that of non-bird eaters (145 g).

6.5.3. Age structure and prolonged reproductive span

In the laboratory, longevity of rats is significantly correlated with BM. However, some rats of the same age can weigh twice as much as others. Bentley and Taylor (1965) suggested that this militates against the use in the field of BM as a guide to age. However, they found that longevity was significantly correlated with both maximum weight and the age at which it was attained. Although BM-age relationship is unlikely to be consistent across all rats, a change in the mean BM of the rat population is likely to be indicative of a change in the mean age of the population (Bentley & Taylor 1965). In my study an increase from one to 27 senior rats trapped could indicate that the rat population has aged (that is if all rats are equally trappable). Rats with increased longevity may now be able to breed in two consecutive sooty tern breeding seasons rather than just in one (Fig. 6.7). Under favourable conditions rodent populations are capable of rapid growth over short spaces of time (Meehan 1964) and it is possible that a prolonged reproductive

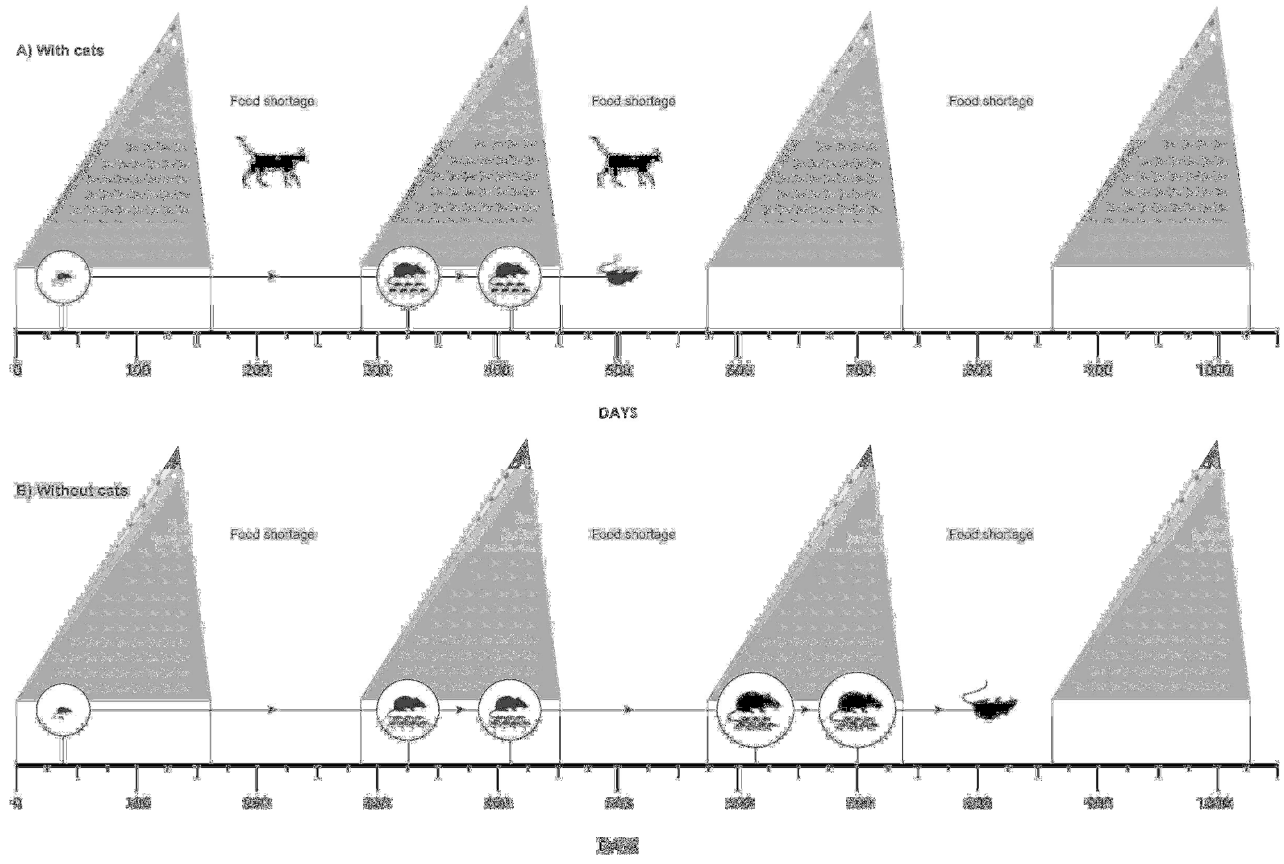

Figure 6.7. Schematic diagram showing the outcomes of the mesopredator release phenomenon on breeding seasons of black rats on Ascension Island as a result of removal of the feral cat, the apex predator. Pyramids of biomass indicate days when sooty terns were on the island and cats and rats had sufficient food to breed. Between breeding seasons of terns cats had few food sources but rodents; few rats survived. When cats were eradicated rats became the apex predator, survived longer during the period when terns migrated and increased longevity. Opportunities for rats to breed during sooty tern breeding seasons have increased from one season before (A) to two seasons after (B) cat eradication.

period, spanning two sooty tern breeding seasons, has mediated a doubling of reproduction activity.

6.5.4. Impact of cat eradication on seabirds

Cat eradication on Natividad Island, Mexico significantly decreased black-vented shearwater *Puffinus opisthomelas* mortality (Keitt & Tershy 2003) and a decline in sooty tern adult mortality also occurred on Ascension when cats were eradicated. The eradication of cats is seen as particularly beneficial to seabirds (Nogales *et al.* 2004) but to the best of my knowledge where beneficial effects have been recorded these were on islands without rats (e.g. Natividad Island, Marion Island in the sub-Antarctic and Baker Island in the Pacific).

Bonnaud *et al.* (2012) reported that cat removal on Port-Cros Island in the Mediterranean was a success for the yelkouan shearwater *Puffinus yelkouan* population despite an increase in mesopredator relative abundance. However, their four year study may not be of sufficient duration to detect changes in the adult population size that may have resulted from an increased interaction between rats and yelkouan shearwaters.

Ratcliffe *et al.* (2009) estimated breeding success of masked boobies, brown boobies and brown noddies that had re-located from offshore predator-free islets to the main island of Ascension to be 0.19, 0.28 and 0.26 chicks fledged per pair, respectively. These estimates are consistent with the 0.31 chicks fledged per pair breeding success that I found. Breeding successes for these seabirds are low when compared with conspecifics elsewhere and were unlikely to lead to an increase in the size of the respective breeding populations. Ratcliffe *et al.* (2009) proposed three possible reasons for low breeding success: (1) low food availability; (2) lack of prior breeding experience; and (3) rats. Low food availability may indeed be a cause but what appears to be relatively satisfactory muscle scores of ≥ 1 and mean masses of 157.6 g of sooty tern chicks in some breeding seasons suggest that food is available during some breeding seasons. Ashmole (1963a) recorded the weight of 19 chicks during a season when there was a food shortage and none weighed more than 120 g. These chicks were approximately one third lighter than the body mass of chicks during my study period. The sooty tern breeding population does not lack breeding experience as the colony has bred on Ascension for > 300 years and has evolved a sub-annual breeding season (Chapter 2) leaving rat predation as the prime reason for low fledging success of seabirds on Ascension. Polynesian rat predation on Kure Atoll in the Pacific Ocean was the cause of low sooty tern fledging successes (i.e. 0.18, 0.24, 0.27 and 0.60 from 1965 to 1968; Woodward 1972) that were similar to the fledging success of 0.31 (chicks fledged per pair) on Ascension.

Counts of bird carcasses are typically used to assess the impact of oil spills and powerlines, for example (Newton 1998). Here, I have compared counts of adults killed by cats with counts of chicks killed by rats to assess their relative impact using an adult:chick ratio of 1:3. This ratio was similar to that found on Bird Island in The Seychelles where Feare and Doherty (2011) estimated that one bird was recruited into the breeding population for every 3.8 chicks that fledged. Carcass counts prior to cat eradication, and adjusted by the adult:chick ratio, and those post-cat eradication were similar, varying by just 1%. In addition, it is probable that rats have a negative impact on at least three other trophic levels (e.g. mice, plants, invertebrates). I was unable to identify any change in egg predation due to rats. While I predicted that the benefits of cat eradication for the sooty tern population would be out-weighed by an increase in rat predation, in reality I found that the single-predator regime (rats) and the pre-existing dual-predator regime (rats and cats) were equally detrimental to the sooty tern population. The eradication of feral cats has not resulted in an increase in the breeding population size of sooty terns. My finding that the eradication of cats on Ascension has resulted in large apparent increases in rat abundance in a seabird colony is bound not to be welcome; however, it does echo the concerns of Stonehouse (2002) about negative outcomes of such a cat eradication programme.

Future research into rat predation on Ascension should focus on the repeat censuses of the sooty tern population until 2016 by which time any changes in the size of the sooty tern population will be apparent. Conclusive photographic evidence of rats killing chicks as seen in video footage of mice eating albatross chicks (Wanless *et al.* 2007) is required. Confirmation that rats in the tern colony time their breeding to coincide with that of sooty terns is also required. Studies are needed to establish the importance of other predators (e.g. mice) and other invasive species (e.g. Mexican thorn) in relation to the diet of rats.

