FROM POPULATION TO INDIVIDUAL: COLONY DYNAMICS AND STRUCTURE IN TIME AND SPACE OF A HIGHLY SOCIAL SEABIRD

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ABSTRACT

Understanding why populations change in size and distribution can help us assess a species' vulnerability to future environmental change (e.g. climate warming) and their conservation status. This thesis focuses on a population of sooty terns, a small seabird, that breed in huge numbers on Ascension Island in the South Atlantic. By combining long-term data on population size and breeding movements with genetic relatedness and chick survival, we explore the effects of environmental and social processes that may underlie population trends. We found evidence for a shift in population size between two breeding sites on the island. Despite high population genetic diversity and low levels of relatedness we found fine-scale genetic structure between neighbours. There was evidence that birds breeding earlier were genetically different to those breeding over one month later. Chick sociality was a key factor influencing daily survival together with the use of habitat cover, both of which are likely responses to predation risk. The shift in population size between breeding sites suggests instability in habitat quality, with potential declines in breeding success driving breeder movements. Overall our findings suggest differences in animal behaviour can have significant effects on population ecology, genetic structure, breeding timing and breeding outcomes.

This thesis is dedicated to my Mum and Dad for always believing in me and having no expectations.

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Chapter 1

General Introduction

Population ecology can be defined as the study of changes in the size and distribution of animal populations and the biological process that underlie such changes (Begon *et al.* 2009). Although the study of population ecology can tell us much about demography and the responses of populations to ecological change, encapsulating differences between individuals can increase our ability to link these responses to fitness outcomes (Sutherland 1998). For example, differences in contact rates between individuals has been shown to affect the speed and direction of the transmission of information (e.g. for foraging areas Weimerskirch *et al.* 2010) and diseases (e.g. via the spread of parasites; Altizer *et al.* 2003). Therefore, the variation in resulting individual fitness (i.e. the number of individuals that locate food) has implications for population trends, structure and ultimately persistence (Kurvers *et al.* 2014). Thus to understand what is occurring at the population level in space and time it is necessary to consider individual level variation and responses to ecological change and the interactions between the two. This thesis explores possible mechanisms that may contribute to population trends and breeding distribution of a highly social seabird, the sooty tern *Onychoprion fuscatus*, on Ascension Island in the South Atlantic Ocean (Fig. 1.1). To achieve this we combine long-term data on population trends with the genetic relatedness and social behaviour of individuals.

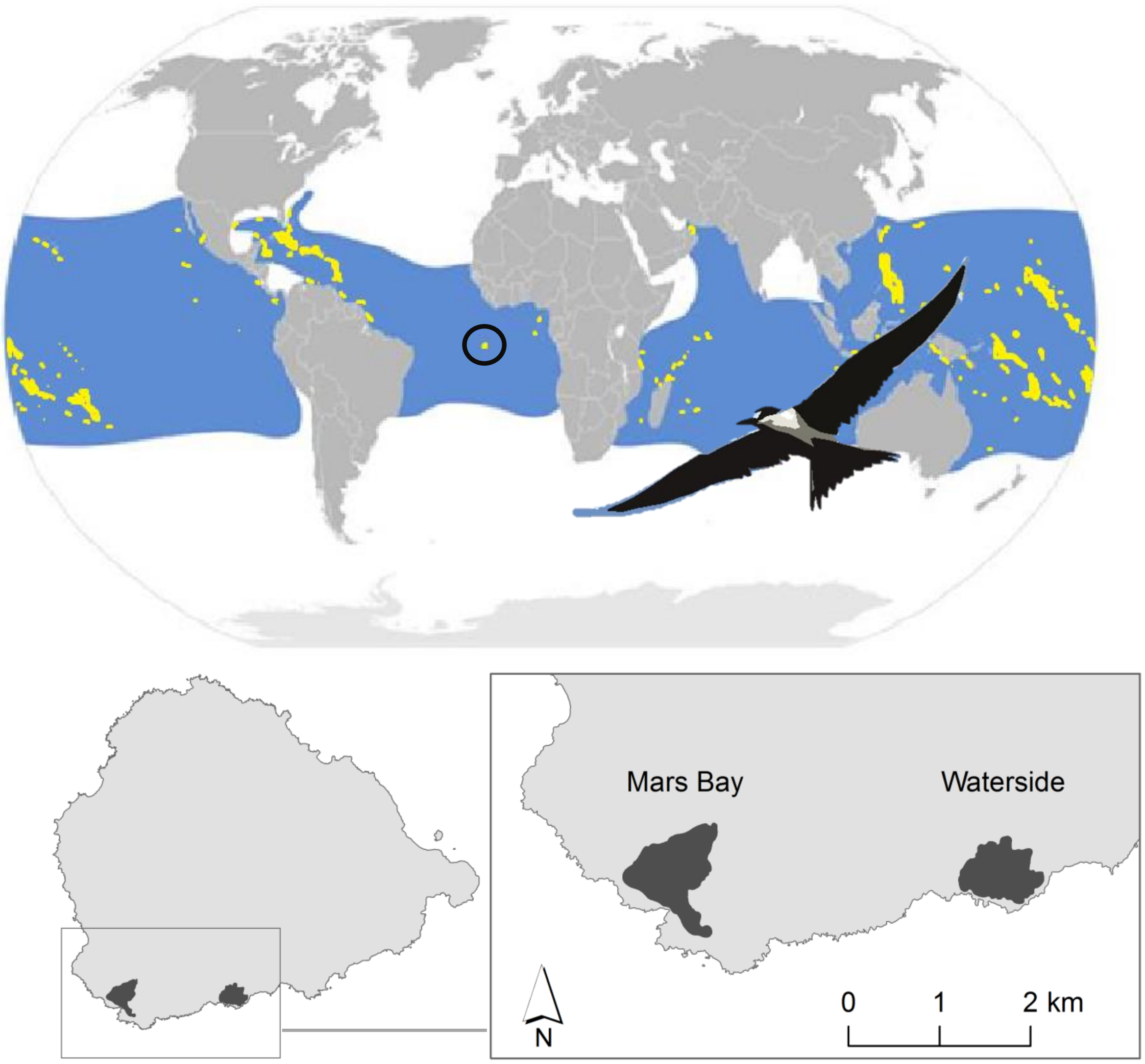

Figure 1.1 The global breeding (yellow) and non-breeding (blue) distribution of sooty terns; map adapted from BirdLife International (2017). Relative locations of Ascension Island in the South Atlantic (indicated by the black circle) and of the breeding sites of sooty terns on the island. Dark grey areas represent the cumulative extent of peak breeding occupancy by birds between 1996 and 2015. Ascension Island base map source: Ascension Island Government Conservation and Fisheries Department.

1.1 Population structure

Population structure is shaped by the interactions between individuals and their environment (Krause *et al.* 2007) at different levels of social organisation. Heterogeneities in such interactions can influence a range of processes such as the transfer of information and diseases as well as dispersal (Kurvers *et al.* 2014), and thus have fitness consequences (Ohtsuki *et al.* 2006). In highly social species that breed in colonies, where individuals raise their offspring in dense aggregations containing no resources (Perrins & Birkhead 1983), the interactions between social, environmental and genetic processes that underlie population structure are poorly understood (Brown & Brown 2001; Kildaw *et al.* 2008). Deciding when and where to breed can directly affect an organism's fitness and survival due to variation in factors such as foraging and breeding success and predation risk (Conradt & Roper 2010). Seabirds are excellent model species to investigate spatio-temporal population trends given their sensitivity to changes in environmental factors (e.g. weather, food abundance) and life-history traits such as longevity and their tendency to congregate in large numbers to breed with often high fidelity, making their occurrence predictable in space and time (Kokko *et al.* 2004).

Temporal fluctuations in population size can be indicative of a species' vulnerability to extinction (Cuervo & Møller 2017), with increasing variability indicating ecosystem instability (Cottingham *et al.* 2001) which can result in lower population persistence (Inchausti & Halley 2003). Long-lived species with delayed maturation that produce few offspring per breeding attempt often exhibit variation in whether individuals choose to breed in any given breeding season. It is therefore necessary to use longitudinal data to detect population trends and assess population persistence (Robinson *et al.* 2013). Migratory species that utilise different habitats between breeding and non-breeding periods are particularly vulnerable to changes in habitat quality due to extrinsic (e.g. food availability, weather, predation) and intrinsic factors (e.g. sociality, body condition, dispersal) (Leyrer *et al.* 2012) with conditions in habitat quality at one breeding stage influencing the outcome at the other through mechanisms such as carry-over effects (Harrison *et al.* 2011). Understanding what drives variation in population ecology (e.g. population size and density) can help us to assess ecosystem stability (Robinson *et al.* 2013) and predict responses to changes under future environmental scenarios such as climate warming and increased predation risk.

Coloniality occurs throughout the animal kingdom and is particularly prevalent in seabirds (Lack 1968). Numbering a few pairs to millions of pairs (Rolland *et al.* 1998), seabirds gather to breed in a roughly centralized location leaving to feed (Siegel-Causey & Kharitonov 1990). Benefits of such breeding aggregations include social information exchange for nesting and foraging sites, reduced predation risk and behavioural coordination (e.g. breeding arrival and departure timing) (see review by Evans *et al.* 2016). However, there are also associated costs of group living, mainly related to density dependence (Sachs *et al.* 2007). Such costs include competition for resources such as space and mates and increased disease transmission (Brown & Brown 2004). However, the benefits of coloniality must outweigh the costs given that inexperienced pairs breed in lower quality sites or defer breeding (Kildaw *et al.* 2008) rather than establish new breeding colonies in available habitat that is often close by to established colonies (Olsthoorn & Nelson 1990).

1.2 Population genetic structure

Given that the movement of breeders is not always indicative of random social and genetic organisation of individuals (Sonsthagen *et al.* 2010), consideration of genetic and social structure adds to our understanding of population structure and associations between individuals.

A population's genetic structure is the spatial distribution and frequency of individual genotypes and which can help us to understand ecological and evolutionary drivers of population structure, persistence in space and time, and a species' genetic adaptability to environmental change (Palestis 2014). However, we know little about what regulates seabird population genetic structure (Schreiber & Burger 2001; Friesen *et al.* 2007a). Genetic differentiation within a population is primarily driven by gene flow, with greater levels of genetic structure and differentiation in populations with limited gene flow (Leedale *et al.* 2018). This can result in isolation by distance, where increasing geographical distance between individuals also increases their genetic dissimilarity with each other (Wright 1943). Limited gene flow may result from a number of factors such as physical barriers that prevent mixing between individuals e.g. roads (Riley *et al.* 2014) or habitat fragmentation (Coulon *et al.* 2004), or behavioural traits such as migratory routes (Rolshausen *et al.* 2013).

Populations that exhibit limited gene flow are at risk of reduced genetic diversity. The level of genetic diversity within a population is mediated by a number of mechanisms, namely genetic drift, mutation, natural selection, inbreeding and gene flow (Frankham 1996). Decreased genetic diversity has fitness consequences (Slate *et al.* 2000) as well as affecting species' adaptation to environmental change (Frankham 2003). Small and isolated populations, or those with low levels of gene flow, can be more at risk from stochastic processes such as mutation and genetic drift (Lande 1995). Understanding population genetic diversity and structure can also aid conservation management by providing base-line data with which to assess genetic adaptability, as well as assisting with delineating conservation management units (Bicknell *et al.* 2012; Palestis 2014; van Rees *et al.* 2018).

Seabirds display high levels of breeding location philopatry (Schreiber & Burger 2001) which may lead to genetic relatedness between individuals nesting in close proximity (genetic autocorrelation) (Banks & Peakall 2012). Within-island genetic diversity was observed between two populations of Abbott's boobies *Papasula abbotti* breeding on Christmas Island, thought to be a result of natal philopatry (Morris-Pocock *et al.* 2012). Such kin-mediated groupings have the potential to increase inbreeding between related individuals and the likelihood of inbreeding depression (Frankham 2005). By breeding with related individuals there is an increase in the frequency of individuals that are homozygous for alleles identical by descent (Keller & Waller 2002). Inbreeding depression is the expression of recessive alleles that may have deleterious consequences for fitness-related measures such as reproduction and survival (Jimenez *et al.* 1994; Frankham 2003) via the loss of heterozygous advantage (Charlesworth & Charlesworth 1987; Hedrick & Garcia-Dorado 2016). Such consequences have been demonstrated to include immunodeficiency and increased susceptibility of disease contraction (Whiteman *et al.* 2005), and reduced reproductive success (Amos & Balmford 2001). Inbreeding depression can occur at a much more rapid pace than other mechanisms that have the potential to reduce genetic diversity, such as genetic drift (the random fixation or loss of alleles) or mutation (Keller & Waller 2002). Indeed, inbreeding has been shown to reduce fertility, hatching rates, fledging survival and recruitment in birds (Daniels & Walters 2000; Jamieson & Ryan 2000).

Inbreeding depression can be assessed via detailed pedigree analysis, although in long-lived species this is often infeasible and the use of neutral microsatellite markers to determine genotype heterozygosity is widely applied (Goldstein & Schlötterer 1999; Hansson *et al.* 2001; Townsend *et al.* 2019). A number of studies have shown links between neutral markers influencing fitness (e.g. Da Silva *et al.* 2006; Agudo *et al.* 2012) or heterozygosity-fitness correlations (HFC) (Chapman *et al.* 2009). Two main hypotheses exist to explain these relationships: namely the local effect hypothesis where heterozygotes exhibit an advantage via dominance (Hansson & Westerberg 2002); and the general effect hypothesis where heterozygotes reflect genome-wide variation (or lack of it) (Luikart *et al.* 2008). However, such indirect effects are often weak (Keller & Waller 2002) and the use of adaptive or candidate loci such as those of the major histocompatibility complex (MHC) that relate to functional diversity (immune response) (Ejsmond & Radwan 2011) are preferred for such direct comparisons between fitness and heterozygosity. Other methods investigating genetic structure and gene flow employ the use of mitochondrial DNA, or a combination of both microsatellites and mitochondrial DNA (Levy *et al.* 2016; van Rees *et al.* 2018). However, molecular markers such as microsatellites are a well-established and economical method for investigating genetic structure and relatedness both within and between populations (Selkoe & Toonen 2006; Townsend *et al.* 2019). A major benefit of using microsatellite markers is the ability to detect kinship due to their high mutation rates that often result in high numbers of alleles at a single locus, and thus unrelated individuals are unlikely to share alleles (Webster & Reichart 2005).

Genetic relatedness is cited as a key factor underlying the formation and benefits of social groups (Rubenstein & Kealey 2010), due to the fitness benefits gained via kin-selection (Maynard Smith 1964). For example, kinship is thought to underlie cooperative behaviour that results in indirect benefits by enhancing the reproductive success of relatives (Hamilton

1964; Dickinson & Hatchwell 2004). Other benefits gained from kin-structured groups include reduced conflict between related neighbours (Pshenichnikova *et al.* 2015), more effective predator defence (Griesser & Ekman 2005), resource sharing (van Dijk *et al.* 2015) and infanticide avoidance (Pshenichnikova *et al.* 2015).