6.5.5. Implications for management

I have shown that an understanding of the consequences of management strategies for invasive species such as eradication of an apex predator can be slow to materialize. The removal of non-native cats from seabird island ecosystems is likely to result in an immediate increase in adult survival of seabirds (Nogales *et al*. 2004) but as many seabirds breed for the first time five or more years after fledging (Schreiber & Burger 2002), the impact on the size of the breeding population as a result of mesopredator release and increased predation of eggs and chicks may be slow to emerge (Towns *et al.* 2006). Managers should plan to monitor the outcomes of apex predator eradication for a period that extends beyond the age of first breeding of the prey species. Mine is one of the few studies to demonstrate that trophic cascades associated with removal of an invasive species (Courchamp *et al*. 1999) can result in a rapid increase in mesopredator abundance that may have a major impact on an island's ecosystem (Bergstrom *et al.* 2009). This finding runs counter to those that support cat eradication as *the* solution to the detrimental impacts of invasive non-native species (Nogales *et al*. 2004). Conservation funding is often limited and conservation managers are frequently restricted to a step-by-step approach to eradication of invasive species (Bell & Ashmole 1995, Bergstrom *et al.* 2009). Eradication of mesopredators can be much more costly than the eradication of apex predators (Bergstrom *et al.* 2009, Lambert 2010) and, thus, apex predator eradication linked to control of mesopredators should be the default position adopted to conserve seabirds. Thus, I think that restoration plans that include apex predator eradication are doomed to failure in most cases unless funds are also available to control mesopredators.

I have been able to quantify the impact of rats on survival and productivity of the sooty tern population on Ascension Island and my findings indicate that there is an urgent need to reduce rat abundance in the tern colony. I have shown that in 2004 rats became a major factor limiting the population size of sooty terns. However, the cause of the historic decline in the sooty tern population has not yet been identified.

In Chapter 7 I will diagnose the cause of the historic decline in population size. (Note: The publication status of Chapter 6 as of December 2013 is that it is currently being prepared for submission).

Chapter 7

DIAGNOSING ENVIRONMENTAL FACTORS LIMITING THE SIZE OF THE SOOTY TERN POPULATION ON ASCENSION ISLAND

7.1. ABSTRACT

Environmental factors frequently limit population size and they must be understood before any desired change in population size can be achieved. Identifying such limiting environmental factors is a prerequisite to successful management of the target population. Feral cats were identified as the major factor limiting the survival of adult sooty terns on Ascension Island. However, the eradication of cats has not resulted in a predicted increase in the size of the sooty tern population but in an increase in rat abundance which is now limiting the breeding success of sooty terns. Here, I investigate competing hypotheses for the causes of the historic population decline of Ascension sooty terns. I explore the hypothesis that sooty terns were limited by feeding conditions in the ocean by assessing the numbers of foraging tuna. Sooty terns are regarded as near-obligate commensals with small tuna. From a stable population size, a stepwise decline in the size of the breeding population of sooty terns occurred in the early 1970s as tuna catches began to rise sharply. I also found that the proportion of squid in the diet of sooty tern chicks was larger than that of conspecifics on other islands but my sample size was small. My results suggest that the sooty tern population on Ascension was limited by insufficient recruits to the breeding population as a consequence of over-fishing and food of poor quality fed to chicks. Trends in the population size of sooty terns, in tuna catches and in rat

abundance were modelled and projections to 2022 revealed a predicted slow decline in the size of the sooty tern population.

7.2. INTRODUCTION

The environment is the ultimate regulator of animal populations (Krebs 2001) and several environmental factors may influence long-term trends in population size (Oro *et al.* 2004). Among the key environmental factors that limit bird numbers are resources (particularly food availability), competition, predation, parasites, weather and human activity (Newton 1998). To identify the major factors that limit the size and/or contribute to the decline of a particular population, it is necessary to distinguish between the various environmental factors that have been proposed to explain population size.

Green (1994) suggested examining different focal periods during which population size presented different trends to identify the cause of decline in a particular population. He suggested using correlations between trends in numbers and measurements of environmental factors. At the very least such an approach requires demographic data from periods when population decline was occurring, and from when population size was stable or increasing. Ideally, the latter would precede the period of population decline. Allied to such data would be those relating to environmental factors during both periods.

The time period when a population decline occurred can be obtained from a long series of population censuses and an analysis of population trends. Environmental factors which changed at the same time as the start of the population decline are implicated as probable causes. Comparison of changes in trends in numbers over time with changes in environmental factors for one population is the study of coincidence and correlation, rather than causality. However, Green (1994) recommended that the danger of correlation revealing non-causal relationships can be minimized by completing an *a priori* list of plausible causes of population change based on studies of the natural history of the species. Of such causes of population decline in birds that have been identified by Newton (1998), weather and parasites are more likely to cause short-term fluctuations in the size of populations rather than a sustained decline; food supply (Fisher & Lockley 1954, Nelson 1980, Nettleship *et al.* 1994, Newton 1998, Oro *et al.* 2004) and predation by non-native species (Nettleship *et al.* 1994, Russell & Le Corre 2009, Hilton & Cuthbert 2010), or a combination of these (Rauzon 2007), are probably the most likely causes of long-term decline in the size of seabird populations.

On Ascension there is an urgent need to diagnose the cause of the decline in sooty tern population size because previous predictions have not been confirmed. Feral cats were observed predating seabirds on Ascension but predictions of Ashmole *et al.* (1994) and Croxall *et al.* (1984) that cat eradication would result in an increase in the size of the sooty tern population have not been supported by my research (Chapter 3). The eradication of cats on Ascension between 2002 and 2004 resulted in a range expansion of five seabird species that were previously restricted to predator-free offshore stacks and islets (Ratcliffe *et al.* 2009). The main aim of the cat eradication programme was to facilitate the return of the Ascension frigatebird (Pickup 1999) and this was achieved in December 2012 when two pairs nested on the main island. However, the sooty tern population that had co-existed with cats on the main island since 1815 has not increased in size despite a decline in adult mortality of 4,500 birds per breeding season (Chapter 6).

The failure of the sooty tern population to increase in size following the eradication of cats indicates that factors other than cat predation were limiting the population or that new (non-feline) factors have come to the fore. Bretagnolle *et al.* (2011) suggested that identifying the factors limiting population growth was fundamental to reversing the decline in the population size of little bustards *Tetrax tetrax* in western France. On Ascension identifying such factors is essential to halt the decline, or to increase the size, of the sooty tern population.

7.2.1. Timing of the population decline of sooty terns on Ascension

More than 2,000,000 sooty terns bred on Ascension Island between 1877 and 1958 (Chapter 3), but less than 500,000 birds (< 25%) bred from 1990 to the present day (Chapter 3). Simmons (pers. comm.) lived on Ascension between 1962 and 1964 and stated that the population began to decline in the early 1960s. When population size declines it might also be expected that the number of colonies would also decline (Mitchell *et al*. 2004); this occurred on Ascension Island. However, changes in the number of colonies may not be contemporaneous with overall declines in population size with a lag of approximately 20 years being detected in a study of black-legged kittiwakes in the British Isles (Coulson 1983). Green (1994) suggested that more reliable diagnosis of factors limiting the abundance of species can be obtained from studies of more than one colony. Of the sooty tern colonies that were monitored on Ascension, the smallest of three colonies (≈ 50 pairs) was lost during the study period. The date when this sooty tern colony was abandoned provides further insight into causes of the population decline.

7.2.2. Factors that may limit the population size of sooty terns

7.2.2.1. *Chick starvation.* Food shortage is a common problem for seabirds; typically, starvation is an isolated occurrence when individual parents cannot locate sufficient food to feed their young, especially after a parent has died (Harrison *et al.* 1983). Sooty terns in the Pacific are known to be severely affected by ENSO events that have caused starvation and extensive chick mortality (e.g. > 90% of sooty terns on Christmas Island 1982–1983; Schreiber *et al.* 2002). On Ascension Ashmole (1963a) used chick body mass to identify breeding seasons when food shortage was the likely cause of chick mortality. Of chicks aged 30 days, mean body mass in 1958 was ≈ 125 g (n = 10 chicks) and in 1959 it was ≈ 60 g (n = 19 chicks). Certainly, in the latter starvation was assumed to be the main cause of chick loss (Ashmole 1963a). During my study period chicks were reported to have died of starvation in 1991 (S. Newlyn-Browne pers. comm.) and in 2003 (D. Boyle pers. comm.) but I have no data to support this contention further.

7.2.2.2. *Infanticide.* Ashmole (1963a) and Harrison (1983) reported adult sooty terns (but not their parents) killing chicks. I observed and quantified similar interactions (see Chapter 5 for full details). Counts of dead chicks were monitored in a strip around the perimeter of four sub-colonies in 2005. The mean count per hectare was 59 dead chicks. My findings support those of Ashmole (1963a) and Harrison *et al.* (1983) that the impact was negligible and was unlikely to be a major limiting factor. However, in The Seychelles more losses were due to pecking by adults than to starvation or predation (Feare 1976).

7.2.2.3. *Predation by feral cats.* In 1958 feral cats were identified as the major predator of sooty terns (Ashmole 1963a) and in 1992 as the main cause of the decline in the size of the sooty tern population (Ashmole *et al.* 1994). However, the eradication of cats has not resulted in an increase in the sooty tern population size and this clearly indicates that population size must be limited by other factors.