Kinship has also been shown to influence dispersal and group dynamics (van Dijk *et al.* 2015). As kin-mediated groups may increase the likelihood of inbreeding depression, sex-biased dispersal is a mechanism by which relatives avoid opposite sex pairings (Clutton-Brock & Lukas 2012). Studies which document the degree of kinship at the population and group levels can add to our understanding of both individual behaviour and population genetic variation (Lacey & Wieczorek 2004). However, studies that focus on genetic structure at the intrapopulation level are lacking (but see Lacey & Wieczorek 2004; Sonsthagen *et al.* 2010; Ibarguchi *et al.* 2011), especially those that focus on seabirds (Pshenichnikova *et al.* 2015). Seabirds are an ideal model species to investigate the impacts of philopatric behaviour on population genetic structure, given that nest-site fidelity of returning adults and natal philopatry of juveniles breeding for the first time are often high (Schreiber & Burger 2001). Evidence of kin-based groups in breeding seabird colonies has been observed in Pacific common eiders *Somateria mollissima v-nigrum* (Sonsthagen *et al.* 2010) and common gulls *Larus canus* (Bukaciński *et al.* 2000). Although weak genetic structuring was evident overall, fine-scale genetic relatedness between females was evident in thick-billed murres *Uria lomvia* (Ibarguchi *et al.* 2011). Information on the levels of natal philopatry and intrapopulation genetic structure is not available for sooty terns.

1.3 Social structure

Being social could provide significant advantages for species breeding in unstable ecosystems where variations in food and environment (e.g. predation risk and habitat quality) are inconsistent between breeding seasons (Francesiaz *et al.* 2017). Familiar connections between individuals may mediate competition (Dávid-Barrett & Dunbar 2012) by reducing aggression (Tourenq *et al.* 1995) and improving the ability to locate foraging areas for example by information through information centres (Ward & Zahavi 1973). A population's social structure requires a diverse range of ecological and evolutionary processes such as dispersal and invasion (Kurvers *et al.* 2014) to shape and stabilise it and mediate its functionality. Network analysis (Whitehead 2008) is a useful tool with which to explore the social structure of breeding seabird populations. Originating in mathematical graph theory, network analysis is increasingly used in the study of non-human animal systems to study group functionality (Pinter-Wollman *et al.* 2013). Its main advantage is that it allows for the analysis of complex social structures through characterisation of interactions between dyads (pairs of individuals) (Kurvers *et al.* 2014). Patterns of interactions between dyads can shape the fitness of individuals within groups and thus impact population structure (Wey *et al.* 2008). A number of studies (reviewed in Brent 2015) have demonstrated a link between social connections and fitness benefits in animal systems, with more centrally placed individuals obtaining the most fitness benefits. For example, grooming networks in baboons *Papio cynocephalus ursinus* reveal that individuals who spend more time grooming and are spatially closer to other females have a higher probability that their young will survive longer than those with weak social bonds (Silk *et al.* 2009). A greater number of familiar neighbours in female great tits *Parus major* is positively related to clutch size (Grabowska-Zhang *et al.* 2012), while reproductive success is positively related to numbers of social bonds in feral horses *Equus caballus* (Cameron *et al.* 2009). However, few studies have investigated the social structure of offspring, despite there being evidence that early life social connections are important. For example, early life associates in barnacle geese *Branta leucopsis* shaped later life networks during foraging (Kurvers *et al.* 2013) and in bottlenose dolphins *Tursiops* sp. Frère *et al.* (2010a) found offspring social structure affected survivorship due to social stress.

1.4 Seabird conservation status: A global concern

Seabirds are globally important ocean sentinels, crucial for their roles as bio-indicators of ecosystem status (Einoder 2009; Mallory *et al.* 2010); however, many seabird species are more threatened than other avian taxa (Croxall *et al.* 2012). Of 340 seabird species 44% are listed on the International Union for Conservation of Nature's (IUCN's) Red List as threatened (i.e. 'Near Threatened, 'Globally Threatened' or 'Critically Endangered'), with pelagic species being most at risk (Votier & Sherley 2017). Between 1950 and 2010 monitored seabird populations declined by 70% in population size (Paleczny *et al.* 2015). The majority of reasons for such drastic declines are linked to human-induced actions (Votier & Sherley 2017). Grémillet and Boulinier (2009) identified six key anthropogenic threats responsible for such declines: 1) direct harvesting of eggs, chicks and adults although this is confined to relatively few seabird populations in more recent years. For example harvesting of sooty tern eggs still continues on the Seychelles (Feare *et al.* 2007) and accidental seabird by-catch during fishing operations is also a major contributor to adult mortality (Anderson *et al.* 2011); 2) introduced species at nesting grounds depredating adults, eggs and chicks. Species such as rats *Rattus* spp. have had devastating effects on seabird populations at nesting grounds (Jones *et al.* 2008); 3) marine pollutants such as heavy metals and plastics are becoming a serious concern for seabird survival and reproductive success. Wilcox *et al.* (2015) predicted that plastics will affect 99% of all seabird species by 2050; 4) over-fishing leading to a reduction in prey availability (both direct and indirect) (Reynolds *et al.* 2019); 5) climate change influences a number of life-history traits such as breeding timing, changes in dispersal or migration routes (Ducklow *et al.* 2007); and 6) an increase in the occurrence of avian pathogens due to climate warming and an increase in human presence at nesting grounds (Ricciardi 2008).

1.5 Sooty tern biology and study population

Sooty terns are a small, long-lived colonially nesting seabird species distributed throughout the circumequatorial zone (Fig. 1.1). They are the most numerous tropical seabirds in the world (Schreiber *et al.* 2002). Although categorised as 'Least Concern' on the IUCN Red List, there is growing concern that their conservation status should be altered to 'Critically Endangered' following severe declines of a number of large populations across their range (Hughes *et al.* 2017b). The population breeding on Ascension Island (Fig. 1.2) is the largest population in the Atlantic Ocean. Sooty terns are a *K*-selected species that typically lay one egg per breeding attempt and have a long maturation time of approximately five years (Hughes 2014). Other life-history traits that align more with *K*- than *r*-strategists are high energy input to produce offspring (hatching to fledging takes approximately 60 days; Ashmole 1963), extended parental care (thought to be at least one month; Ashmole 1963), and long life expectancy (an adult recaptured on Ascension Island was 34 years old; Hughes 2014) that permits multiple opportunities to reproduce. In comparison *r*-selected taxa have a small body size, early reproduction producing many offspring, rapid development and short life expectancy (Jeschke *et al.* 2019). Extreme *K*-strategists live in relatively stable and persistent environments, close to carrying capacity due to density dependence; hence they are more likely to survive to old age (Putman & Wratten 1985). Although no one strategy is an ‘exact fit’ for any given organism, *K*-selection is described by Nicholson (1954) as ‘contest’ competition compared to ‘scramble’ competition of *r*-selection. The former leads to low adult mortality and, in turn, low recruitment but relatively stable population sizes. Competition between adults is fierce, which is exhibited by many colonially breeding species where competition for space and other resources is often high (Danchin & Wagner 1997). In *r*-selected species the opposite is true, with high adult mortality and high juvenile survival. *K*-selected species can withstand some environmental disturbance but when disturbances lead to population declines below some lower threshold, they cannot recover (Putman & Wratten 1985). Indeed, Arctic terns *Sterna paradisaea* nesting in the Gulf of Maine abandoned 90% of the breeding colony when breeding failures occurred in 25% or more of the colony (Scopel & Diamond 2017). In comparison, *r*-strategists grow rapidly at low numbers in unstable environments where resources are likely to change, hence the need for rapid growth before environmental conditions alter. Although the concept of *r*- and *K*-selection has met with controversy (Jeschke *et al.* 2019), the use of fast and slow life-history traits to describe a species’ biology is useful for our understanding of its ecology and evolution.

Sooty terns are sexually monomorphic although males are generally larger than females (Reynolds *et al.* 2008). During incubation both parents incubate the egg and once hatched the chick is guarded for a few days before being left alone to allow both parents to forage at sea (Dinsmore 1972). Chicks are highly mobile after a few days post-hatch and leave the nest sheltering under rocks and vegetation often in social groups of conspecifics from other nests. Chicks have been recorded up to 56 m from the nest on Ascension Island (Ashmole 1963).

Sooty terns are surface feeders having poor waterproofing and rely on larger fish, such as tuna *Thunnus* spp. to drive smaller prey to the surface in so-called ‘facilitated foraging’ (Maxwell & Morgan 2013). Ashmole (1963) also noted that individuals frequented nesting grounds at night before egg laying commenced, and would largely nest in the same location as these preliminary gatherings.

Figure 1.2 Sooty terns nesting in large colonies at the Waterside breeding site on Ascension Island in the South Atlantic in Nov 2015. (Photo: L.J.H. Garrett).

The population on Ascension Island has been recorded from as early as 1501 when eggs were collected by early colonisers (Ashmole 1963). Ascension Island is a remote volcanic island 97 km^2 in size located in the South Atlantic (07°57’S, 14°24’W) just south of the equator and around 2,000 km from continental land masses (Fig. 1.1). Unlike most other populations, individual sooty terns on Ascension Island can breed sub-annually every 9.6 months, resulting in differences in the time of year that breeding takes place (Reynolds *et al.* 2014). Sub-annual breeding has been recorded in other pelagic seabirds such as albatrosses *Diomedea* spp. (Jouventin & Dobson 2002), although it is relatively rare, occurring in only

25% of all bird species (Chastel 1995). Reasons for sub-annual breeding are thought to be linked to food abundance and distribution, which in the tropics is ephemeral and unpredictable, as opposed to temperate conditions that give rise to more predictable peaks in food abundance, resulting in annual breeding cycles that coincide with such peaks (Lack 1968). Sub-annual breeding has been noted in other tropical seabird populations, such as bridled terns *Sterna anaethetus* in the Seychelles breeding every 7.5 months (Diamond 1978) and swallow-tailed gulls *Creagrus furcatus* that breed every 9 to 10 months in the Galapagos Islands (Harris 1970). Another population of sooty terns that breeds sub-annually is at Michaelmas Cay, Queensland where some birds breed every 8.6 months (King *et al.* 1992). Breeding sub-annually increases the number of breeding attempts an individual can make in their life-time, and Reynolds *et al.* (2014) showed that individual sooty terns on Ascension Island have shorter return times when their nesting attempt fails to produce a chick. Relaying in this population is also low (30%; Ashmole 1963) compared to other populations of sooty terns (e.g. 90% in the Seychelles; Feare 1976a).

In comparison to other seabird species, sooty terns tend to share behaviour and life-history traits with other pelagic species such as petrels Procellariiformes and noddies such as brown noddies *Anous stolidus* rather than other terns (Dinsmore 1970). For example, most tern species forage in marshes and coastal waters, produce more offspring that take longer to develop and have younger first breeding ages (reviewed in Dinsmore 1970). Compared with polar species, tropical species tend to have larger wing spans, longer bills and tails, and less body fat, presumably for catching sparse and highly mobile prey and in response to warmer climatic conditions (Schreiber & Burger 2001). Offshore feeders have larger foraging ranges over which to find prey. Diamond (1978) noted that those tropical species with populations in excess of 10 million individuals, including sooty terns, were all offshore surface feeders. Tropical seabirds tend to have fewer young than coastal species or those that use coastal environments during the non-breeding period (Croxall *et al.* 2012). As a result of these life-history traits pelagic species are much slower at recovering from human-induced threats such as over-fishing and those negatively impacting breeding grounds.

The extent of the sooty tern colony in terms of range, size and distribution has changed markedly since it was initially mapped and recorded in 1942 (see Hughes *et al.* 2017b). When a large airstrip was built in 1942 sooty terns represented a hazard to aircraft resulting in the removal of eggs as well as adult birds in consecutive years, which eventually prevented nesting in the area (Chapin 1954). The population has been subject to a range of human-induced limiting factors, which are thought to have contributed to the decrease in population size from approximately 2 million birds in 1942 to 500,000 individuals in 2005 (Hughes *et al.* 2017b). Reasons for such declines have been linked to the rapid expansion of industrialised fisheries of both large and forage fish (Reynolds *et al.* 2019). Introduced predators have also negatively impacted the sooty tern breeding population with feral cats *Felis silvestris* depredating adults and chicks before their removal in 2003 (Hughes *et al.* 2008). Common mynas *Acridotheres tristis* cause widespread destruction of seabird eggs while black rats *Rattus rattus* depredate both seabird eggs and chicks (Hughes *et al.* 2019).

Since the crash in sooty tern breeding population size in the 1950s there have been marked changes not only in size but also the spatial location of breeding colonies, with a shift from larger more inland clusters to smaller clusters closer to the coast (Hughes *et al.* 2017b). Since the 1990s sooty terns have occupied two main breeding areas termed ‘breeding sites’ in this thesis, namely Mars Bay and Waterside (Fig. 1.1). Within each site the placement of breeding aggregations termed ‘colony clusters’ in this thesis varies in both spatial location and size between breeding seasons.

Although sooty terns are considered one of the most abundant seabirds with population estimates globally of 60 to 80 million birds and the number of annual nesters predicted to be between 18 and 23 million birds (Schreiber *et al.* 2002), the overall trends in population size are not currently known (Birdlife International 2017). One of the reasons for this is that populations are spread over such wide areas with long-term monitoring on any one population lacking (but see outputs from the Florida Keys: Schreiber *et al.* 2002, Bird Island: Feare & Doherty 2004, and Ascension Island: Hughes *et al.* 2019). There is evidence that the number of tropical islands which once supported breeding sooty tern colonies has declined (Hughes 2014). Hughes *et al.* (2017b) recently highlighted concerns for the conservation status of sooty terns, recommending that they be re-classified from 'Least Concern' to 'Critically Endangered' based on declines of multiple populations, including on Ascension Island. Two other abundant colonial nesters inhabiting the tropics (wedge-tailed shearwater *Puffinus pacificus* and guanay cormorant *Phalacrocorax bougainvillii*) are currently listed as declining (BirdLife International 2017). Presently, we lack quantification of population trends particularly for tropical species (Croxall *et al.* 2012), and there are many gaps in our knowledge of their breeding and population ecology. For example, in highly social species a breakdown in social systems can result in declines that exceed declines in population size, through impacts such as reduced reproductive success (Archie *et al.* 2006), foraging success (Claidière *et al.* 2013), and increased risk to depredation (Dunbar & Shultz 2010).