7.2.2.4. *Predation by frigatebirds*. Losses of chicks to frigatebird predation in 1958 and 1959 ran into the thousands (Ashmole 1963a) and I found that between 1996 and 2009 chick mortality from adult and juvenile frigatebirds was 2,463 and 262 chicks per breeding season, respectively. Taken together, frigatebirds predated 5% of chicks per season (further details in Chapter 5). In the Shetlands, UK great skuas *Stercorarius skua* are known to predate black-legged kittiwakes and there is some evidence that they may detrimentally affect their breeding success (Votier *et al.* 2008b). However, in general, native avian predators do not regulate the size of prey populations (Newton 1998) and as frigatebird predation was relatively low, frigatebirds were unlikely to limit the size of the sooty tern population.

7.2.2.5. *Predation by mynas and rats*. Ashmole (1963a) reported that mynas and rats were effectively absent from the tern colony in 1958 and 1959. During my study period the number of eggs per season destroyed by mynas varied between 2,443 and 35,970 (mean: 16,483 ± 3,366 eggs, $n = 10$ field seasons; see section 5.4.3). In 2009 the number of chicks killed by rats was 19,500 chicks (see section 6.4.5.3). During my study period the intensity of predation from both of these non-native predators could be major limiting factors (Chapters 5 and 6).

7.2.2.6. *Nest sites*. Shortages of suitable nest sites have been reported as limiting the size of some seabird populations (Newton 2003, Feare *et al.* 2007). However, on Ascension the large area (≈ 1 km^2) previously occupied by colonies, but now unoccupied, suggests that nest site availability for sooty terns has not been a factor that has limited the size of the population historically.

7.2.2.7. *Egg harvesting and disturbance by humans*. In 1958 and 1959 some sooty tern eggs were harvested for human consumption (Stonehouse 1960). During periods of war the human population on Ascension fluctuated markedly and so too have the impacts of military personnel on the tern colonies. In 1942 one large colony was destroyed to accommodate the military airfield (Clarke 1944, Chapin 1946) and in 1983 Mars Bay (the site of one of the tern colonies) was used as a target range (McQueen 2005, H. Pike pers. comm.). Therefore, it is important to assess the impact of such human interference on the size of the sooty tern population.

On land (i.e. on the breeding grounds) the potential candidates that may have limited the size and growth of the sooty tern population on Ascension are human activities, and predation by cats, rats and mynas. Throughout the literature sooty terns are described as among the most aerial of extant bird species in the world (e.g. Schreiber *et al.* 2002). I have shown that this pelagic species spends ≈ 9% of its life on land (see section 4.5.6). Sooty terns spend most of their life foraging over the ocean and food availability in the marine environment is critical to their survival.

7.2.3. Marine environment

Marine fish populations have collapsed (Hutchings & Reynolds 2004) and larger bodied marine taxa have led the decline (Myers *et al.* 2007). The loss of these apex consumers in the marine ecosystem has affected the process of trophic cascade. It has had unanticipated consequences (e.g. coralline algae diminished in concert with removal of large fish; Estes *et al.* 2011) and can negatively impact the demography of seabirds (Le Corre & Jaquemet 2005). For most fish populations reliable quantitative data on abundance have been available for the last 20–30 years. The median maximum decline among 232 populations of marine fish is 83% (Hutchings & Reynolds 2004). In the oceans, commercial fishing has greatly reduced the abundance of apex consumers (Safina & Klinger 2008). Compared with only 50 years ago, the abundance of large pelagic fishes such as tuna in tropical, international waters has declined by roughly 90% (Safina 2003). Longline and purse seine fishing for Atlantic yellowfin tuna *Thunnus albacares* commenced in the 1960s and rapidly expanded. The International Commission for the Conservation of Atlantic Tuna (ICCAT) reported that by 1980 the annual catch in the tropical Atlantic had reached an unsustainable level of 130,000 tonnes (t) and peaked in 1990 at 160,000 t (ICCAT 2010).

7.2.4. Sooty tern association with tuna

Pelagic seabirds rely almost entirely on the marine ecosystem for their diet, but the distribution of marine food can be patchy in both time and space (Ballance & Pitman 1999, Schreiber & Burger 2002, Jaquemet *et al.* 2007). Some seabirds appear to be attracted to large fish because the latter’s foraging activity forces small prey species to the surface where seabirds have access to food that otherwise would be unobtainable. Tuna are large oceanic species that school primarily by size in single or multi-species groups (Au & Pitman 1986, Le Corre & Jaquemet 2005). Flocks of seabirds associated with surface-feeding schools of tuna, in particularly yellowfin tuna, are characteristic of tropical oceans. The association of seabirds with yellowfin tuna has been observed in all oceans of the world (Ashmole & Ashmole 1967, Burger 1988, Clua & Grosvalet 2001, Gaston 2004, Le Corre & Jaquemet 2005). Tropical seabirds in flocks appear to feed mainly on prey driven to the surface by tuna, which are the only sizeable pelagic fishes known to form abundant and large surface schools in the tropical oceans (Au & Pitman 1986, Burger 1988). Sooty terns are regarded as near-obligate commensals with small tuna (Ashmole & Ashmole 1967, Au & Pitman 1986) when they feed on micronekton (mainly small fast-swimming fishes such as those of the Exocoetidae) driven to the surface (Ribic *et al*. 1997). Sooty terns do not have waterproof feathers and quickly become water-logged if immersed in water (Johnston 1979). Bird do not plunge dive but catch prey within a few centimetres (<10 cm) of the surface while on the wing by air dipping or contact dipping (Ashmole & Ashmole 1967). Single-species flocks of foraging sooty terns are associated with small surface-feeding tuna. These small tuna are now being harvested at an increasing rate with the average weight of individual tuna landed declining by more than 50% between 1970 (> 20 kg) and 2000 (< 10 kg) (ICCAT 2010). As a result, within the foraging distance (≈ 500 km; Flint 1991) of sooty terns breeding in the Ascension Island colonies, stocks of tuna that sooty terns rely on to drive their prey to the surface have probably declined in both number and in size of individual fish.

7.2.5. Food availability and dietary shifts

Measuring food availability for pelagic seabirds is notoriously difficult (Gaston 2004, Le Corre & Jaquemet 2005). Quantitative information on seabird diet composition (Wanless *et al.* 2005) and shifts in diet of seabirds may provide indications of ecological change within marine systems (e.g. Käkelä *et al.* 2010). For example, over-fishing of tuna can affect those species such as sooty terns that depend upon tuna to drive small fishes to the surface with the result that birds may change their diets. Removal of the tuna, the apex consumers, by commercial fishing has resulted in an increased abundance of squid (Teuthida) and possibly small fish for seabirds (Rodhouse 2005). However, despite a possible increase in small fish abundance sooty terns are unable to feed on these fish if they remain below the surface. Thus, removal of apex marine consumers may have unforeseen consequences as did the removal of apex species (i.e. cats) on the land (Chapter 6).

Variation in the diet of seabird chicks can provide clues to food availability within the range of the breeding colony (Ashmole 1963b, Flint 1991, Gaston *et al.* 2008). The diet of sooty terns is well studied and largely consists of pelagic fish from more than 33 families and squid (Hensley & Hensley 1995, Schreiber *et al.* 2002, Colchero 2008). Sooty terns in the Hawaiian Islands in the Pacific have a diet of 46.5% fish and 53.5% squid by volume (Harrison *et al.* 1983) and on Houtman Abrolhos Island in the Indian Ocean diet comprises 39% fish and 61% squid by volume (Surman & Wooller 2003). Fish are an important constituent of the diet of sooty terns because pelagic fishes have a high lipid content (Cowey & Sargent 1977, Croxall & Prince 1982, Iverson *et al.* 2007) and lipid is needed for successful breeding (Wanless *et al.* 2005).

7.2.6. Identifying limiting factors – objectives

Diagnosing the major environmental factors limiting the size and growth of the sooty tern population is essential for halting further declines. I have shown that a previous attempt to diagnose the cause of population decline was problematic (Chapter 6) but support for the hypothesis that feral cat predation was a major limiting factor remains (Ratcliffe *et al.* 2009). Given the controversy, and to support my argument that cat predation was not the major factor limiting the size of the sooty tern population on Ascension, I investigated trends in a population of sooty terns that nested on a predator-free islet (BBI). Furthermore, I determine trends in the population sizes of cats, mynas, rats, and human populations on Ascension Island, trends in the tuna population in the Atlantic Ocean, and trends in the quantity of squid consumed by sooty tern chicks. I have used variation in tuna catches and sub-annual censuses of the sooty tern population over decades to establish if the two variables are correlated. I investigated the influences of environmental factors on the size and growth of the sooty tern population by examining how they co-vary and by using them to predict the future demography of sooty terns on the island.

7.3. MATERIALS AND METHODS

7.3.1. Study area and period

The study area was the same as described in section 2.2.1 with the addition of BBI. The islet is a bird sanctuary and an Important Bird Area (IBA reference number SH002; Sanders 2006). BBI is free of non-native predators, is 5 ha in area and is a steep-sided rock ≈ 100 m off the eastern corner of the main island of Ascension (Fig. 7.1; further details in Stonehouse 1962a, Sanders 2006). The

Figure 7.1. Boatswainbird Islet (BBI), Ascension, South Atlantic viewed from the Letterbox peninsula. The islet was the location of a small sooty tern colony until it was abandoned between 1958 and 1990. (Photo: D. Thomas).

study period encompassed years between 1958 and 1990 when the size of the sooty tern population on Ascension declined rapidly (Chapter 3). I added to my datasets, which cover the breeding seasons between 1990 and 2012, other data, the earliest of which was from 1942. These were derived from a literature review targeting population data on humans, cats, rats, mynas and tuna.