There is also the issue of 'shifting baselines' as introduced by Pauly (1995), where a population is described as stable or even increasing even though it is much reduced from historic levels. The coining of this hypothesis largely arose as a result of fisheries research, where each generation of researchers would accept the baseline by which to measure change as the fish stock levels and composition at the start of their careers (Pauly 1995). This results in a gradual shift in baselines and an acceptance of disappearing stocks as well as inappropriate reference points by which to set future targets (e.g. for conservation or fishing quotas). For example, coral reef conservation is largely inhibited by the lack of a pristine or undisturbed baseline from which to derive indicators of vulnerability or assess conservation efforts given that most reefs have already been impacted by human disturbance (Knowlton & Jackson 2008). In some cases pre-population decline levels may be unrealistic targets for restoration programmes but even so it is important that historical levels are considered in the design of recovery programmes or a species classification status (Seminoff & Shanker 2008). For example, green turtles *Chelonia mydas* nesting in the Seychelles increased from 1,700 females in 1968 to 5,000 in the 1990s, seemingly showing a significant population recovery. However, historic accounts put the number of nesting females at > 10,000 in the early 1900s (Seminoff & Shanker 2008). The relevance of shifting baselines in shaping conservation priorities for other apex marine species comes was highlighted by declines in pelagic sharks. Not only have the historical numbers of oceanic whitetip sharks *Carcharhinus longimanus* in the Gulf of Mexico been relatively ignored, but their distributional changes have also gone largely unrecognised in current assessments of their vulnerability (Baum & Myers 2004). Despite accounts from before the 1960s reporting very large numbers of these sharks compared to the present when they are largely absent, their approximate 92% decline has resulted in a revised conservation status of 'Near Threatened' (Smale 2009). Therefore, understanding and acknowledgment of historic 'pristine' species compositions and population sizes are essential when investigating population trends, stability, and current and future threats to species' population persistence.

1.6 Thesis aims and hypotheses

The aim of this thesis is to investigate trends in population size and structure of sooty terns on Ascension Island, and factors (e.g. inbreeding, sociality, habitat) which may affect such trends together with their implications for conservation management. This will provide a baseline by which to assess the likely impacts of future changes in the environment, such as climate warming, and to conduct population forecasting.

Specifically, I look to address the following aims and hypotheses:

1) Evaluate trends in intra-island breeding timing, synchrony, success and movements and how these relate to trends in population size.

Given that the population on Ascension Island has remained relatively stable between 1990 and 2013 (Hughes *et al.* 2017), it follows that breeding site population stability should also be evident. High levels of breeding success will likely result in an increase in time to arrive on-island in subsequent breeding seasons, and in general breeders should exhibit high levels of breeding site fidelity given site faithfulness is high in seabird species.

2) Examine the links between genetic structure and social organisation, levels of inbreeding depression and potential barriers to gene flow.

It follows that the presence of site faithfulness is predicted to result in landscape level genetic structuring between breeding sites. Given the benefits of kin group structure, this may also lead to higher relatedness of neighbouring individuals, although this is likely to be biased by sex to avoid inbreeding.

3) Assess factors influencing contemporary reproductive success as measured by daily survival rates of chicks to fledging.

The survival of chicks to fledging is predicted to be influenced by group structure, given the benefits of social aggregations and the presence of crèching in this species. Larger and more socially connected groups may stand better chances of surviving against the threat posed by predators given heightened vigilance from many eyes and prey dilution effects.

1.7 Thesis structure

In this thesis I focus on a breeding population of sooty terns on Ascension Island, that has seen declines of 84% in population size between 1950 and 2005 (Hughes et al. 2017). To answer the questions set out in section 1.6 I utilise an extensive mark-recapture database covering over 20 years of monitoring by the Army Ornithological Association (AOS) and the Ascension Island Government Conservation and Fisheries Department (AIGCFD), combined with additional field research as part of this PhD to investigate genetic population structure and breeding success.

Chapter 2 describes the spatial and temporal distribution of breeding colonies of sooty terns on Ascension Island. Using long-term data spanning 22 breeding seasons, I examine population trends at the whole island and breeding site scale. Factors influencing population size and breeding timing, such as breeding success and seasonality, are also explored together with the movement of individuals between two main breeding sites (i.e. Mars Bay and Waterside) that are located approximately 3 km apart (Fig. 1.1).

In **Chapter 3** I develop a set of microsatellite markers with which to assess the genetic structure and relatedness of the sooty tern population on Ascension Island. **Chapter 4** utilises these markers to assess the genetic structure of sooty terns on Ascension Island at various spatial scales. I investigate fine-scale spatial and temporal structure, and find parallels between our findings and those from other taxa – such as fish. I argue that analyses accounting for within-season temporal effects on population structure need further investigation in other species and taxa.

Chapter 5 details a set of field methods for estimating breeding success and offspring sociality of seabirds with precocial offspring. Using data outlined in Chapter 5, I explore connections between the offspring social environment and survival to fledging of sooty tern chicks on Ascension Island in **Chapter 6**. I investigate factors that may influence chick survival including social group size, connectedness and habitat parameters. I also evaluate how early life sociality varies with age and discuss potential reasons for such patterns.

Chapter 7 is a general discussion of our findings and their implications for population ecology and evolution, and the long-term management of the sooty tern population on Ascension Island.

Chapter 2

The influence of timing, synchrony, and breeding success on the movements and population trends of a socially nesting seabird, the sooty tern *Onychoprion fuscatus*

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LJHG analysed the data and wrote the manuscript. SJR, JPM, JPS, and JKC assisted with writing the manuscript.

2.1 Abstract

Temporal variation in population size and movement behaviour can be used as indicators of ecosystem stability, with increased variability and movement indicating ecosystem instability. Long-term data are required to study such trends, given that not all individuals in a population breed at any given time. Seabirds are an ideal study system to investigate population trends and breeding movements given that they are long-lived, produce few offspring per breeding attempt and generally exhibit high breeding site fidelity. We investigated the population trends of a large population of sooty terns nesting on Ascension Island in the South Atlantic that has been subject to severe historical population declines. Although the population remained stable between 1997 and 2015, we observed a dramatic shift in intra-colony population size. We found seasonal effects were acting on the number of terns choosing to breed as well as their body condition, with greater numbers of birds of higher condition breeding in warmer months. We found high levels of asynchrony in breeding timing and heterogeneity in breeding density as well as the movement of birds between breeding sites across breeding seasons. Breeding success had a positive effect on the return time of breeders, with successful seasons resulting in longer delays until their return. The compensatory change in population size between breeding sites was likely a result of the observed movement of breeders together with recruitment of first-time breeders. Our findings indicate a shift in intra-colony level habitat stability which has implications for conservation management, such as predator control, and highlights the importance of within-population scale analyses.

2.2 Introduction

Socially aggregating species that gather in large numbers to breed and rear young, are found in a wide range of taxa, including invertebrates (Uetz *et al.* 2002), fish (Huggins & Thompson 1970), reptiles (Doody *et al.* 2009), and mammals (Campagna *et al.* 1992). They are widespread in birds making up 13% of all bird species, and 98% of seabird species (Lack 1968). Adaptive benefits of aggregating behaviour or coloniality include social information exchange for nesting and foraging sites, reduced predation risk and behavioural coordination (e.g. breeding arrival and departure timing) (see review by Evans *et al.* 2016). The costs of colonial breeding include increased risk of kleptoparasitism (Jovani & Grimm 2008), disease and parasite transfer (Danchin & Wagner 1997; Silk *et al.* 2014) and competition for resources (Danchin & Wagner 1997). The mechanisms that operate on when and where breeders nest are complex (Conradt & Roper 2010). These include interactions between life history stages, and environmental conditions that in turn impact food availability both prior to (Sorensen *et al.* 2009) and during breeding (Barrett & Krasnov 1996), as well as factors such as predation risk at breeding grounds (Nisbet & Welton 1984; Naves *et al.* 2006; Kildaw *et al.* 2008). In long-lived organisms, understanding factors that affect if and where individuals decide to breed is crucial given the consequences for lifetime reproductive success, and their impacts on the structure and size of local populations (Martinez-Abrain *et al.* 2003). However, long-term studies that are required to answer such questions are often limited (Dunn & Weston 2008) and rarely consider the effects of both extrinsic and intrinsic factors on population parameters, such as the breeding timing (Votier *et al.* 2009).

Climate and time of year effects have been shown to influence breeding timing and success of common guillemots *Uria aalge* (Votier *et al.* 2009). Adverse weather conditions led to a delay in breeding which was thought to be due to reductions in food availability. Breeding success was also higher in breeding seasons which commenced earlier in the year suggesting that food availability affected fitness outcomes. Indeed, global climate change has consequences for the phenology of most organisms with shifts in seasonal activities, including breeding timing, leading to potential asynchronies in available resources (Root *et al.* 2003; Thackeray *et al.* 2016). The sensitivity of organisms to shifts in the availability of resources through phenological shifts that lead to misalignments between species such as predator prey interactions are uncertain (Cohen *et al.* 2018). Cohen *et al.* (2018) found that factors such as arrival time to breeding areas was poorly correlated to climate variables such as precipitation and temperature; this was thought to be due to climatic conditions differing between pre-arrival and destination locations. Peak abundance proved to be better predicted by changes in climate (Cohen *et al.* 2018). In a meta-analysis of the impacts of climate change on 145 seabird populations, Keogan *et al.* (2018) found only limited changes in breeding timing in response to changes in sea surface temperature (SST), though argue that if lower trophic levels are shifting in parallel with changes in SST that seabirds may be at risk from increasing mismatch in prey availability. Schroeder *et al.* (2009) found that winter climate was an important determinant of pre-breeding condition of Cassin's auklets *Ptychoramphus aleuticus* and common guillemots, with positive associations between winter up-welling and SST, and breeding timing. However, the effects of climatic conditions on breeding timing and success are variable with a number of studies showing the opposite trend in warmer climatic conditions having a negative effect on breeding timing and cooler temperatures delaying breeding onset (Frederiksen *et al.* 2008; Robinson *et al.* 2013).

Both breeding timing and breeding synchrony can have significant effects on breeding success, with earlier and more synchronous breeders having higher breeding success (Feare 1976a; Murphy & Schauer 1996; Faivre *et al.* 2001; Ramos 2002; Antolos *et al.* 2006; Minias *et al.* 2013). The benefits of greater synchrony to breeding success are thought to include predator satiation, enhanced mate finding and the formation of crèches containing offspring (Jovani & Grimm 2008). Several studies have shown within-colony variability in breeding synchrony (e.g. Murphy & Schauer 1996; Faivre *et al.* 2001; Dey *et al.* 2014). Differences in breeding synchrony could be due to the clustering of experienced or inexperienced birds, those in similar body condition, or genetically similar individuals (Murphy & Schauer 1996; Brown 2016). Indeed, Coulson and White (1960) found that older, more experienced black-legged kittiwakes *Rissa tridactyla* bred earlier than inexperienced breeders, and densely nesting birds showed lower variation in breeding synchrony.

Breeding site fidelity, where breeders return to the same nesting ground, and sometimes the exact nest site (Kokko *et al.* 2004), can be used as predictors of habitat quality and ecosystem stability given that movement between nesting sites is often related to breeding success of either individuals or of conspecifics. This is often referred to as the 'win-stay, lose-move' strategy (Schmidt 2004). By experimentally manipulating breeding success, Boulinier *et al.* (2008) were able to show that public information regarding the quality of breeding areas was important in determining the level of nest-site fidelity in black-legged kittiwakes. Low quality areas where breeding failure was high prompted residents to prospect for new sites the following year. Martinez-Abrain *et al.* (2003) also found a 90% likelihood of colony desertion in the year following low levels of breeding by Audouin's gulls *Larus audouinii*. Site fidelity may also be affected by the stability of the nesting habitat with more stable sites (e.g. less prone to flooding) leading to greater site faithfulness (Cuthbert 1985). In slender-billed gulls *Chroicocephalus genei* breeding colonies occupied different sites each season but the social structure of colony membership was dependent on breeding success in the previous season, with successful breeding leading to greater social group tenacity (Francesiaz *et al.* 2017). Several studies have highlighted the importance of previous experience on individual breeding movement and dispersal through the use of multi-event models that incorporate memory effects (Hestbeck *et al.* 1991; Rouan *et al.* 2009). A classic example that highlights the existence of the use of previous breeding sites predicting future breeding site choice uses a large dataset of mark-recaptures of Canada geese *Branta canadensis* (Hestbeck *et al.* 1991; Pradel 2005). Pradel (2005) found that past experience influenced subsequent breeding movements and dispersal between breeding locations. This phenomenon has also been found in other species including greater flamingoes *Phoenicopterus roseus* (Pradel *et al.* 2012) and black-headed gulls *Larus ridibundus* (Péron *et al.* 2010), but also in other taxa, such as amphibians (Cayuela *et al.* 2017).

The degree of natal philopatry by recruiting first time breeders can have important consequences for population dynamics and future breeding success and fitness of recruited individuals (Serrano *et al.* 2003). However, in species with long maturation times such as seabirds, recruitment is often difficult to assess and therefore it is rarely studied (Becker 2015). Many studies have illustrated that recruiting (or first –time) breeders often arrive later than more experiences breeders and occupy less favourable habitats (e.g. Aubry *et al.* 2009; Becker 2015). Recruitment can also be sex-biased, with males nesting closer to their natal sites than females (Mougin *et al.* 1999; Ibarguchi *et al.* 2011). Serrano *et al.* (2003) showed that dispersal distance of lesser kestrels *Falco naumanni* was dependent on the distance between colonies, with shorter distances resulting in shorter natal dispersal distances. In Cory's shearwaters *Calonectris diomedea* recruitment to natal sites was high (> 80%), with first time breeders settling within 20 m of their original nest site when nesting in the same colony as they fledged from, and otherwise travelling in excess of 1 km from their original nest site (Mougin *et al.* 1999). Pre-breeder dispersal to non-natal areas also tends to be higher than dispersal of established breeders to other breeding areas (Greenwood & Harvey 1982; Bradley & Wooller 1991). For example, in roseate terns *Sterna dougalli*, the probability of natal dispersal by recruiting first-time breeders was 2-6 times higher than breeder dispersal (Lebreton *et al.* 2003). However, the existence of long-term memory has been shown in black-headed gulls breeding for the first time (Péron *et al.* 2010) with recruiting individuals having a higher probability of returning to their natal colony later in life. Age at first recruitment to a breeding population can also vary, and this is especially true in long-lived seabird species occupying stable habitats (Lebreton *et al.* 2003; Becker & Bradley 2007; Aubry *et al.* 2009). For example, black-legged kittiwakes can reproduce at two years old but recruitment is highest between three and six years or older (Aubry *et al.* 2009). Such variation can be due to heterogeneities in individual body condition, the availability and quality of the breeding site habitat, and the interaction between them. In great cormorants *Phalacrocorax carbo*, recruitment was delayed in areas of highest quality compared to younger recruiting ages in lower quality areas (Hénaux *et al.* 2007).