7.3.2. Monitoring sooty terns on BBI

Until recently the longest established colony of sooty terns on Ascension was located on BBI (see Chapter 3 for mainland colony movements). Breeding on the islet was roughly in phase with colonies on the mainland (Stonehouse 1962a). Historical records of sooty terns breeding on BBI prior to the study period (1876 to 1990) were also obtained from the literature. I visited the Islet in 1990, 1996 and

2001, and recorded sooty tern breeding events. More recently, permits to land on BBI were restricted and records of breeding in 2002 and 2009 were obtained from conversations with RSPB ornithologists (R. White & M. Bolton pers. comm.) who visited BBI during the breeding seasons of sooty terns.

7.3.3. Dietary shift

Temporal variations in chick diet were monitored by collecting prey items brought to the colony by adult terns and regurgitated by them (or regurgitated by the chicks) during breeding seasons in 2004, 2009 and 2012. Mass of prey was recorded with a Pesola spring balance to the nearest 1 g and total length of each prey was recorded with a stopped metal rule to the nearest 1 mm. Regurgitated prey fed to chicks by adults was categorised as either fish or squid. The numbers of fish or squid passed by adults to chicks were also counted (Fig. 7.2). The

Figure 7.2. A sooty tern on Ascension Island in the South Atlantic in 2009 feeding squid to a chick. (Photo: D. Osborn).

percentages of fish and squid prey fed to chicks were calculated. A literature search revealed six islands in the Pacific and Indian Oceans where counts of prey items fed to sooty tern chicks were recorded and the literature search also described the diet of sooty tern chicks on Ascension in 1958.

7.3.4. Identifying key environmental factors

To identify environmental factors that limit the size of the Ascension sooty tern population, I used census data as presented in Table 3.4 in combination with changes in the abundance of humans (Clarke 1944, Hart-Davis 1972, McQueen 2005, Knipe 2009), cats (Chapin 1946, Ashmole 1963a, Davies 1966, Hart-Davis 1972, Merritt *et al.* 1992, Bell & Boyle 2004), mynas (Stonehouse 1962a, Packer 1983, Varley & Dickey 1994, Saavedra 2009), rats (Chapin 1946, Ashmole 1963a, Hart-Davis 1972, Packer 1983, Chapter 6) and tuna (ICCAT 2010). All of these parameters have the potential to limit the size and/or growth of the sooty tern population. I tested if variation in the abundance of these species could account for the decline in the population size of sooty terns that occurred between 1959 and 1990. I constructed graphs to illustrate the abundance of species before, during and after the dramatic decline in the size of the sooty tern population. I used the results of the statistical tests and the illustrative graphs to identify species predicted to limit the size of the sooty tern population. Time series of both sooty tern population censuses (1942–2012) spanning the period of sooty tern population decline (1959–1990), and of population estimates of species predicted to limit sooty tern population size and growth were constructed to project population trends for sooty terns for the 2013–2022 period and, thereby, to predict their future population size.

7.3.5. Statistical analyses

Spearman Rank Correlation was used to test for a relationship between sizes of populations of cats, rats, mynas and humans, and the population size of sooty terns between 1942 and 2012. Differences between the provisioning of chicks on Ascension and on other islands were tested for with a Mann-Whitney *U*-test.

7.4. RESULTS

7.4.1. Loss of the sooty tern breeding colony on BBI

The colony on BBI which has been occupied since the late 1800s was abandoned in the 1990s. Saunders (1881) and Gill (1878) recorded sooty terns breeding on BBI in 1876 and 1877, respectively. Sooty terns were collected from the islet in 1876 by the Challenger Expedition and by the Blossom Expedition in 1925 (Simmons 1927). In 1957 the governor of St Helena recorded sooty terns breeding on the islet (Harford 1958). In 1958–1959 there were about 20 pairs nesting on the north side of the islet (Stonehouse 1962a). During my study period I saw no sooty terns breeding on BBI during breeding seasons of 1990 and 1996, and in 2001 just a single pair of birds bred. None was seen breeding in 2002 (R. White pers. comm.) or 2009 (M. Bolton pers. comm.). The loss of the breeding population of sooty terns on BBI occurred between 1958 and 1990.

7.4.2. Trends in environmental factors

There was a non-significant negative correlation between the size of the sooty tern population and that of rats ($r_s = -0.46$, $n = 8$, $P = 0.22$; Fig. 7.3a) and humans ($r_s = -0.21$, $n = 8$, $P = 0.58$; Fig. 7.3b) and, based on anecdotal data, a non-

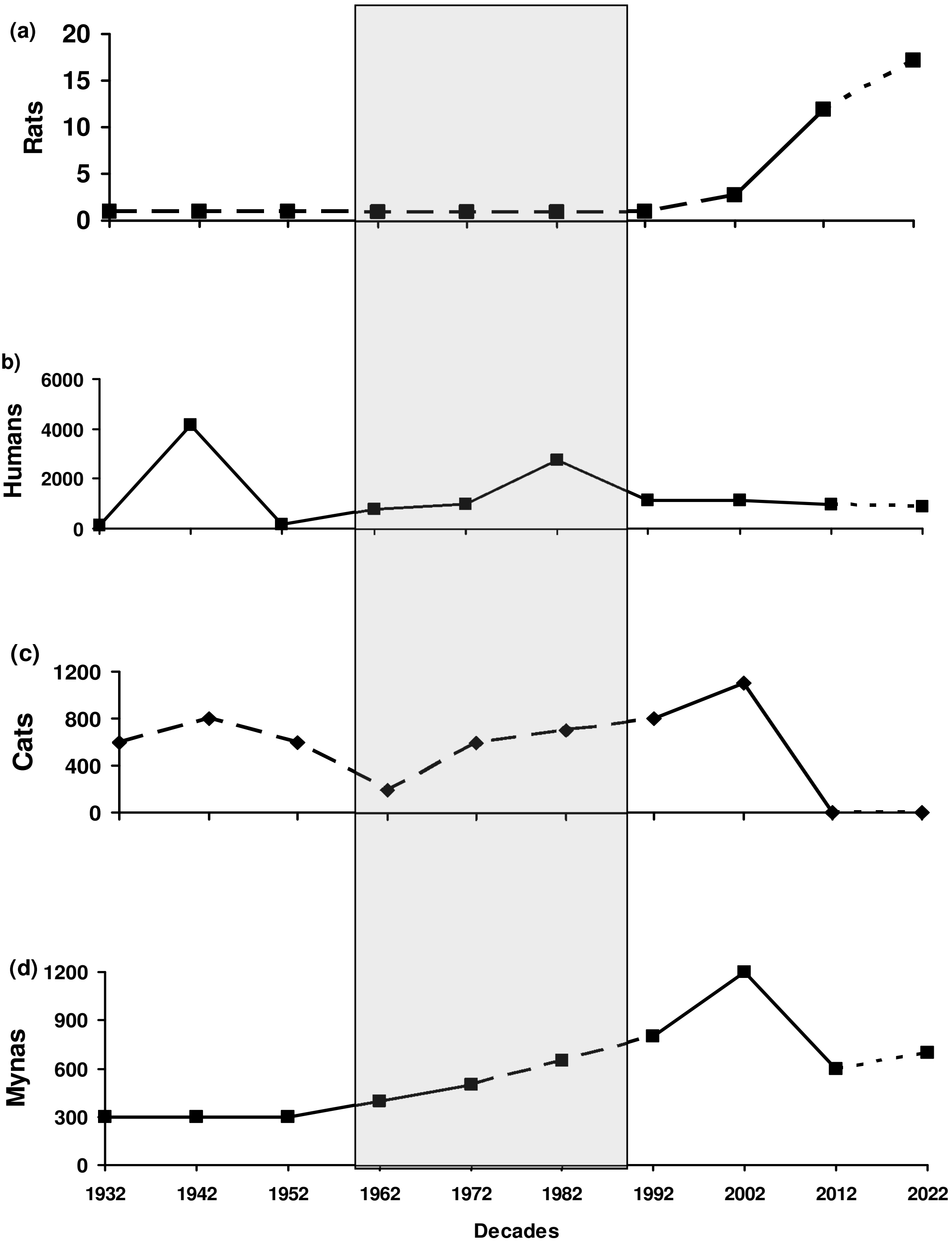

Figure 7.3. Population trends of (a) rats (relative abundance [/100TN]), and (b) humans, (c) cats and (d) mynas (all individuals) spanning decline in the population size of sooty terns (1959–1990; grey shading) on Ascension Island in the South Atlantic. Long-dashed lines indicate anecdotal data and short-dashed lines are projections based on data collected in 2012.

significant positive correlation between that of cats (*r*$_S$ = 0.07, *n* = 8, *P* = 0.62; Fig. 7.3c) but a significant negative correlation with that of mynas (*r*$_S$ = -0.80, *n* = 8, *P* = 0.03; Fig. 7.3d). However, during the period of rapid decline in the size of the sooty tern population (i.e. 1958–1990), the population size of rats in the tern colony appears to have been low and stable, the size of the myna population may have increased from approximately 400 to 800 birds and there was a spike lasting approximately 2 years in the human population during the Falklands War.