Here, we investigate the effect of breeding timing, synchrony and breeding success on the movements and population trends of breeding sooty terns on Ascension Island in the South Atlantic. Sooty terns are socially breeding pelagic seabirds found throughout the tropical oceans. Although widespread, dramatic population declines prompted a recent call to reclassify their conservation status from ‘Least Concern’ to ‘Critically Endangered’ (Hughes *et al.* 2017b). The Ascension Island population is significant in that it accounts for 40% of the Atlantic population and has been monitored in some form since the late 1800’s. The population has declined by 84% from > 2 million individuals in 1942 to approximately 500,000 in 2005 (Hughes *et al.* 2017b). The reasons for this decline are thought to be due to predation by introduced predators, namely feral cats and black rats, together with food shortages caused by commercial fisheries that appear to have resulted in a dietary shift from predominantly teleost fish pre 1950 to nutrient poor squid and other invertebrates post-1970s (Reynolds *et al.* 2019). Consistent long-term monitoring of the population began in the 1990s and from this time the population has occupied roughly the same two breeding sites located on the south coast of the island and are approximately 3 km apart (Fig. 2.1).

Although the population has remained relatively stable since the early 1990s (Hughes 2014), finer scale analyses at the local breeding site level have not previously been explored. Using an extensive long-term dataset spanning 22 breeding seasons, we investigated population trends at the two breeding sites, the influence of timing, synchrony and breeding success on the breeding heterogeneities in the strength and direction of movements between breeding sites and their implications for population growth and recovery following the eradication of feral cats in 2003 (Hughes *et al.* 2012). We used a long-term mark-recapture dataset to estimate breeder dispersal between breeding sites on Ascension Island. We used multi-event models that included the influence of imperfect detection of birds (Pradel 2005; Gimenez & Choquet 2010) and past experience on the likelihood of movement (Rouan *et al.* 2009). We also investigated the probability of recruitment and natal philopatry at each breeding site by first time breeders. Finally, we discussed how these findings may be used to assist the long-term management and monitoring of such populations. Improving the effectiveness of survey efforts is crucial for maintaining accurate longitudinal studies (Mitchell *et al.* 2004), data from which are fundamental for monitoring future responses to changes in environmental conditions such as climate warming (Clutton-Brock & Sheldon 2010).

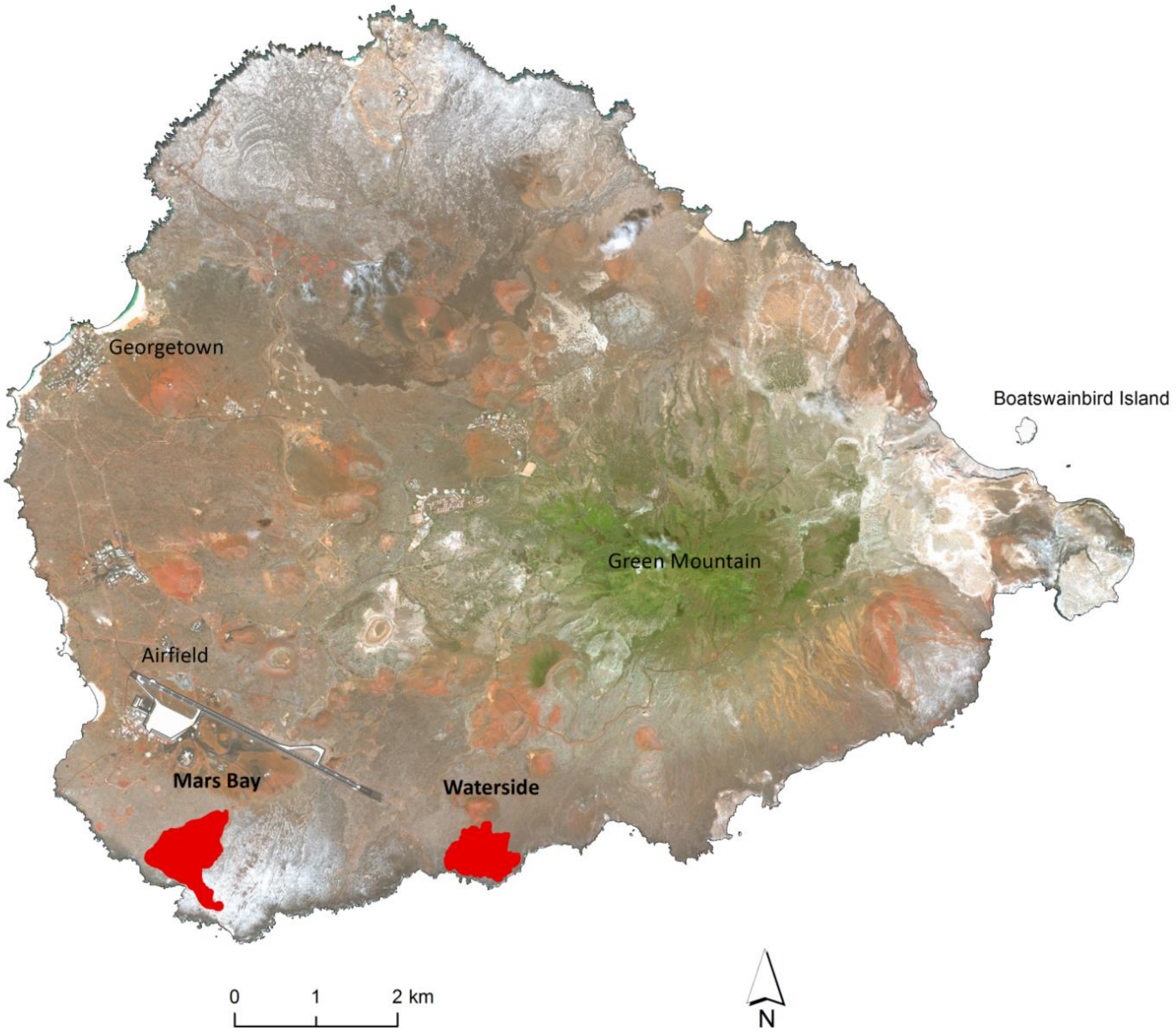


Figure 2.1 The locations of the two main sooty tern breeding sites (Mars Bay and Waterside) in relation to Green Mountain on Ascension Island in the South Atlantic. The red areas represent the cumulative extent of peak breeding occupancy between 1996 and 2016 (inclusive). Ascension Island base map courtesy of the Ascension Island Heritage Society.

2.3 Materials and Methods

The ringing and recapture dataset contains 35,817 captures of 30,960 individuals between 1975 and 2016 from the sooty tern breeding population on the mainland of Ascension Island (see Table 2.1 for breakdown by breeding season). The dataset includes 4,762 recaptures of 4,049 ringed birds (13.1% of the total ringed population) as well as 95 recoveries of ringed dead individuals. Recapture effort was recorded in person hours, with a total of over 1,100 hours.

Where possible, data were collected during peak breeding times defined by Ashmole (1963) as 40 to 60 days after the first egg is laid at a breeding site, based on a 9.6 month breeding cycle (Reynolds *et al.* 2014). Birds were captured with a long-handled net mainly during the incubation stage to minimise disturbance to the more vulnerable newly hatched chicks. Sooty terns usually lay only one egg per breeding season, with low rates of relaying as a result of nest failure (Ashmole 1963). Re-trapping was undertaken by a team of two to 14 people who systematically searched the colony for ringed individuals. Birds were ringed each breeding season under a British Trust for Ornithology (BTO) ringing licence number A4318, in groups of 50–100 birds in order to minimise disruption in a given area. Fledged juveniles take on average 5 years to return to breed as adults (Hughes 2014). For each captured bird the following data were recorded: date, ring number, breeding site (Mars Bay or Waterside; Fig. 2.1), and GPS coordinates (records begin in 2003 as hand-held GPS devices became more readily available).

Individual capture rate varied with the majority of birds being caught twice and the maximum number of captures for a single individual being six. The number of individuals caught on multiple occasions was 3,435 (twice), 537 (three times), 62 (four times), 13 (five times), and 2 (six times).

Nesting density was recorded where possible at each breeding site using transects (*sensu* (Hughes *et al.* 2008). Colony area was calculated in ArcGIS version 10.2 (ESRI 2013) from GPS perimeter shape files of each area occupied by breeding individuals taken at the time of visit.

Table 2.1 Ringing records of breeding sooty terns on Ascension Island by breeding season peak.

Breeding season peak*	No. adults ringed	No. chicks ringed	Total no. birds ringed	Total no. recaptures	Total no. recoveries	Re-trapping effort (hrs)
1975	-	200	200	-	-	-
Oct 1996	150	50	200	-	-	-
June 1998	186	314	500	1	-	-
Nov 2000	546	1	547	-	-	-
Sep 2001	186	51	221	-	1	-
July 2002	1,379	50	1,429	7	-	10
April 2003	399	250	649	45	-	19
Feb 2004	2,000	-	2,000	154	-	64
Dec 2004	500	-	500	153	-	32
Oct 2005	375	1,625	2,000	112	72	18
Aug 2006	376	624	1,000	190	2	55.75
May 2007	2,498	1,498	3,996	260	9	53.25
Feb 2008	2,000	-	2,000	414		70.5
Dec 2008	2,200	-	2,200	538	1	52
Oct 2009	62	1,033	1,095	101	8	22
May 2010	-	-	-	16	1	3
Apr 2011	2,570	-	2,570	379	-	81.5
Jan 2012	511	39	550	259	-	47
Dec 2012	1,401	699	2,100	629	-	166.75
Aug 2013	731	469	1,200	362	1	166
May 2014	1,998	-	1,998	547	-	182
April 2015	1,080	500	1,580	474	-	147
Dec 2015	2,416	9	2,425	121	-	23.5
Total	23,548	7,412	30,960	4,762	95	1,189.75

*The peak is 40 to 60 days after the first egg is laid, based on a 9.6-month breeding cycle

For each breeding period an estimate of population size (number of breeding pairs) at each colony was then calculated and confidence intervals (CIs) produced from the variance in breeding density. Population estimates for breeding seasons where density estimates were not available were calculated using the overall average breeding density by breeding colony (mean eggs/m^2 ± CI: Mars Bay = 1.41 ± 0.92, n = 2,358, Waterside = 1.87 ± 1.06, n = 2,849). In years where the peak breeding period was missed (as defined by 30 days before/after peak breeding), population estimates were not included in the analysis (n = 4 seasons). Total population size was estimated by summing the two colony estimates with 95% CIs calculated from the pooled standard deviation (SD_{pooled}) of the variance in breeding density at each breeding site (Cohen 1988):

$$SD_{pooled} = \sqrt{\frac{(n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2}{n_1 + n_2 - 2}}$$

where $n_{1,2}$ = the number of quadrats sampled at each site (1,2) and $SD_{1,2}$ = the standard deviation of the variance in nesting density at each site (1,2).

Colony areas were plotted in ArcGIS version 10.2 (ESRI 2013) for breeding seasons between September 1997 and November 2015 for approximately every six breeding seasons to visualise heterogeneities in the breeding areas occupied. To compare colony areas with historical records of breeding extent pre-population crash (pre-1960) we also plotted outlines of breeding colony occupancy in 1877, 1958 and 1942. Breeding success estimates were recorded at the population level for 20 seasons between 1997 and 2015 defined as: 'Good' - < 40% desertion of breeding areas by breeding adults shortly after peak breeding; 'Average' - ~ 40% desertion of breeding areas after peak breeding; and 'Poor' - > 40% desertion of breeding areas after peak breeding. Eggs were measured on an *ad hoc* basis along transects at each breeding site between 1994 and 2018 (n = 8 breeding seasons, n = 1,824 eggs measured). The lengths and breadths of eggs were measured with Vernier dial callipers (± 0.1 mm, dialMax, Wiha, Switzerland).

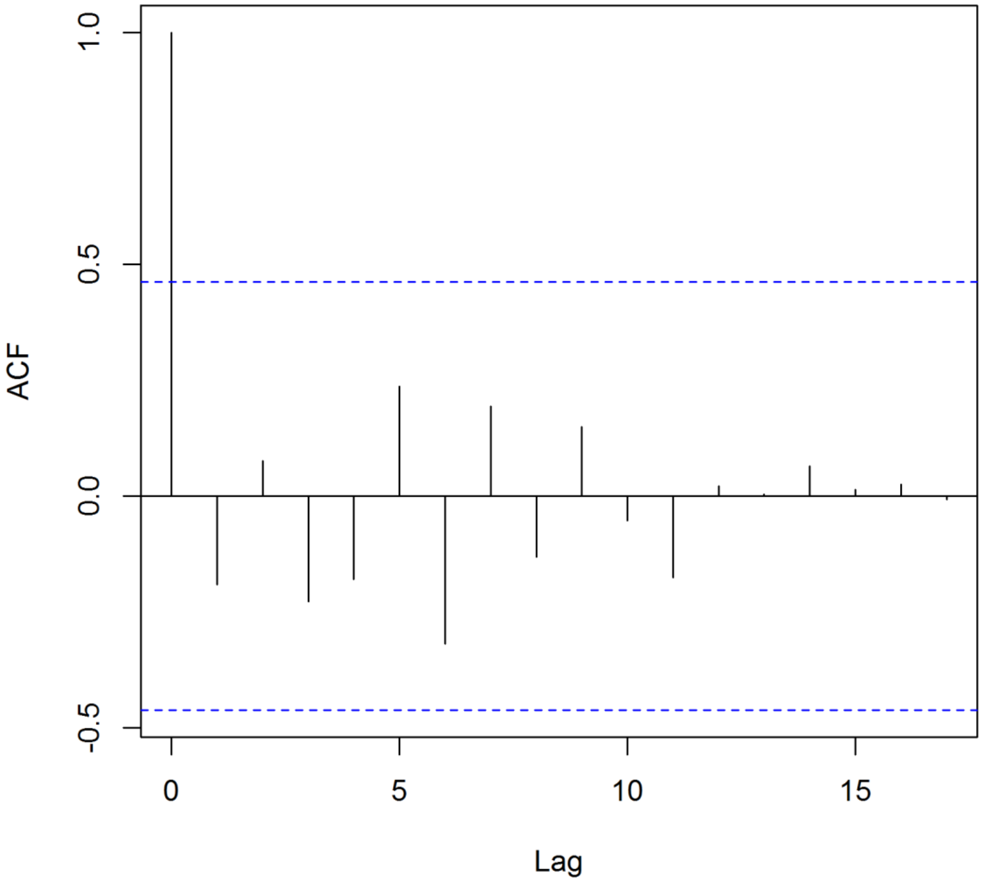
2.3.1 Statistical analyses

All analyses were undertaken in R version 3.6.0 (R Core Team 2019). Chicks were not included in analyses except where specified. We checked that assumptions were met for all using for example Shapiro-Wilk's test for normality and from examination of diagnostic plots (e.g. residuals vs fitted, normal Q-Q. scale-location residuals vs leverage) (Zuur *et al.* 2010).

2.3.1.1 Colony population trends

We used linear regression to investigate temporal trends in population size both at the population and site levels between 1997and 2015 (inclusive). Models were checked for temporal autocorrelation by examining correlograms using the acf function in the R package 'nlme' (Pinheiro *et al.* 2020). The autocorrelation plot displayed no obvious oscillations around zero correlation and correlations did not reach the significance boundary (i.e. the dashed lines in Fig. 2.2). Therefore, an autocorrelation term was not included in the final models. To account for variation in breeding density, 95% CIs were included as an offset in the models. To examine whether factors affecting population change at breeding sites were occurring at a global level a Pearson's correlation test was used.

a



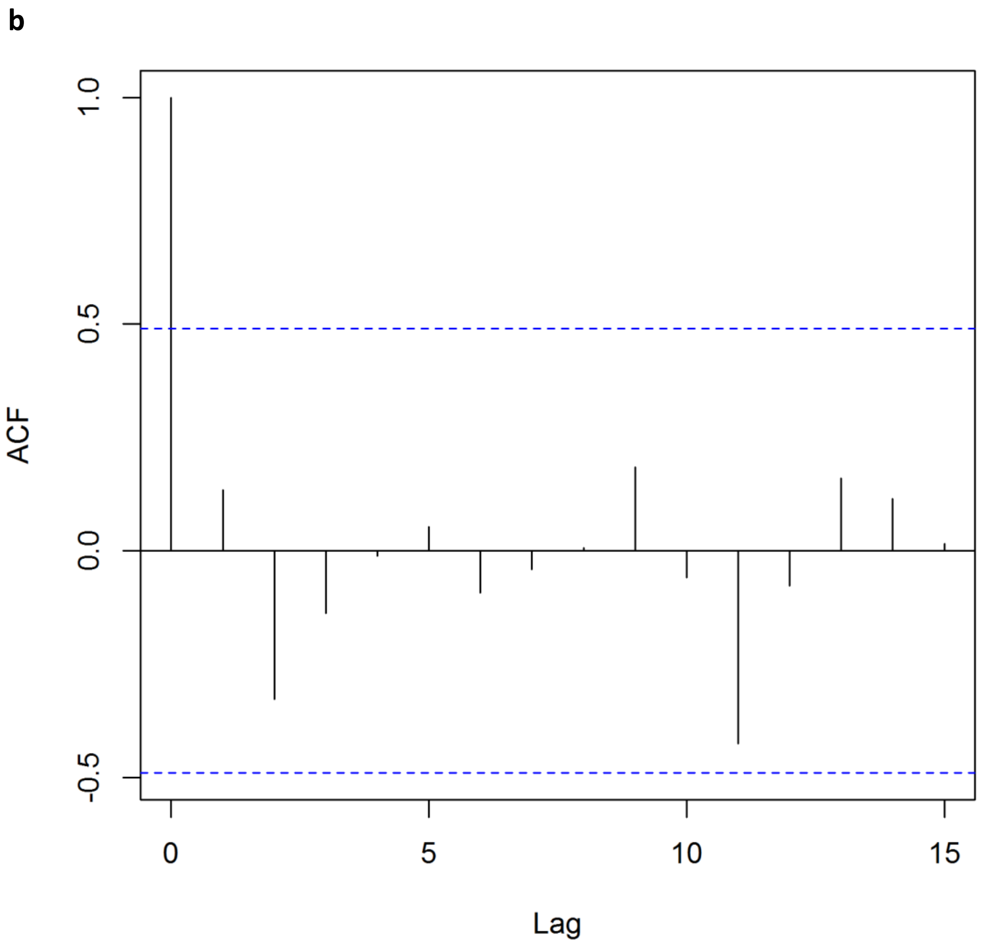


Figure 2.2 Correlograms to check for the presence of temporal autocorrelation in population size of sooty terns at **a)** Mars Bay and **b)** Waterside. Dashed blue lines represent significance boundaries. ‘ACF’ = Auto Correlation Function, ‘Lag’ refers to the breeding seasons time lag.

Time of year effects on populations change were explored using a binomial generalized linear mixed-model (GLMM), with binary change in population size as the response variable. Predictor variables included time of year (binary: warmer/cooler months) for the current and previous breeding seasons using the glmer function in the lme4 package (Bates *et al.* 2015), with breeding season and breeding site as random effects. Given that the climate in the tropical South Atlantic does not have pronounced seasons we defined time of year effects into two main periods of warmer and cooler months. Ashmole and Ashmole (2000) stated that Ascension Island has the warmest weather in April and the coolest in September. Therefore, we defined the warmer season from 1st April to 31st August and the cooler season from 1st September to 31st March and assigned breeding seasons using first lay dates.

To assess whether adult body condition and investment varied with time of year, we used egg volume as a proxy, given that female investment in eggs is a reflection of female body condition (Lack 1968; Barrett *et al*. 2012), with larger eggs, and thus investment, laid by females with higher body condition (Minias *et al*. 2013). More specifically, food abundance prior to laying is considered to be one of the most important determinants of egg size (Sorensen *et al*. 2009; Barrett *et al*. 2012), with higher food availability leading to larger eggs. Egg volume (V) was calculated from the following equation from Hoyt (1978):

$$\mathrm{V} = K_v \cdot LB^2$$

where L = length, B = breadth, and K_v = the volume coefficient, a term describing egg shape. K_v was taken as 0.51 from Hoyt (1979) who compiled 124 measures of K_v from 115 species (accurate to within 2% of the fresh egg weight for most species). We ran a Welch's t-test for unequal sample sizes to compare egg volume between warmer and cooler months.

2.3.1.2 Breeding synchrony and success

To assess potential heterogeneity between breeding sites in both breeding density (mean number of pairs/m^2) and first hatch dates we used linear mixed-effects models using the lmer function in the package lme4 (Bates *et al.* 2015) with season as a random factor to account for potential variance over time. A reference point of 1st January was used to compare first hatch dates between breeding sites.

To assess whether carry-over effects from breeding outcome were operating on breeding timing in successive breeding seasons, we used population-level breeding success data (as breeding site level data were not collected) and the lagged number of days between first hatch dates at the earlier breeding site (i.e. Waterside). We used a general linear model (GLM) with breeding success set as the predictor variable.

2.3.1.3 Nest and breeding site movement

To assess the levels of nest and breeding site tenacity, we used a combination of fine and wider spatial scales. At the fine scale, individual adult nest locations were obtained from GPS positions of breeding birds captured at the time of ringing and when recaptured during subsequent nesting attempts between 2003 and 2015. The average distance travelled between nest locations in successive breeding attempts was calculated at the population and breeding site scale in Arc GIS version 10.2 (ESRI 2013). Site-based differences in distances moved were compared in a linear mixed-effects model using the lmer function in package lme4 (Bates *et al.* 2015). Individual was included as a random factor to account for the nested nature of the data. Distance travelled was square root transformed to meet model assumptions.

2.3.1.4 Multi-event models

At the site-based scale we used multi-event models built in the program E-SURGE V 2.1.2 (Choquet *et al*. 2009). Multi-event models are appropriate for studying heterogeneity in individual movement patterns (Péron *et al*. 2010) where there is uncertainty of states. An individual's underlying state is determined by their current location and the probability of emigration. Uncertainty can be accounted for by the inclusion of unknown states, such as 'individual not seen' (Pradel 2005). The 'real' observed data, derived from field observations, are the events and in our case these are the breeding locations of individuals. E-SURGE uses three different parameters: the initial state probabilities, the probability of transitioning between states (which includes movement and survival probabilities), and finally the probability of the events conditional on the underlying states (i.e. the probability of capture).

To investigate the movement probabilities of breeding adults between breeding sites we employed the use of memory models, which account for the tendency of individuals to return to breeding areas that they previously used, as opposed to random settlement models (Cole *et al*. 2014). The most simple memory model that considers the site currently occupied to predict settlement at time t + 1 is the Arnason-Schwartz model (hereafter referred to as model 'AS') (Arnason 1973; Schwarz *et al*. 1993). To account for memory that extends beyond one breeding season we also employed the Pradel model (hereafter referred to as model 'P'; Pradel 2005). Model P considers the previous site used (at time t - 1) and the current location (at time t) to predict the probability of being present at a particular site in the following breeding period (i.e. at time t + 1). In both models events (directly observed) were: 'not encountered' (code = 0), 'encountered at site 1' (Mars Bay:

code = 1), ‘encountered at site 2 (Waterside: code = 2). For model AS we defined three states (i.e. those not directly observed), given that transitions depend on the current site occupied only: adult alive at site 1 (Mars Bay: code = 1), adult alive at site 2 (Waterside: code = 2), and adult dead (code = 3). For model P we defined five different states dependent on the previous and current locations: 11 (alive at site 1 at time t - 1 and alive at site 1 in the following breeding period t: code = 1), 12 (alive at site 1 and alive at site 2 in the following period: code = 2), 21 (alive at site 2 and then at site 1: code = 3), 22 (alive at site 2 and then at site 2 again: code = 4), and dead (code = 5). E-SURGE uses matrices of parameters to denote each stage of the model and we use the same notation as given in Rouan *et al*. (2009) and Cole *et al*. (2014). For each of the three matrices these are defined in Table 2.2 for both models. It is important to note that rows define the state at departure, columns the state at arrival and the sum of each row is equal to one. In the initial state and transition matrices both rows and columns represent states, and in the event matrices the rows represent states and columns the events.

For both models we also set capture probabilities conditional on effort (man hours spent searching for ringed individuals) at each site, given that this varied by year and site. For the full parameterisation in E-SURGE please see Appendix 1. Data used in the adult breeding movement models comprised 27,913 individual capture histories ringed and recaptured during 20 breeding periods from 2000 to 2015 with known breeding site locations.

Table 2.2 Matrices for the model parameters used for the multi-event models run in E-SURGE for adult sooty tern movements between sites (1: Mars Bay, and 2: Waterside) during breeding periods on Ascension Island. Model AS is the Arnason-Schwarz model and model P is the Pradel model. In model AS states were: site 1, site 2, and dead. In model P states were: 11, 12, 21, 22, and dead (†). Events were: seen at site 1, seen at site 2, and not seen [see section 2.3.1.4 and Appendix 1 for further details).

Model	Initial state	Transition	Event
Model AS	$\Pi_t = (\pi^t_1\ \pi^t_2\ 0)$	$\Phi_t = \begin{bmatrix} \Phi^t_{11} & \Phi^t_{12} & \Phi^t_{1\dagger} \\ \Phi^t_{21} & \Phi^t_{22} & \Phi^t_{2\dagger} \\ 0 & 0 & 1 \end{bmatrix}$	$B_t = \begin{bmatrix} 1-p^t_1 & p^t_1 & 0 \\ 1-p^t_2 & 0 & p^t_2 \\ 1 & 1-p^t_1 & 1-p^t_2 \end{bmatrix}$
Model P	$\Pi_t = (\pi^t_{11}\ \pi^t_{12}\ \pi^t_{21}\ \pi^t_{22}\ 0)$	$\Phi_t = \begin{bmatrix} \Phi^t_{111} & \Phi^t_{112} & 0 & 0 & \Phi^t_{11\dagger} \\ 0 & 0 & \Phi^t_{121} & \Phi^t_{122} & \Phi^t_{12\dagger} \\ \Phi^t_{211} & \Phi^t_{212} & 0 & 0 & \Phi^t_{21\dagger} \\ 0 & 0 & \Phi^t_{221} & \Phi^t_{222} & \Phi^t_{22\dagger} \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}$	$B_t = \begin{bmatrix} 1-p^t_1 & p^t_1 & 0 \\ 1-p^t_2 & 0 & p^t_2 \\ 1-p^t_1 & p^t_1 & 0 \\ 1-p^t_2 & 0 & p^t_2 \\ 1 & 1-p^t_1 & 1-p^t_2 \end{bmatrix}$

2.3.1.5 Natal site philopatry

We assessed the level of natal site philopatry by analysing data collected from individuals ringed as chicks that were later captured for the first time as breeding adults. We included an unobservable state to control for the possibility that birds could have returned to breed in the seasons before they were recaptured but were missed. We assumed that recruiting breeders had not bred elsewhere prior to breeding on Ascension Island, given that site fidelity is strong in seabirds once a breeding site is selected (Lebreton *et al.* 2003; Palestis 2014).

We analysed the capture histories of 5,489 sooty terns marked as chicks from 2000 to 2011 and recaptured as breeding adults for the first time until 2015. We used E-SURGE to model recruitment and site philopatry and the probability of breeding at different ages. Events were coded as ‘not encountered’ (code = 0), ‘encountered at site 1’ (Mars Bay: code = 1), and ‘encountered at site 2 (Waterside: code = 2). We defined five states as: non-breeder at site 1 (code 1), breeder at site 1 (code2), non-breeder at site 2 (code 3), breeder at site 2 (code 4), and dead (code 5). We built models with age, site and effort effects. We kept the initial state constant in all models. As first time breeders did not breed for the first time until at least three breeding seasons had passed since fledging, we set possible recruitment age to ≥ 3. Note that breeding seasons are used as a proxy for age, but as sooty terns on Ascension Island breed every 9.6 months, age in years is actually lower. Model structure is given in Appendix 2 and included parameters for initial state, survival, breeding recruitment and capture probability (see Pradel *et al*. 2012 for similar model design). Given the sparseness of the data per breeding season, we did not attempt model recruitment estimates over time (i.e. breeding seasons).

2.3.1.6 Goodness-of-fit tests and model selection for multi-event models

No test is available to assess the goodness-of-fit (GOF) for multi-event models, so we carried out GOF tests using the Jolly Move Model (JMV) which is an extension of the AS model (Pradel *et al*. 2005). We used the program U-CARE V2.3.4 (Choquet *et al*. 2005).

Model selection was undertaken in E-SURGE (Choquet *et al*. 2009) using Akaike's Information Criterion (AIC; Burnham & Anderson 2002). A variance inflation factor ($\hat{c}$) was applied from GOF tests by correcting AIC for extra-binomial variation (see section 2.4). Discriminating between two models was done by assuming difference where their QAIC was > 2. If models had redundant or partial parameter redundancy they were not included in model selection given uncertainty in the estimates.

2.4 Results

2.4.1 Colony population trends

Although the sooty tern population size on Ascension Island remained relatively stable across breeding seasons between 1997 and 2015 ($F_{1,15} = 0.12$, $R^2 = 0.06$, $P = 0.73$; Fig. 2.3a), there were considerably different temporal trends at the breeding site level. The population nesting at Mars Bay significantly increased ($F_{1,16} = 34.87$, $R^2 = 0.67$, $P < 0.001$; Fig. 2.3b), while it decreased significantly at Waterside ($F_{1,15} = 11.58$, $R^2 = 0.40$, $P = 0.007$; Fig. 2.3c). This represents a 337% increase in population size at Mars Bay and a 62% decrease at Waterside across the study period (Fig. 2.4). There was a significant negative correlation between the change in population size in successive seasons at Mars Bay and Waterside ($t_{11} = -2.55$, $R^2 = 0.61$, $P = 0.03$; Fig. 2.5).