7.4.3. Relationship between population sizes of sooty terns and tuna

During the period of rapid decline in the size of the sooty tern population, the relationship (Fig. 7.4) between tern population size and catches of yellowfin tuna

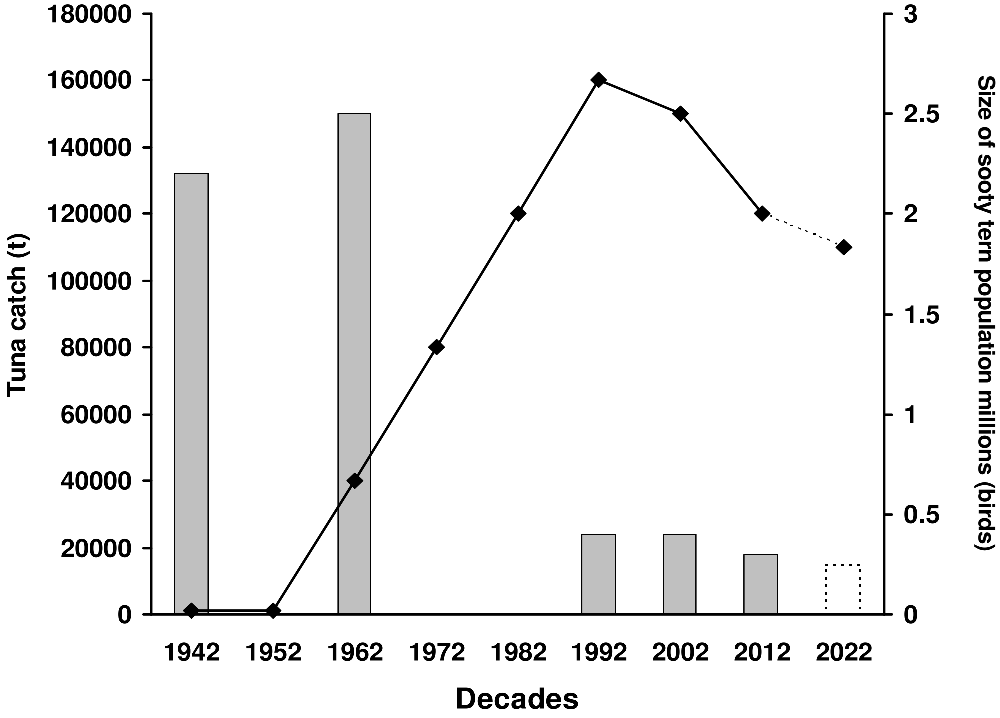

Figure 7.4. The relationship between sooty tern population size from censuses (bars) and yellowfin tuna catch (points and line) between 1942 and 2012 on Ascension Island in the South Atlantic. The dashed bar represents the projected population size of sooty terns on the island in 2022 while the dashed line represents the projected trend in yellowfin tuna fishing between 2012 and 2022.

in the South Atlantic was negative but only marginally significant ($r_s = -0.70$, $n = 8$, $P = 0.06$). A step-wise decline in the size of the sooty tern population occurred in the early 1970s as tuna catches began to rise sharply. When the tuna catch peaked in 1990 the sooty tern population reached a lower and approximately stable level similar to that found in censuses between 1990 and 2011 (Fig. 7.4).

7.4.4. Dietary shift

Four datasets provided estimates of fish and squid in the diet of sooty tern chicks (Table 7.1). The mean fish prey in 2004, 2009 and 2012 in the diet of chicks on Ascension was 17% of all food deliveries by adults (Table 7.1). Of the three fish prey delivered which are not normally associated with fish driven to the surface by tuna, two were pipefish (most closely resembling needlefish *Platybelone argalus trachura* that are commonly found in Ascension waters), and one a pelagic sucking fish *Remora remora.* Other changes in diet may have occurred during the

Table 7.1. Dietary composition as percentage of observations (*n*) made up of fish or squid fed to sooty tern chicks from observations and counts of prey regurgitated by birds during ringing on Ascension Island in 2004, 2009 and 2012.

Year	**Percentage composition of diet made up of:**		***n***
	fish	**squid**	
2004 – regurgitation by adults during ringing	27	73	18
2009 – regurgitation by chicks during ringing	6	94	48
2009 – direct observation through binoculars	17	83	42
2012 – direct observation through binoculars	16	84	19
Mean	17	83	127

1991 breeding season when much of the tern colony contained fresh guano of an unusual pink colour (unfortunately, no further details were collected). Prey, (Fig. 7.5) other than fish and squid, were recorded most breeding seasons; incubating sooty terns were seen on occasions to catch and eat endemic crickets *Gryllus abnormis* and tropical migratory locusts *Locusta migratoria migratorioides* that

Figure 7.5. Food items fed to sooty tern chicks on Ascension Island in 2012: top – megalopa larvae of Ascension Island rock crab; and bottom – common purple snails. (Photos: N. Day & S.J. Reynolds).

passed close to their nest. In 2012 I observed for the first time sooty terns feeding chicks with large quantities of megalopa larvae of Ascension Island rock crabs and common purple snails *Janthina janthina* (Fig. 7.5).

7.4.5. Predictive population trend

Sooty tern population census data, the relative abundance of rats in the tern colony and tuna catches were projected to illustrate the predicted trend in the size of the sooty tern population (Fig. 7.6). The trends in rat relative abundance and

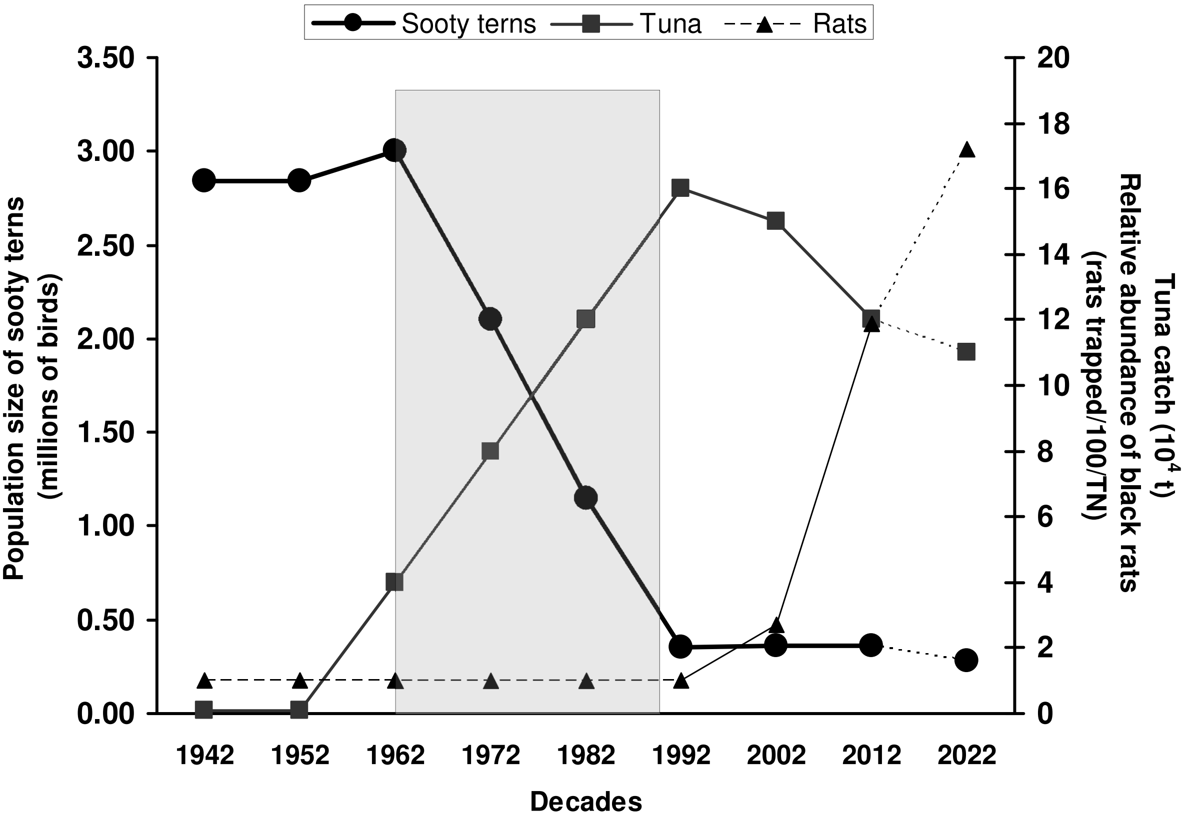

Figure 7.6. Population model illustrating trends in sooty tern population census data and the relative abundance of rats in the tern colony on Ascension Island in the South Atlantic, and tuna catches in the Atlantic, from 1942 to 2012. The time series spans the period of rapid decline in the size of the sooty tern population between 1959 and 1990 (grey shading). Dashed lines indicate anecdotal data and trends for the three parameters are projected to 2022 as dotted lines.

tuna harvested between 2005 and 2011 suggest that a new tipping point in the size of the sooty tern population occurred in 2012. Poor breeding success between 2005 and 2011 will result in fewer recruits to the sooty tern breeding population in the forthcoming decade. Cats have been eradicated and trends in the human population suggest that its size on Ascension has not limited the size of the sooty tern population. In 2009 there was a major cull of mynas (Saavedra 2009) and until the population recovers, mynas are not likely to be a factor limiting the size of the sooty tern population.

7.5. DISCUSSION

The aim of this chapter was to diagnose the key ecological factors that have limited the size of the sooty tern population on Ascension Island. The results provide addition support for my hypothesis (as outlined in Chapter 6) that feral cats were not the major factor limiting their population size. The timing of the loss of the sooty tern breeding colony on BBI was significant because it occurred on a predator-free islet and in the period before cats were eradicated on the main island. This suggests that factors not associated with cat predation were limiting the tern population on both BBI and on the main island. Interestingly, the time lag between the decline in population size and in the number of colonies was similar to the 20 years found by Coulson (1983) in black-legged kittiwakes. Other potential factors such as human pressures and myna predation that had the potential to limit tern population size were also rejected.

Overall, my results suggest that changes in the marine environment (i.e. a shortage of schooling tuna) may have had the most influence on the size of the sooty tern population on Ascension Island. My results also suggest that variations in rat abundance in the breeding colony were also a major factor. Examining trends in these limiting factors allowed projections of them and of the population size of sooty terns, revealing that in the next decade the size of the tern population may shift from a position of relative stability, as has been the case over the last 20 years, to one of slow decline.

7.5.1. Dietary shift

During the last 50 years cape gannets *Morus capensis* (Grémillet *et al.* 2008), macaroni penguins *Eudyptes chrysolophus* (Cresswell *et al.* 2008), marbled murrelets *Brachyramphus marmoratus* (Norris *et al.* 2007) and other seabirds (Harris *et al.* 2007) have changed their diet and now eat less nutritious marine prey. Previous research has shown that fish discards from the fishing industry have roughly half of the calorific value of birds' natural prey and this has had a negative impact on young chicks (Grémillet *et al.* 2008). Breeding success improved when murrelets fed at higher trophic levels (Norris *et al.* 2007), but it can decline when seabirds shift diets to less nutritious prey (e.g. snake pipefish *Entelurus aequoreus*; Harris *et al.* 2007). In fish, lipids are the major source of energy reserves (Cowey & Sargent 1977). Squid contains significantly less lipid than fish (Croxall & Prince 1982) and low-lipid prey are inadequate to meet the energetic demands of breeding (Wanless *et al.* 2005). Typically, lipid-rich prey such as pelagic schooling fish are needed for successful breeding of seabirds (Wanless *et al.* 2005). Kitaysky *et al*. (2006) and Hipfner (2008) have shown that lipid-poor diets during development reduce the body condition of young seabirds, resulting in reductions in survival and in recruitment.

On Ascension there is some limited evidence that a dietary shift in chick provisioning has occurred, probably in the early 1970s. During the BOU expedition (of 1958–1959), the diet of sooty terns on Ascension Island was similar to that in the Cook Islands in the Pacific where fish comprised 60% of the foods observed (Ashmole & Ashmole 1967). On Ascension in 1972 levels of polychlorinated biphenyls (PCBs) were recorded from lipid extracted from sooty tern adults and chicks (Johnson 1973). PCB concentrates were much higher in pelagic fish than in squid (Schiff *et al.* 2007). Half of the samples analysed had high levels of PCBs which suggests that birds were eating fish rather than squid. Accordingly, it may be concluded that in 1972 sooty terns were probably still feeding their chicks primarily on fish. On Ascension between 1972 and 2004 the proportion of fish fed to sooty tern chicks had declined from 50–60% in 1972 to 17% in 2004. The percentage of fish in the diets of chicks in 2004, 2009 and 2012 on Ascension was 16.5% (Table 7.1), compared with 62.2% on islands in the Pacific and Indian Oceans (Table 7.2). Furthermore, the percentage of fish in the diet of chicks on Ascension was significantly smaller (Mann-Whitney U-test, $U = 24$, $P < 0.05$) than that percentage of fish fed to chicks at other sooty tern colonies. This apparent dietary shift did not occur in all subsequent breeding seasons as in 2007 small fish 59 mm long ($n = 5$) and possibly rudderfish *Centrolophus niger*, were found as sun-dried regurgitants on the nesting substrate. In 2012 chicks were predominantly fed on squid but also on megalopa larvae and common purple snails (Fig. 7.5). Megalopa larvae are rarely recorded foods taken by sooty terns and I was unable to find any records of sooty terns preying on purple snails; both observations suggest that small pelagic fishes were not readily available.

Table 7.2. Sample size (*n*) and percentage counts of prey (fish and squid) in the diet of sooty tern chicks on islands in the Pacific and Indian Oceans.

Year(s)	**Location**	**% of prey counts that were:**		***n***	**Source**
		fish	**squid**		
1963-1964	Christmas Is., Pacific	60	40	803	Ashmole & Ashmole 1967
1971	Manana Is., Hawaii	42	58	356	Brown 1976
1976	The Seychelles	70	30	10	Feare 1976
1983	Hawaiian Archipelago	69*	31*	?	Harrison 1983
1993-1999	Houtman Abrolhos, Australia	61*	39*	449	Surman & Wooller 2003
2002	Mozambique Channel	71	29	348	Le Corre & Jaquemet 2005

*Prey volume converted to prey counts using 60% fish = 38% volume (*n* = 803) and 40% squid = 62% volume (*n* = 498) (based on Schreiber *et al.* 2002).

The low abundance of fish in the diet of chicks on Ascension may have been due to a shortage of schooling tuna. Sooty terns are diurnal and nocturnal foragers (Mörzer Bruyns & Voous 1965) taking prey close to the surface without plunge diving (Schreiber *et al.* 2002). Fish driven to the surface by schooling tuna during the day and squid on the surface at night provide feeding opportunities. When fish cannot be caught, despite their abundance, sooty terns will feed on squid. A similar dietary shift by sooty terns was recorded in the North Atlantic on the Dry Tortugas in the Caribbean. Between 1920 and 1941 squid were absent from the diet of sooty terns whereas they were commonly found in their diet between 1992 and 1994 (Colchero 2008). The distance of 8,000 km between the sooty tern breeding colonies on Ascension and on the Dry Tortugas implies that species' demography may be influenced by ecological phenomena occurring across the entire tropical Atlantic. It is interesting to note that in the Atlantic common terns, which feed by plunge diving, continue to feed nearly exclusively on small pelagic fish (Granadeiro *et al.* 2002).

7.5.2. Predictive population trend

The analysis suggested that the population of sooty terns on Ascension (Fig. 7.4) has moved from a stable and relatively large size during the period preceding 1942 and extending to 1958, to a second smaller but stable size between 1990 and 2011. These two stable population states can be explained by a change in the density of tuna rather than by a change in the level of cat predation. The rapid increase in tuna fishing in the second half of the 20th century negatively correlated with the rapid decline in the size of the sooty tern population (Fig. 7.4). Food-supply and predation by non-native species have been identified as the major factors limiting avian population size (Fisher & Lockley 1954, Nelson 1980, Nettleship *et al.* 1994, Newton 1998, Oro *et al.* 2004, Rauzon 2007, Russell & Le Corre 2009, Hilton & Cuthbert 2010). Here, I have also identified food supply (i.e. the dietary shift from small fishes to squid) and now non-native species (i.e. an increase in rat abundance) as the major factors limiting the size of the sooty tern population on Ascension. I have used projections of trends in the size of tuna catches and in rat abundance to predict the likely population size of sooty terns in 2022 (Fig. 7.4). However, some care needs to be taken with interpretation of the population trend as data are not sufficiently comprehensive to make the predictions highly reliable (Sæther & Engen 2002).

7.5.3. Limitations and future directions

Some of the potential factors that may have limited the population size of sooty terns have been rejected. However, they may have the potential to limit the size of the sooty tern population and should be subject to further investigation in analyses encompassing more years of sooty tern census data. For instance, sooty terns have been recorded as suffering significantly from ant infestations (Feare 1999) and disease. Bartsch (1922) recorded “vast numbers of dead birds” (i.e. sooty terns) on Midway in the Pacific which were assumed to have been killed by a new unidentified disease. I also rejected cats and mynas as factors likely to limit the breeding success of sooty terns, at least during the period 2012 to 2022. However, the myna population may recover more quickly than expected (Holzapfel *et al*. 2006, Peacock *et al.* 2007) and domestic cats that are still found on Ascension might once again become feral; both should be monitored closely.

Green (1994) suggested that conclusions based on correlations between trends in numbers of a focal species and external factors may be misleading, instead recommending manipulative experiments to test such conclusions. Manipulative experiments in the marine environment are likely to be difficult to achieve but rat abundance on the site occupied by tern colonies (area < 100 ha) could be manipulated relatively simply by introducing effective rat control measures (i.e. using anticoagulant soaked in water at bait-stations every 20 m throughout the colonies; Meehan 1984, Wegmann *et al.* 2008). The preliminary conclusion that a dietary shift (from predominantly fish to more squid in diets) has been a major factor limiting the size of the sooty tern population was based on samples collected in three breeding seasons during 2004, 2009 and 2012. There is clearly a need to extend such a study by monitoring chick feeding during future breeding seasons. Käkelä *et al.* (2010) showed that switches in feeding between pelagic fish and other marine species can be clearly detected through analysis of lipid signatures of seabirds. Diet data could be obtained retrospectively from Stable Isotope Analysis (SIA) of feather samples from old museum specimens and compared with samples from birds found in the colony at the present time (Norris *et al.* 2007, Bond & Jones 2009, Weiss *et al.* 2009).

The decline in the size of the sooty tern population, the dietary shift and the increase in rat abundance can all be attributed to changes in the abundance of the marine (i.e. tuna) and terrestrial (i.e. cats) apex predators brought about by man. The general conclusion of this study is that trophic cascades, in both the marine and terrestrial environments, need to be considered when understanding declines in population sizes of pelagic seabirds and when devising management regimes for their reversal.