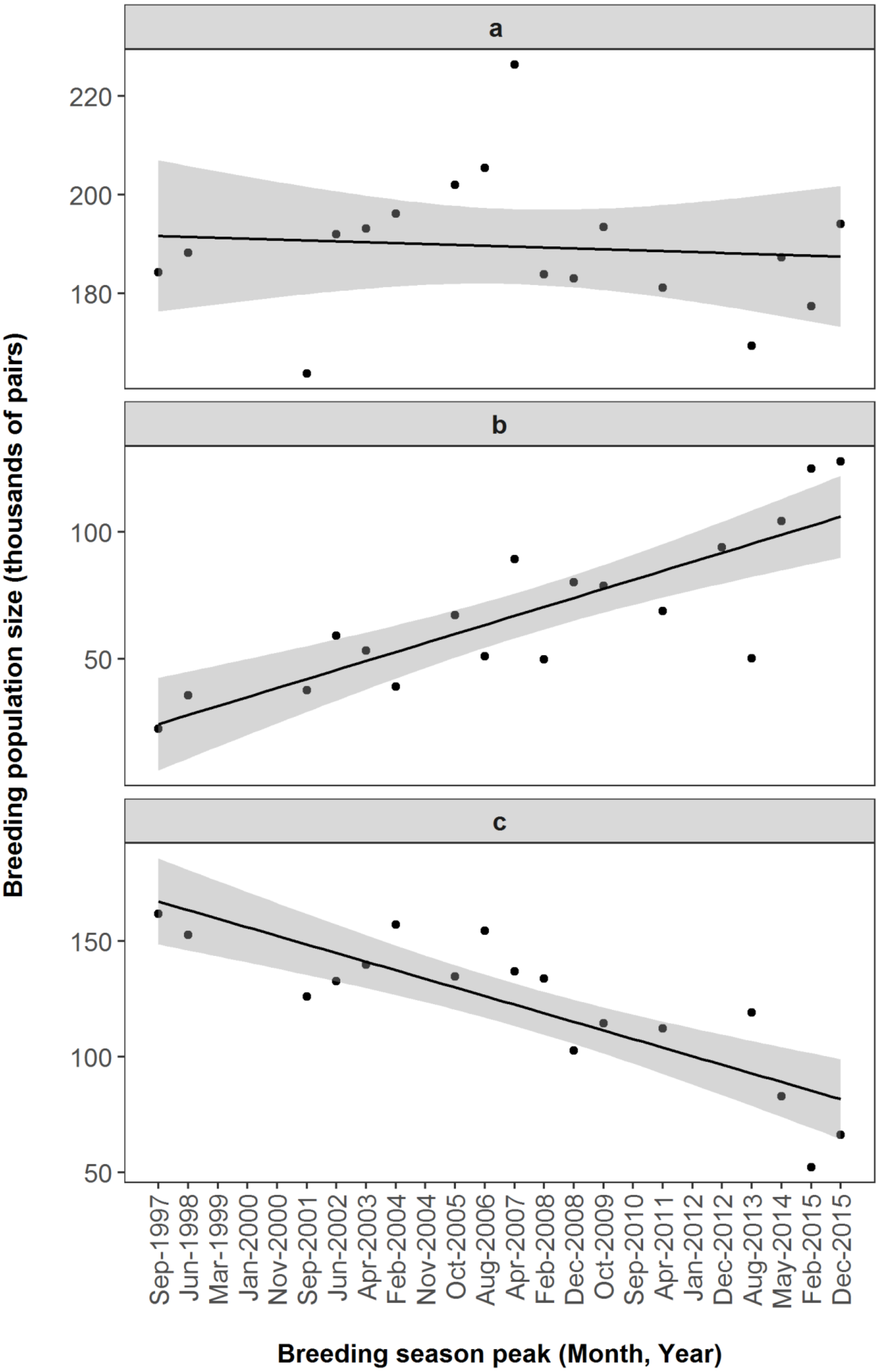


Figure 2.3 The total population sizes of sooty terns breeding on Ascension Island in the South Atlantic between 1997 and 2015 (inclusive) on **a)** the island, and at **b)** Mars Bay and **c)** Waterside. Black dots represent the individual season totals and shaded grey areas are the 95% confident intervals around solid lines that represent least squares regression lines.

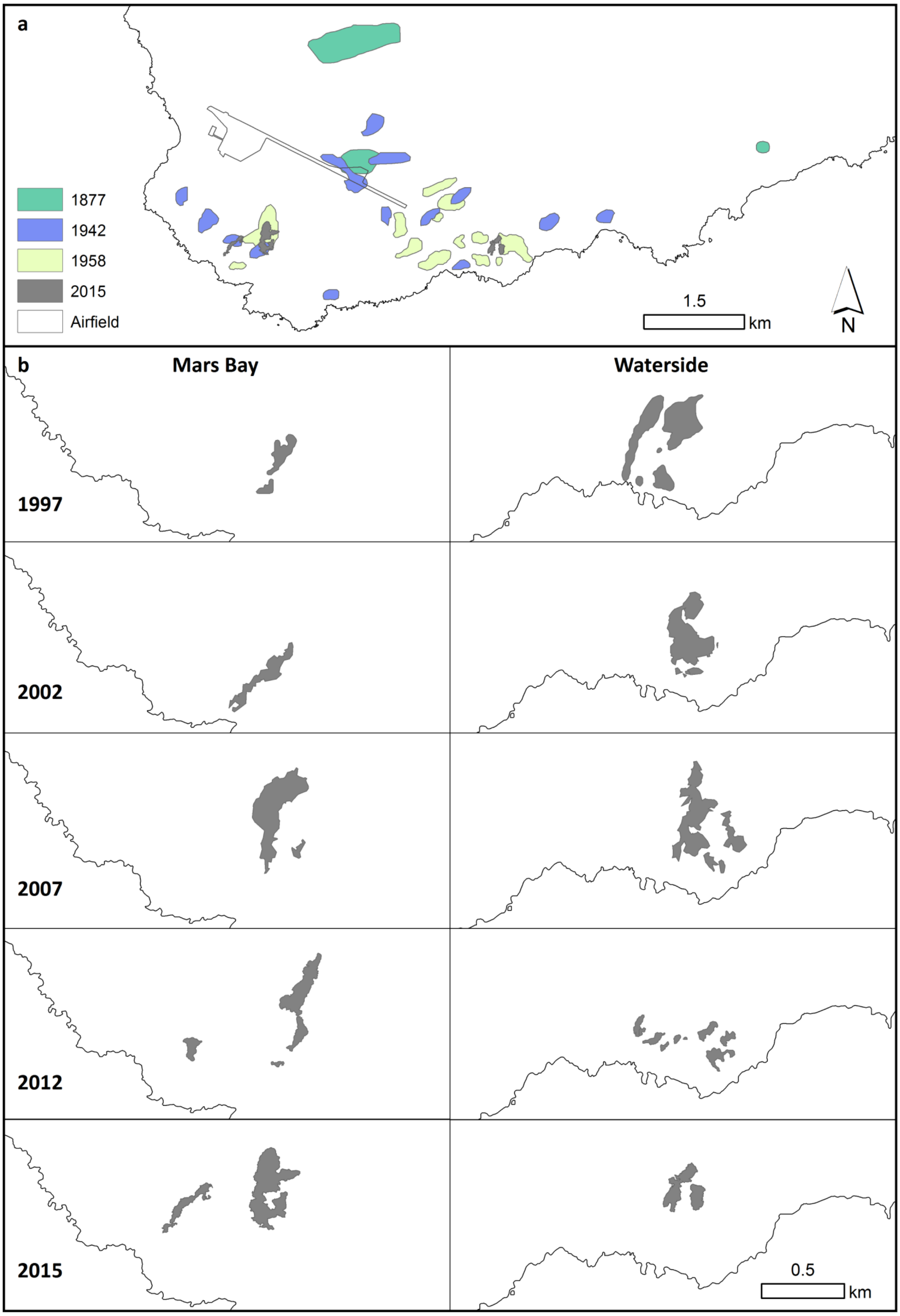


Figure 2.4 The extent of breeding areas **a)** on the island pre-population crash for 1877, 1942, 1958 (with 2015 post-population crash shown for reference), and **b)** at Mars Bay and Waterside breeding sites separately for breeding seasons after the population crash.

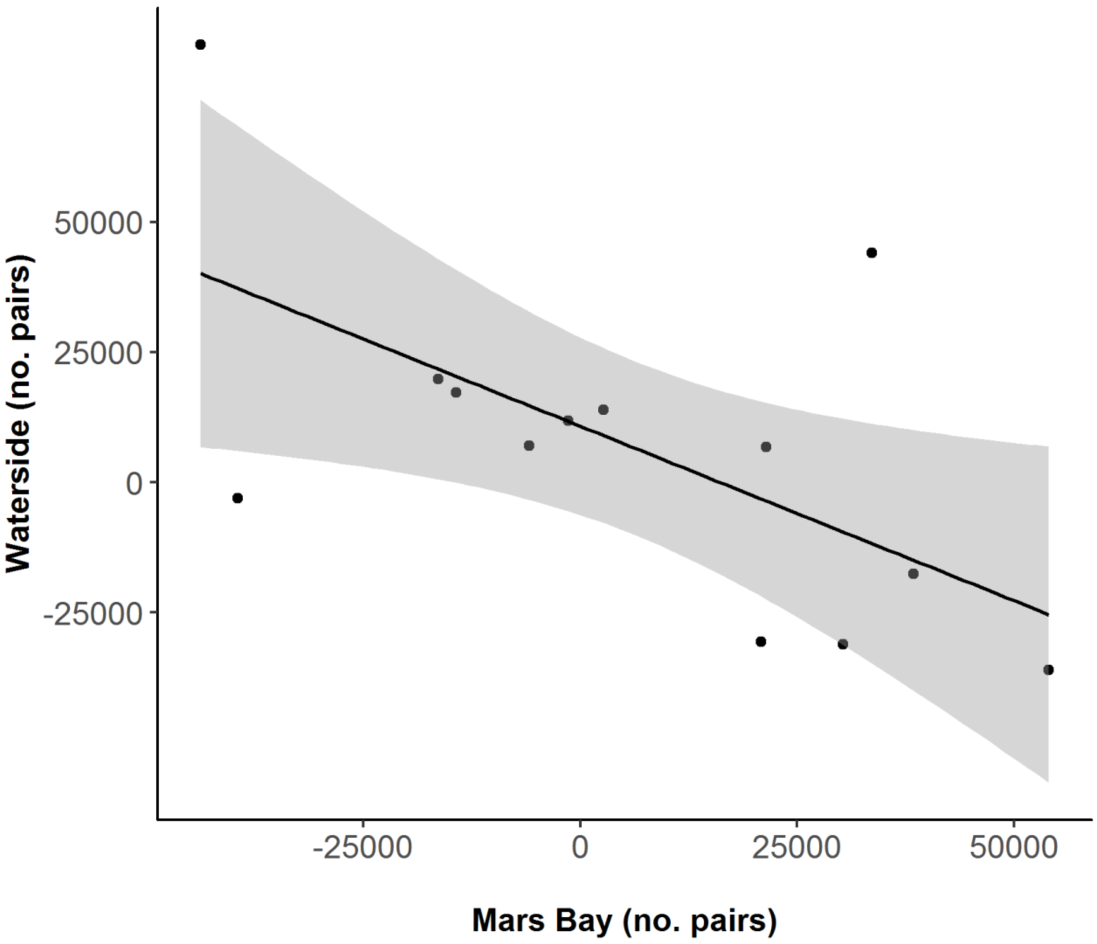


Figure 2.5 The relationship between the change in population size from the previous breeding season at Mars Bay and that at Waterside in breeding seasons between 1997 and 2015. Black dots represent the individual season changes and shaded grey areas are 95% confident intervals around the solid line that represents the least squares regression line.

2.4.2 Time of year effects on population size and adult condition

Population size differed in accordance with time of year across the breeding seasons between 1997 and 2015. The current time of year had a significant effect on the change in population size from the previous breeding season ($\beta = 1.86$, SE = 0.89, $P = 0.04$; Fig. 2.6a), but there was no time of year effect from the previous season on population change ($\beta = 0.38$, SE = 0.88, $P = 0.67$). More birds chose to breed during the warmer months (i.e. 1st April to 31st August), while fewer were present in cooler months (i.e. 1st September to 31st March), resulting in a decline in population size from the previous breeding season. Egg size also varied according to time of year, with females producing significantly larger eggs in warmer (34.78 ± 2.77 cm^3, n = 705) than in cooler months (34.04 ± 2.66 cm^3, n = 1119), t (1447.1) = - 5.70, $P < 0.001$ (Fig. 2.6b).

2.4.3 Breeding synchrony and success

Returning breeders systematically chose to nest at Waterside first, with birds breeding significantly earlier than those at Mars Bay. The mean number of days between first chick hatch and 1st January was 173 ± 51 at Waterside and 187 ± 50 at Mars Bay ($F_{1,17} = 39.46$, $P < 0.001$). The average difference between first hatch dates of the two breeding sites was 13.4 ± 4.5 days between 1997 and 2015, but this difference varied markedly between breeding seasons (minimum of 2 days and maximum of 35 days; Fig. 2.7). There were also differences in the breeding densities of birds between sites, with consistently and significantly higher densities at Waterside (1.87 ± 0.04 nests per m^2, n = 2,849) than at Mars Bay (1.41 ± 0.04 nests per m^2, n = 2,358) across the whole study period ($F_{1,4689.61} = 114.87$, $P < 0.001$).