(Note: Chapter 7 was published as part of Hughes *et al*. 2008).

Chapter 8

GENERAL DISCUSSION

8.1. Summary of findings

My study of the breeding and population ecology of sooty terns on Ascension Island in the South Atlantic has revealed that rates of birth and death of this remote and large population have not been in balance since 1958 and that the population which breeds sub-annually has undergone a large and significant decline in size. It can be argued that sub-annual breeding should enhance lifetime breeding success, assuming that if birds were breeding annually their longevity would be similar to that of birds which breed at less than annual intervals. However, this potential advantage was curtailed by introduced predators (i.e. cats, rats and mynas) and by a suspected decrease in the quality of food fed to chicks; their combined influence has brought about a decline in population size. Counter-intuitively, the eradication of cats has not resulted in an increase in the size of the sooty tern population.

During the study period the breeding periodicity of the Ascension Island population of sooty terns was significantly less than one year and in each breeding season the majority of pairs failed to raise a chick. I have presented strong evidence that the population consistently bred sub-annually as did most individual birds contained within it. Breeding periodicity of birds that were successful in the earlier breeding attempt was annual but the evidence was less convincing. The timing of breeding seasons is predictable and appears not to be influenced by El Niño–Southern Oscillation events (Chapter 2). The size of the sooty tern breeding population was stable during the study period but there has been a precipitous decline of nearly 90% in the size of the sooty tern population since the mid-20th century (Chapter 3). As a result of this apparent stepwise decline, I argue that the species' current IUCN Red List category of 'Least Concern' should be reviewed. In the Ascension Island population of sooty terns immigration and emigration are fairly minimal. Terns show peer group-fidelity but they rarely re-occupy the same nest sites in successive breeding seasons. Compared with conspecific populations on other islands, the longevity of Ascension sooty terns was similar, breeding success was less and age at first breeding was older. The impact of sub-annual breeding on senescence was not studied (Chapter 4). Breeding success recorded at the end of the study period may be insufficient to maintain the sooty tern population at its present size. The causes of breeding failure have changed over time with non-native predators (i.e. rats and mynas) now emerging as one of the primary causes of breeding failure. Frigatebirds predated sooty tern chicks but mynas caused more absolute losses (Chapter 5). Following the eradication of feral cats on Ascension, there was a significant increase in the relative abundance of rats. The impact of these mesopredators on the size of the sooty tern population was similar to the previously combined impact of both cats (i.e. the apex predator) and rats (i.e. the mesopredator that was formerly preyed upon by cats; Chapter 6). I found that the proportion of squid in the diet of sooty tern chicks was significantly larger than that fed to conspecific chicks on other islands. My results suggest that the sooty tern population on Ascension may have been limited by recruitment to the breeding population as a consequence of over-fishing of tuna in the waters of the South Atlantic which resulted in chicks being fed a diet of poor quality (Chapter 7). My study concluded with projections to 2022 of the factors which appear to control the size of the sooty tern population on Ascension and this predicts a slow decline in population size.

8.2. Breeding and population ecology

In this thesis I set out to bridge gaps that had been identified in previous research into the breeding and population ecology of sooty terns. Specifically, I wanted to confirm that individual birds as well as the population of sooty terns bred sub-annually (Schreiber & Burger 2002) and this was achieved in Chapter 2. This is an important finding because it further highlights the large diversity in the breeding strategies of different and geographically dispersed populations of sooty terns (Ashmole 1965, Colchero 2008). Surveys of historical tern colonies were identified as a priority research focus by Schreiber *et al.* (2002) and this thesis has ‘answered that call’ to an extent through surveying of the Ascension breeding colonies that have allowed determination of size and trends in the population (Chapters 3 and 7). Croxall *et al.* (2012) identified urgent research priorities for seabirds and these included monitoring (as a tool to permit evaluation of population size and trends), studies of life history and ecology, and the identification of threats from fisheries. My thesis provides valuable information addressing these research priorities using sooty terns as a model for tropical seabird species.

There are numerous calls in the literature for empirical evidence of the phenomenon of mesopredator release (Courchamp *et al.* 1999, Crooks & Soulé 1999, Le Corre 2008, Ritchie & Johnson 2009, Towns *et al.* 2011). I provide an example of the impact of mesopredator release by monitoring prey, apex predators and mesopredators for a decade before and after apex predator eradication. My findings differ from those reported for the population of 180 pairs of yelkouan shearwaters on Port-Cros Island in the Mediterranean where Bonnaud *et al.* (2012) found that cat removal was beneficial despite an increase in relative abundance of black rats. My findings on the outcomes of apex predator eradication also differ significantly from the outcomes predicted in the management plan of Pickup (1999) for the eradication of cats on Ascension and need further explanation. Ratcliffe *et al.* (2008) reported, as was predicted, positive outcomes of cat eradication for the populations of five seabirds. The seabird species that benefit from cat eradication are those that generally return from foraging trips each evening, roost during the night and are then vulnerable to predation from nocturnally hunting cats. In addition, the breeding cycles of these seabirds vary (Ashmole & Ashmole 2002) and eggs and young of either frigatebirds or boobies are available to cats most months of the year. On the other hand, individual sooty terns spend < 9% of adult life on land (Chapter 3). Sooty terns are able to swamp predators with their large numbers of closely synchronised breeding birds. Equally important, the entire population migrated for three months each year leaving cats with little alternative sources of food but rodents. The key point is that sooty terns are not typical of other seabird species on Ascension. It can now be argued that cat predation did not limit their population size and, consequently, their population size did not respond as predicted to the eradication of cats (Chapters 2, 3 and 5). I identified a strong negative correlation between the size of the sooty tern population on Ascension and the magnitude of tuna fish catches in the South Atlantic (Fig. 7.4). Sooty terns are regarded as obligate commensals with schools of small tuna (Au & Pitman

1986). If tuna stocks are reduced in the Indian and Pacific Oceans, populations of sooty terns may also decline in size there.

8.3. Unexpected findings

Some unpredicted results from my research have important applications in the fields of conservation management, reproductive biology and demography at a global scale. My analysis of historical maps has identified that a stepwise decline in the size of the sooty tern population occurred in the 1960s and 1970s from its previously steady state. The technique I used to make this discovery has wide applications for censuses of other colonially breeding taxa. Many explorers and scientists from the 19th and 20th centuries were excellent cartographers and some drew maps delineating accurately the perimeter of breeding colonies. These historical maps can provide data on the areas of colonies while densities of constituent breeding animals can sometimes be obtained from contemporary surveys, producing an estimate of historical population size (see full details in Chapter 3).

I found that mynas ‘pricked’ and destroyed many more sooty tern eggs than they consumed (Chapter 5). Why mynas prick eggs (Fig. 5.3) is a mystery and, to the best of my knowledge, this is the first time that the impact of mynas on the breeding ecology of a seabird species has been evaluated. Therefore, these findings reveal much about the ecological threats posed by this non-native species that is rightly included in the list of the top 100 of the world’s worst invaders (ISSG 2011b).

Despite there being many more adults than juvenile frigatebirds on Ascension, approximately equal numbers hunted over the breeding colonies.

Adults captured six times more chicks than juveniles (Chapter 5). Frigatebirds are usually solitary at sea (Harrison 1990); therefore, how young frigatebirds learn to forage is a mystery. Juvenile frigatebirds must hone their foraging skills in order to be successful kleptoparasites (Stonehouse & Stonehouse 1963). Previously unreported is my suggestion that interactions with sooty tern chicks may provide juvenile frigatebirds with opportunities to learn essential foraging skills on land that can be applied in other foraging situations later in life.

Another unexpected finding of my research was that rats significantly increase their body mass, and head and body lengths when ‘released’ from cat predation. There were also good indications that in the absence of cat predation, rats in the population lived longer and were able to reproduce more frequently. Conservation managers should be aware that when predation pressures on rats are removed, they are able to prey on animals that previously were too large for them to overpower.

8.4. Future research

Long-term studies are worthy but funding them is problematic (Collins 2001). This long-term study developed from simply monitoring the population of seabirds on Ascension by a group of amateur ornithologists (Nash *et al.* 1991) into a serious long-term scientific exercise studying their breeding and population ecology. In hindsight, there was much that could have been improved. During the early part of the study records were poorly maintained and monitoring activities were erratic and poorly focussed. Many hours in the field were spent sea-watching (i.e. looking for vagrants and conducting timed counts of birds on passage; Hughes 1994) but time could have been more usefully employed answering more targeted questions about breeding ecology of the focal species. Poor predictions of the start of the sooty tern breeding season resulted in failure to arrive in the study area at the height of the sooty tern breeding season in 1992 and 1994, preventing reliable censuses of the population. Research methods (e.g. population census techniques, monitoring of predator abundance and sooty tern breeding success) improved with time and there is now an ongoing and systematic study that will continue monitoring of the breeding and population ecology of sooty terns, extend the ringing programme and expand the research into the identification of foraging range. AOS teams that are largely self-funded have already been identified for the next field seasons in 2014 and beyond.

The most pressing need for further research is to identify the geographical area over which sooty terns from the Ascension population forage, especially the foraging locations of these birds when breeding on the island. The availability of food in the marine environment is a major factor limiting seabird population size (Chapter 7). Sooty terns are well known for their ability to stay airborne for years (Schreiber *et al.* 2002), but virtually nothing is known of their range during the non-breeding season. It is thought that during breeding sooty terns have foraging ranges of between 500 and 700 km (Flint 1991) but just where in more than 1 million km^2 of ocean around Ascension the birds find food for themselves and their young is unknown. Incubation shifts of sooty terns on Ascension last up to 6 days (Ashmole 1963a) and are considerably longer than in most other colonies (Schreiber *et al.* 2002), suggesting perhaps that food for Ascension birds is relatively scarce. Pre-breeders are assumed to be on the wing for about 8 years because they are rarely seen on land (Schreiber *et al.* 2002), but where they go is also unknown. Geolocators can track the foraging range of individuals and if the birds are recaptured data can be downloaded from these archival light tags that can provide the answer to where they forage during the non-breeding season (Egevang *et al*. 2010). However, water temperature sensors and salt water switches are unlikely to provide more fine-scale parameters that could inform geolocation and thereby refine fixes because sooty terns are rarely on the water long enough. The foraging sites of sooty terns feeding offshore from Ascension Island can be obtained from boat surveys (RNBWS 2012) but the mystery of where juveniles go is more difficult to solve. Satellite tracking devices could be used (Pütz *et al*. 2008) and are now small enough to fit to sooty terns. However, resolving issues of how to deploy such devices on juvenile sooty terns that are 'on the wing' for 8 years and ethical concerns for pre-breeding sooty terns whose annual survival rate is 0.26 (Feare & Doherty 2011) remain to be resolved. SIA might be a more fruitful avenue in the study of dispersal of pre-breeding sooty terns (Hobson 2005, Votier *et al.* 2011). Pre-breeders from populations in the Caribbean are known to forage in the Gulf of Guinea (Robertson 1969). One pre-breeder (age 10 months) from the Ascension sooty tern population was recovered in Abidjan, Ivory Coast, Gulf of Guinea (Chapter 4). Hobson (2005) has shown that it is theoretically possible to identify individuals in a population that have moved from one isotopic 'landscape' (i.e benthic or inshore) to another (i.e. pelagic or offshore). A comparison of outputs from SIA between first-time breeders (that may forage inshore) and older adults (that are known to be pelagic foragers) is worthy of investigation.

As the marine environment is taking a more dominant position in research priorities for Ascension sooty terns, it is high time that we turn our attention to their foraging ecology and nutritional needs. Earlier in the thesis, I stressed the need to confirm dietary shifts over recent decades (see section 7.5.3.). Data on dietary shifts can be obtained retrospectively using SIA (Norris *et al.* 2007) of feather samples from old specimens held in museums in the UK and the USA (see section 7.4.1) compared with feather samples from birds found in the colony at the present time and with small fishes from the stomachs of tuna caught in Ascension waters.

8.5. Conservation recommendations for Ascension

Effective rat control measures in the tern colonies on Ascension are essential to maintain the present size of the sooty tern population. My findings support the contention of Fitzgerald *et al.* (1991) who found that removal of cats without simultaneous action to control rats did little to restore seabird populations. While the eradication of cats on Ascension cost £650,000 (Ratcliffe *et al.* 2009), the budget for additional rat control measures that were envisaged in the management plans (Pickup 1999) was minimal and no funds were made available during the 2007–2008 financial period (RSPB 2008). It is my strong recommendation that rat relative abundance is monitored in the seabird colonies and effective rat control measures are maintained around the colonies (Moors *et al.* 1992). This management intervention is relatively low cost but will require a regular annual budget (possible less than £20,000). Other taxa such as turtles, whose breeding populations are threatened by rats (e.g. in Diego Garcia; ISSG 2011a) and other seabirds such as Ascension frigatebirds that returned to nest on the main island of Ascension in November 2012 for the first time since 1836 (McKie 2012; Fig. 8.1), may also benefit from rat control measures. While technically feasible, and theoretically

Figure 8.1. A female frigatebird nesting on the south side of the Letterbox peninsula of Ascension Island in the South Atlantic in November 2012. (Photo: A. Bray).

achievable, rat eradication from Ascension would be a huge undertaking (Brown 2002) in terms of finance and practical on-the-ground measures and is probably, therefore, not viable.

8.6. General conclusions

This study of a seabird species on a remote tropical island in the UKOTs has provided useful insights into the breeding and population ecology of seabirds worldwide. The contribution that this research has made to the study of seasonality in birds may turn out to be significant (A. Dawson pers. comm.). Strong evidence that free-living birds can have a regular sub-annual breeding cycle is scarce and my findings will be of interest to reproductive biologists working across many taxa (Dawson 2008). My findings indicate that some seabird populations have adopted a life-history strategy of sub-annual breeding as a viable alternative to seasonal breeding.

The significance of diet shift and trophic cascade (a sequence of events in a food web; Allaby 1998), as was apparent in Scottish waters (Wanless *et al.* 2005, Votier *et al.* 2008b) and on Ascension has received insufficient recognition (Estes *et al.* 2011). With the global human population set to expand in size, pressures on apex predators and large consumers are likely to continue as demands for food from humans increase. Eradicating cats on the island, and the dramatic human-induced changes in the abundance of tuna in the fishing grounds around the island, have resulted in a cascade effect that has the potential to alter the Ascension Island ecosystem significantly. Therefore, studies such as mine are important in advancing our knowledge of how to manage the unintentional consequences of apex predator eradication.

8.7. Final remarks

Science is always ‘work in progress’ and as new data are collected and analysed, our understanding grows. The more recently gathered data have challenged some of my initial conclusions (see Hughes *et al.* 2008, 2010). This is one of only a very few long-term studies conducted in any of the UKOTs (Pienkowski 2010). It has not been reliant on grants or government funding (Collins 2001), but it has proved very valuable in addressing many ecological questions. Despite the urgent need for long-term research, sustained funding for work in the UKOTs is difficult to acquire (Pienkowski 2010). Determined individuals have conducted long-term research (Greenwood 2007), but all too often their results are not published. W.B. and M.J. Robertson spent 40 years studying the breeding biology of sooty terns on the Dry Tortugas, Florida, USA, and they were conducting such essential ecological research when both sadly passed away. Here, I present findings of phase two (the first phase was the BOU expedition) of the study into the breeding and population ecology of sooty terns and I make them available to all upon request (see www.armybirding.org.uk). I now confidently leave the next phase of this long-term study to my friends at the University of Birmingham and in the Army Ornithological Society.

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APPENDIX 1

AOS field researchers in 1990 and 2012. Figures A1 and A2 show AOS expeditions in 1990 and 2012, respectively.

Figure A1. AOS field team on Ascension Island, South Atlantic in March 1990. From left to right: Philip Ashmole, John Hughes, Myrtle Ashmole, Martin Howell (RNBWS), Billy Bowles, Hilary Nash (expedition leader), Richard Seargent, David Earp, Tim Cowley, John Walmsley and Gez Thompson.

Figure A2. AOS field team on Ascension Island, South Atlantic in December 2012. Bottom row from left to right: John Hughes, Jim Reynolds (University of Birmingham), Andrew Bray, Roger Dickey and Lynne Millard. Top row from left to right: Mark Cutts (RNBWS), Martin Routledge (RAFOS), Tony Giles (expedition leader) and Colin Wearn (RAFOS).

APPENDIX 2

PDFs of papers from thesis work

(1) **Hughes, B.J.**, Martin, G.R. & Reynolds, S.J. 2008. Cats and seabirds: effects of feral Domestic Cat *Felis silvestris catus* eradication on the population of Sooty Terns *Onychoprion fuscata* on Ascension Island, South Atlantic. *Ibis* **150** (Suppl. 1): 122–131.

(2) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J**.** 2010. Sooty Terns *Onychoprion fuscata* on Ascension Island in the south Atlantic are a reproductively isolated population. *Revista Brasileira de Ornitologia* **18**: 194–198.

(3) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J. 2011. The use of Google Earth™ satellite imagery to detect the nests of Masked Boobies (*Sula dactylatra*). *Wildlife Biology* **17**: 210–216.

(4) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J. 2012. Estimate of Sooty Tern *Onychoprion fuscatus* population size following cat eradication on Ascension Island, central Atlantic. *Bulletin of the African Bird Club* **19**: 166–171.

(5) **Hughes, B.J.,** Martin, G.R. & Reynolds, S.J. 2013. Sublingual fistula in a Masked Booby (*Sula dactylatra*) and possible role of ectoparasites in its etiology. *Journal of Wildlife Diseases* **49**: 455–457.

(6) **Hughes, B.J.** & Wearn, C. 2005. Longevity of Sooty Terns *Sterna fuscata* on Ascension Island. *Atlantic Seabirds* **7**: 42–43.

(7) Ratcliffe, N., **Hughes, B.J.** & Roberts, F.A. 1999. The population status of Sooty Terns *Sterna fuscata* on Ascension Island. *Atlantic Seabirds* **1**: 159–168.

(8) Reynolds, S.J., Martin, G.R., Wallace, L.L., Wearn, C.P. & **Hughes, B.J.** 2008. Sexing sooty terns (*Onychoprion fuscata*) on Ascension Island from morphometric measurements. *Journal of Zoology* **274**: 2–8.

(9) Reynolds, S.J., Martin, G.R., Wearn, C.P. & **Hughes, B.J.** 2009. Sub-lingual oral fistulas in sooty terns (*Onychoprion fuscata*). *Journal of Ornithology* **150**: 691–696.