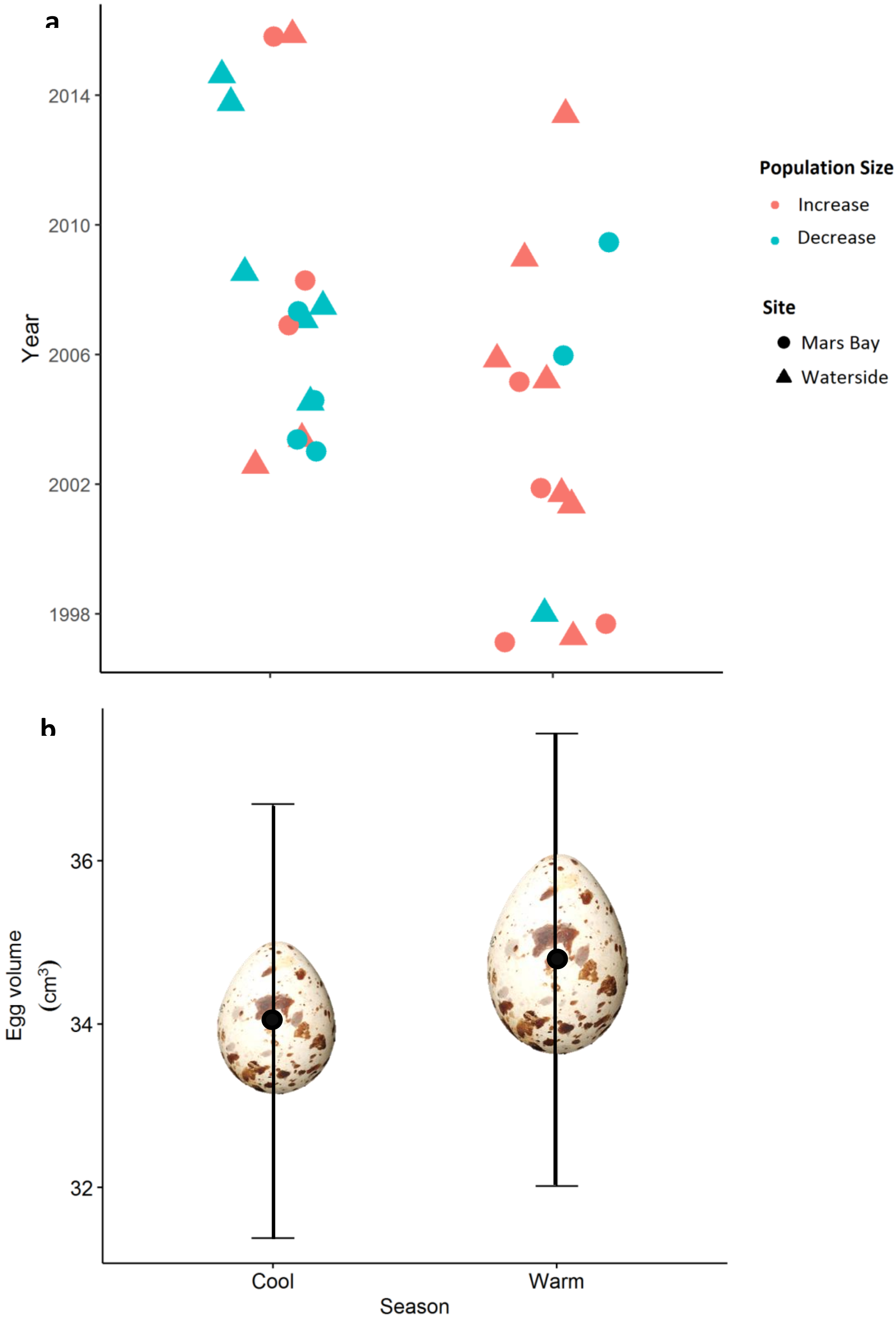


Figure 2.6 Seasonal effects on **a)** population change and **b)** egg size in breeding sooty terns on Ascension Island. Breeding sites are shown by shape. Seasonal effects were defined as warm (1st April to 31st August) and cool (1st September to 31st March) months. Population change is for breeding periods from 1997 to 2015. n = 24 breeding seasons. **b)** Mean ± SD sooty tern egg volume during cool and warm months Larger eggs were recorded in warmer months compared to cooler months (egg pictures are not to scale). (Photos: J.-C. Stahl).

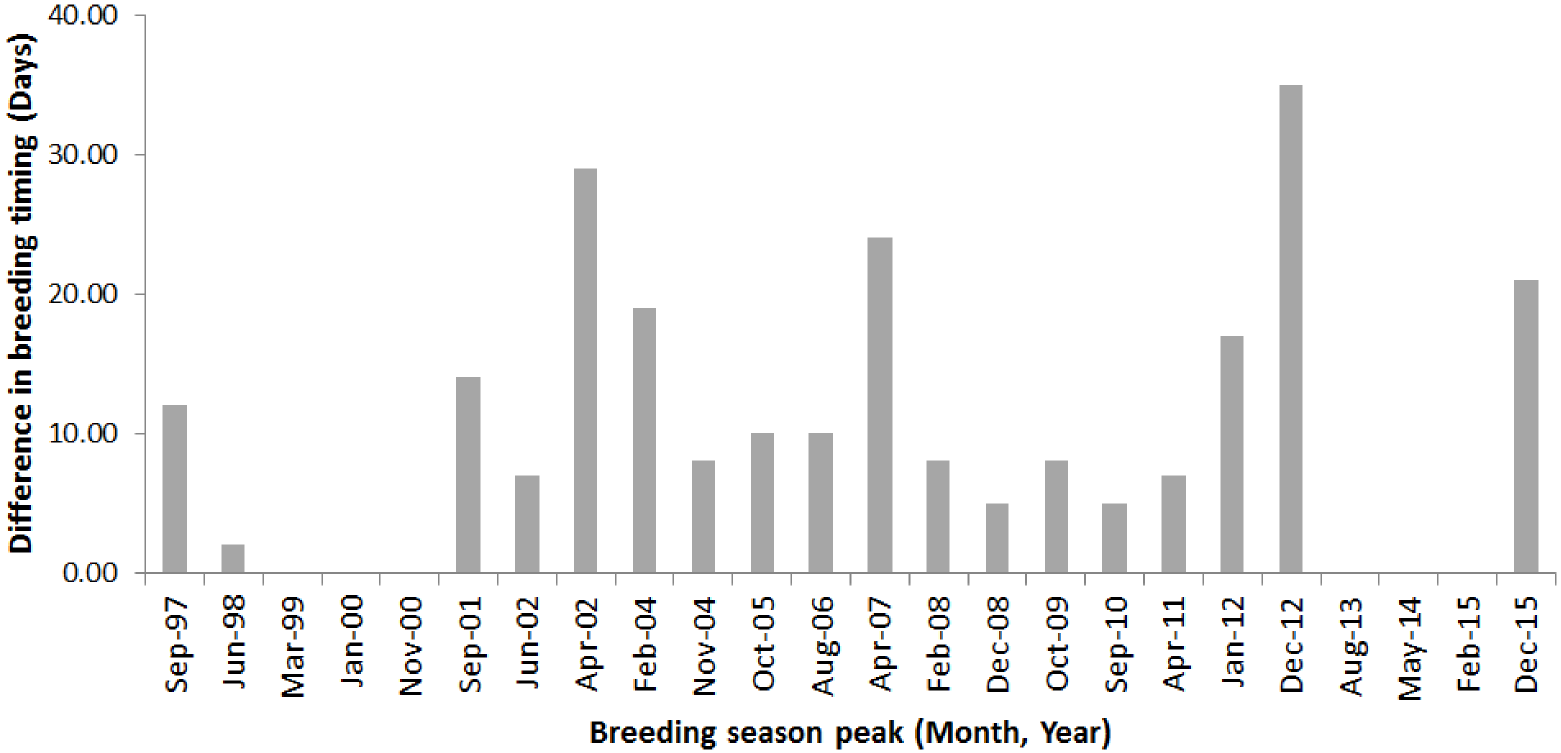


Figure 2.7 Difference in breeding timing of first hatch dates at Mars Bay and Waterside breeding sites between 1990 and 2015 on Ascension Island. Breeding at Waterside always commenced earlier than at Mars Bay. Missing data are breeding seasons during which first hatch dates were not recorded for either or both breeding sites.

At the island-wide population scale, more successful breeding seasons resulted in longer delays until the return of birds the following breeding season ($F_{1,17}$ = 12.07, R^2 = 0.41, P = 0.003; Fig. 2.8).

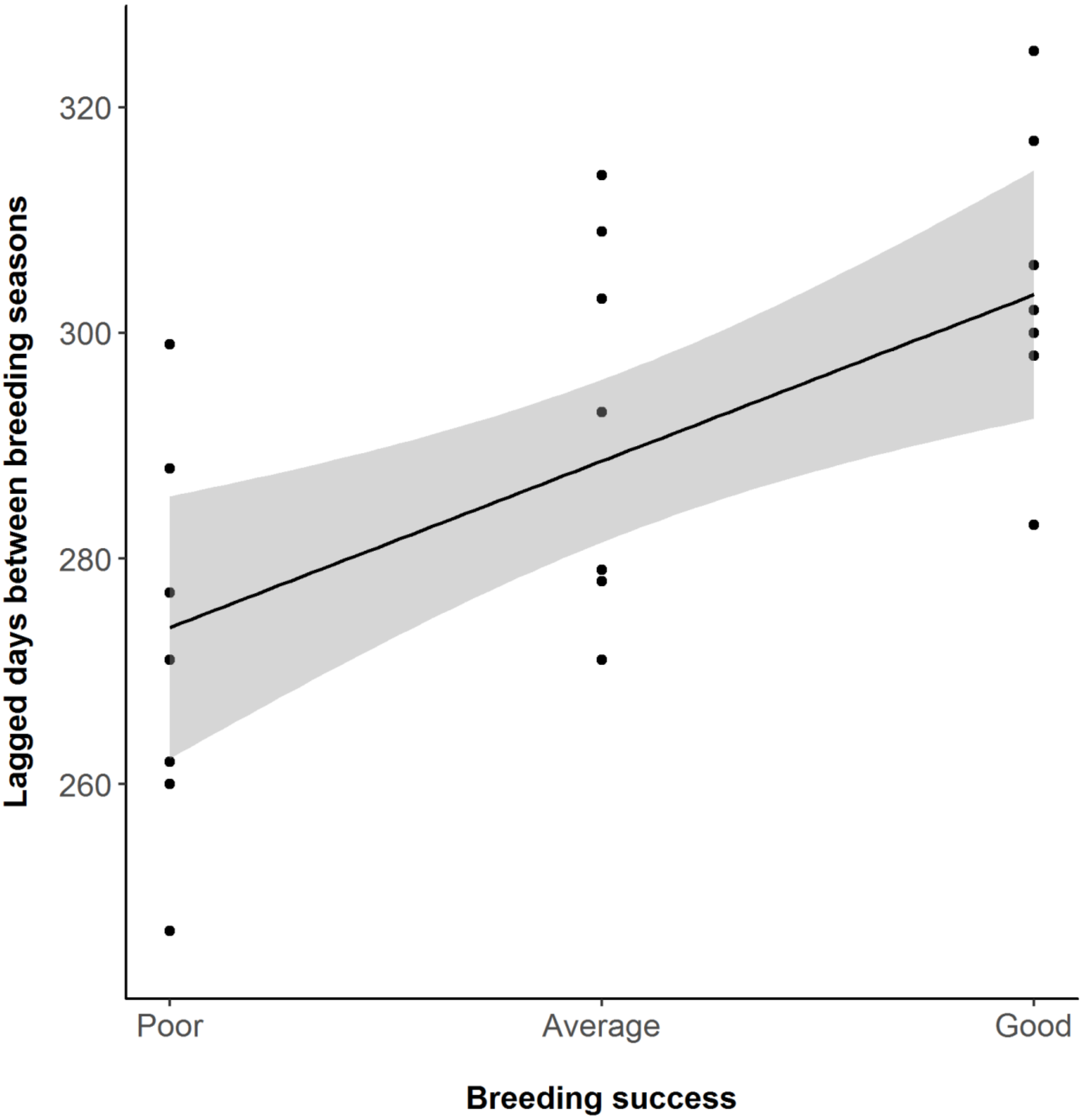


Figure 2.8 The relationship between breeding success and the lagged days between 20 successive breeding seasons (first dates at the earliest breeding site) of sooty terns nesting on Ascension Island in the South Atlantic between 1997 and 2015 (inclusive). Black points are data from individual breeding seasons and shaded grey areas are 95% CIs around the solid line that represents the least squares regression line. Breeding success estimates were defined as: 'Good' < 40% desertion of breeding areas by breeding adults shortly after peak breeding; 'Average' ~ 40% desertion of breeding areas after peak breeding; and 'Poor' > 40% desertion of breeding areas after peak breeding.

2.4.4 Nest and breeding site movement

Some individual adult birds moved considerable distances between breeding seasons, with the overall mean distance being 920.32 ± 49.76 m (± 95% CIs) (n = 2,290 nests) (Figure 2.9a,b). Mean within breeding site distance moved was also high: 352.97 ± 9.48 m (n = 1,868 nests). There was site level variation in the distances travelled between breeding seasons with birds nesting at Mars Bay moving significantly greater distances (376.79 ± 11.84 m, n=1,364 nests) than those at Waterside (288.51 ± 12.81 m, n= 504 nests; $F_{1,168.03} = 45.89$, $P < 0.0001$).

GOF tests revealed some deviations from the JMV model assumptions. In-line with previous knowledge of the tendency for long-lived species display high levels of breeding site philopatry, test WBWA (see Pradel *et al.* 2005 for explanations of each test) was significant (Table 2.3), indicating memory within our dataset (see Pradel *et al.* 2005). We therefore accounted for this by the use of memory models (Rouan *et al.* 2009). There was no evidence of transience in the data (3GSR and 3GSM, Table 2.3) (i.e. no effect of marking individuals on the probability that they will return to the population or of individuals that are passing through the study area. However, there was evidence for the influence of trap-dependence with significant results for M.ITEC and M.LTEC (Table 2.3). This could be due to the biennial breeding strategy of sooty terns on Ascension Island, where successful breeding may result in skipped breeding the following season following a 9.6 month breeding cycle (Fay *et al.* 2015). To some extent this would be considered through the use of the unobservable state, but we accounted for this by using a variance inflation factor for model selection by summing the components of the M.ITEC and M.LTEC giving a ĉ value of 1.4.

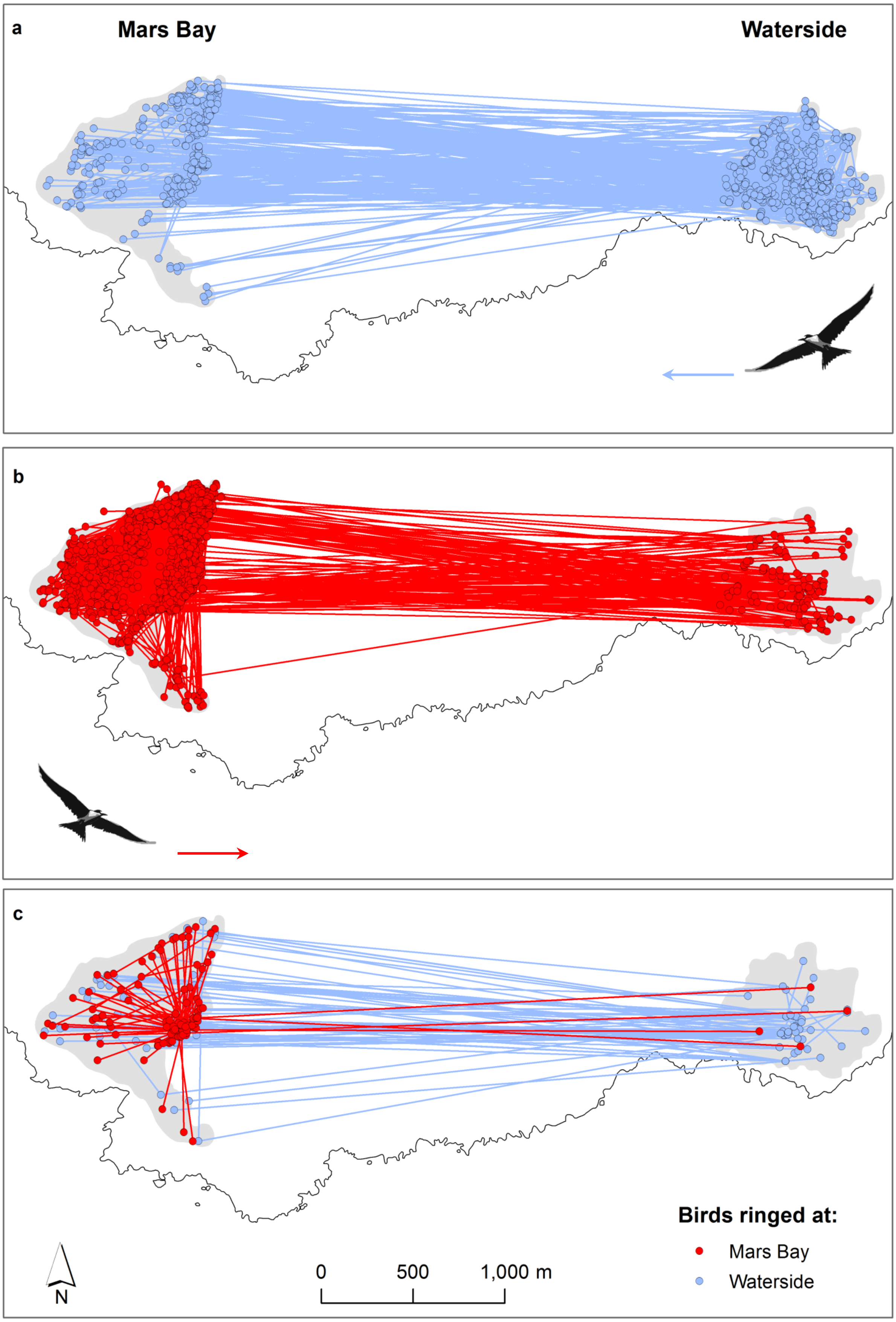

a
Mars Bay
Waterside
b
c
Birds ringed at:
● Mars Bay
● Waterside
0
500
1,000 m
N

Figure 2.9 The movement of sooty terns between successive breeding seasons on Ascension Island between 2002 and 2016. Points represent individual capture events and lines show movements between subsequent captures between 2003 and 2016. **a)** Breeding adults initially ringed at Mars Bay (n = 2,679), **b)** breeding adults initially ringed at Waterside (n = 1,511), and **c)** chicks initially ringed at Mars Bay (n = 89) and Waterside (n = 75) returning as first time breeders. Note that only individuals that had > 1 GPS location are shown. Grey areas show the extent of cumulative breeding areas at the two breeding sites between 1997 and 2016.

Table 2.3 Results from the goodness-of-fit (GOF) tests performed on the breeding adult sooty tern mark-recapture dataset with known states in U-CARE. Bold type indicates tests that displayed significant deviation from the assumptions of the Jolly Move (JMV) model.

Test	X^2	df	*P*
WBWA	**58.71**	**20**	**< 0.001**
3G.SR	40.93	32	0.134
3G.SM	172.00	173	0.507
M.ITEC	**90.82**	**42**	**< 0.001**
M.LTEC	**275.46**	**220**	**0.007**

The most parsimonious model selected (P model 5 in Table 2.4) was one which had transitions varying by site. Adding search effort to the models increased model fit but time varying models which predicted movement across breeding seasons were not fully parameterised, or had partial parameter redundancy (AS model 3 and P model 6 in Table 2.4). In general, the Pradel memory models outperformed the Arnason-Schwartz models (Table 2.4). The average recapture probability of the best fitting model over the entire study period was 0.04 ± 0.001. Birds showed high levels of breeding site memory, with the two states with complete site faithfulness having the highest transition probabilities (111 and 222 in Figure 2.10). The probability of moving from site 2 (i.e. Waterside) and then remaining in site 1 (i.e. Mars Bay) for the subsequent two breeding seasons was also high (211 in Figure 2.10). Breeders that had bred consistently at a site for two occasions were least likely to transition to the other site (112 or 221 in Figure 2.10).

Table 2.4 Modelling of breeding movement probabilities of adult sooty terns between breeding sites on Ascension Island between 2000 and 2015. n = 20 breeding seasons based on a 9.6-month breeding cycle.

Model	**Model structure**				**Deviance**	**AIC$_C$**	**ΔAIC$_C$**
	π	**Φ**	***p***	**k**			
AS Model 3[a]	*C*	site**t*	site**t**effort	75	30214.59	21761.18	0
P Model 6[a]	*C*	site**t*	site**t**effort	143	30325.14	21976.25	215.07
P Model 5	***C***	**site**	**site**t**effort**	**11**	**75601.93**	**54096.76**	**32120.51**
AS Model 2	*C*	site	site**t**effort	7	75774.41	54212.13	115.37
P Model 4	*C*	site	*C*	10	76429.64	54686.79	474.66
AS Model 1	*C*	site	*C*	6	76653.35	54838.80	152.01

The selected model is displayed in bold. [a]Models that contained boundary parameters or were not fully parameterised and were therefore excluded from model selection. π is the initial state, Φ is transition dependent on survival, *p* is recapture probability, and k is the model rank. *C* is constant, site is breeding site, *t* is time, and effort is re-trapping effort (man hours by site and time) that used an external covariate. AIC$_C$ is Akaike's information criterion (corrected for small sample size) and ΔAIC$_c$ is the difference between the lowest and highest AIC$_C$ values.

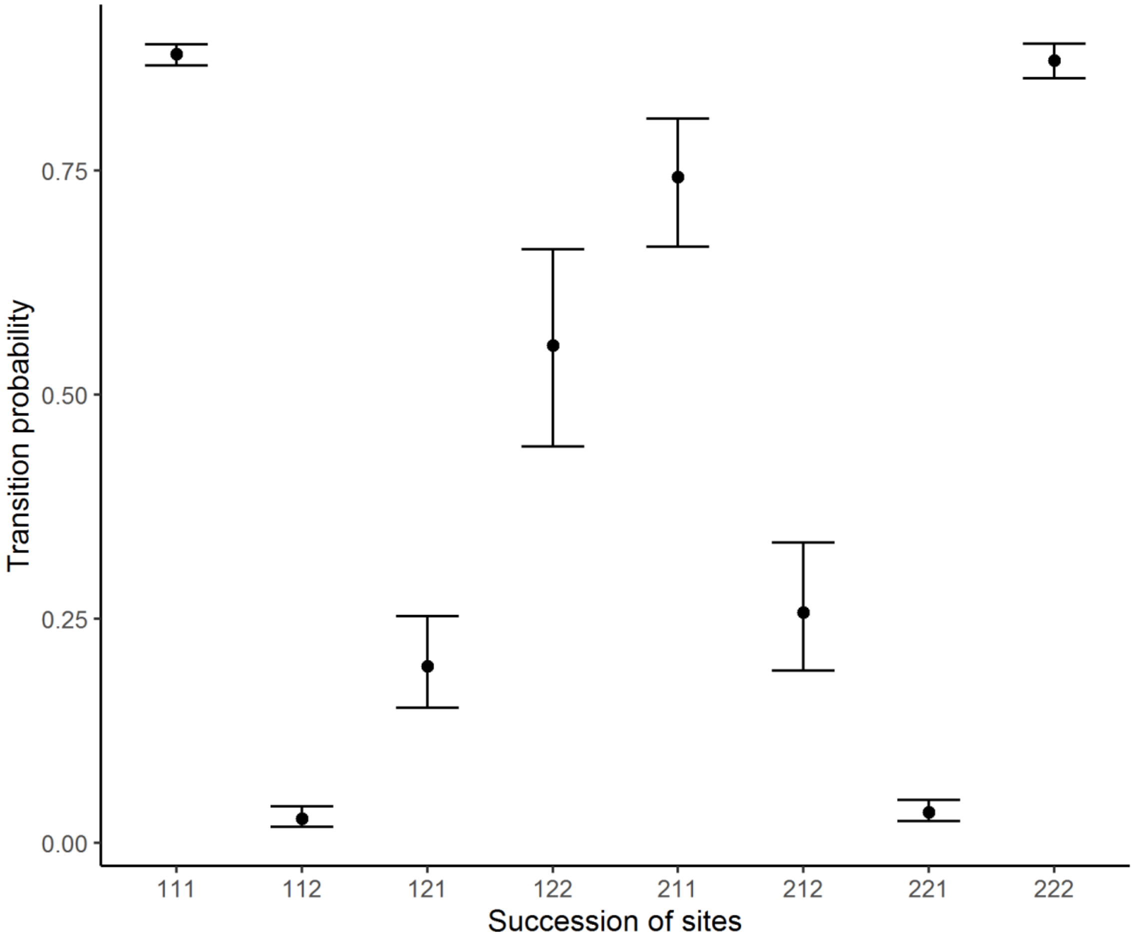


Figure 2.10 The probability of adult sooty terns transitioning between breeding sites on Ascension Island between 2000 and 2015 (n = 20 breeding periods). Site 1 is Mars Bay and site 2 is Waterside. Succession of sites are the eight combinations of breeding at each site at times *t* - 1, *t* and *t* + 1 (see section 2.3.1.4 for further details). Error bars are shown ± 95% CI.

2.4.5 Natal site philopatry

Goodness-of-Fit tests revealed some deviation from the global JMV model assumptions (specific tests could not be performed on the chick dataset given n occasions was < 3 (Choquet *et al.* 2005). Therefore, we accounted for this by using a variance inflation factor for model selection with a ĉ value of 2.849.

Natal site philopatry was high at Mars Bay and recruiting breeders also dispersed to Mars Bay from Waterside (Fig. 2.11). However, at Waterside there was a low probability of breeder recruitment from both natal and dispersing breeders (Fig. 2.11). The overall probability of survival was 0.74 ± 0.023, and the probability of recapture was 0.07 ± 0.004.

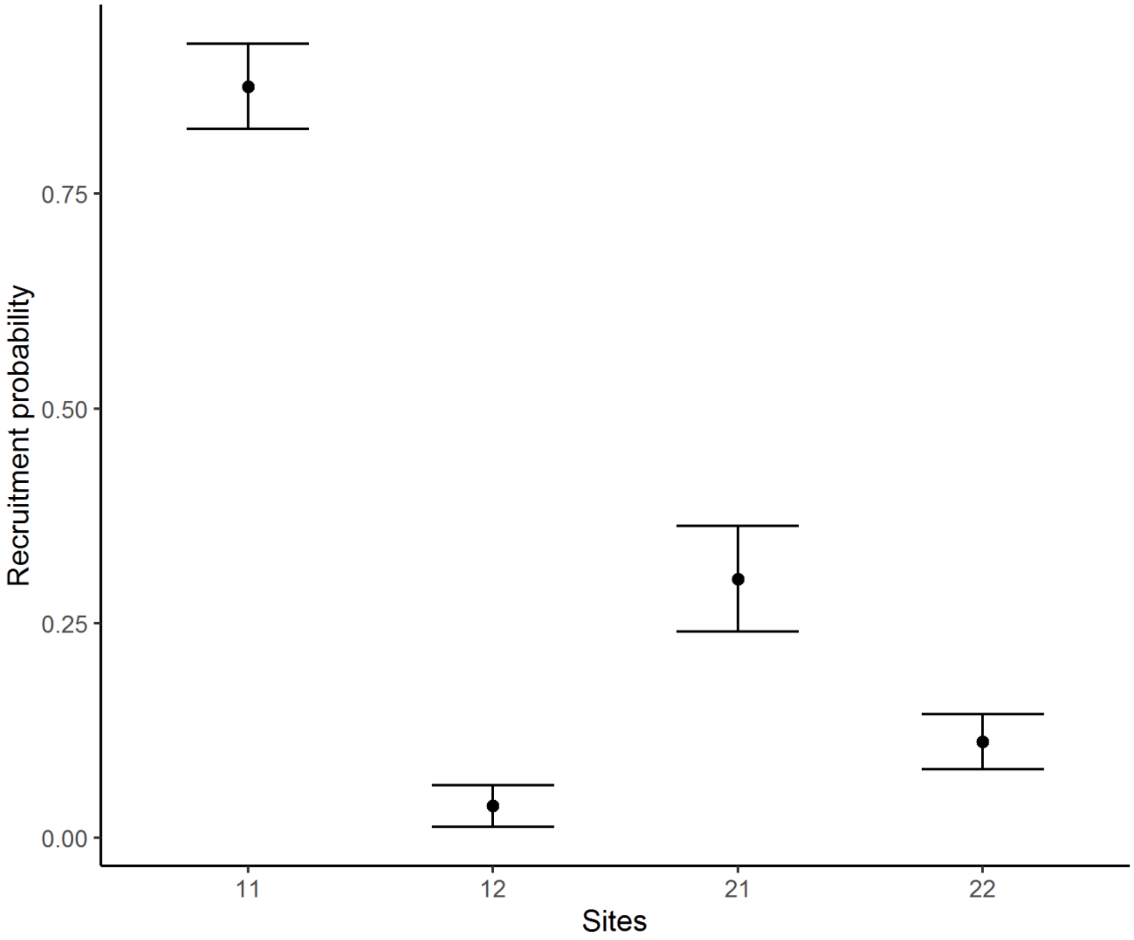


Figure 2.11 The probability of recruitment by first time sooty tern breeders from natal and dispersing breeding sites on Ascension Island. Sites are the initial ringing site of chicks followed by the site of first breeding. For example, site 12 represents a bird ringed as a chick at site 1 and recaptured breeding for the first time at site 2. n = 5,486 birds ringed as chicks.

Survival did not differ between age 1 and other age classes, so was not included in the final models (Table 2.5). The inclusion of search effort for birds as a covariate improved model fit (Table 2.5). Age at recruitment was the second highest ranked model (model 4 in Table 2.5).

Given limited data at higher age classes, we grouped the number of breeding seasons post-fledging from 13 to 16 and set ages > 16 to zero. The addition of site to the model could not be supported given an increase in boundary estimates, most likely due to sparse data (model 5 in Table 2.5). Recruitment age increased until 12 breeding seasons post-fledging (approximately 9.6 years old based on sooty terns breeding on average every 9.6 months on Ascension Island; Fig. 2.12). There was a low probability of breeding before individuals had survived beyond seven breeding seasons since fledging (or approximately 5.6 years old) (Fig. 2.12).

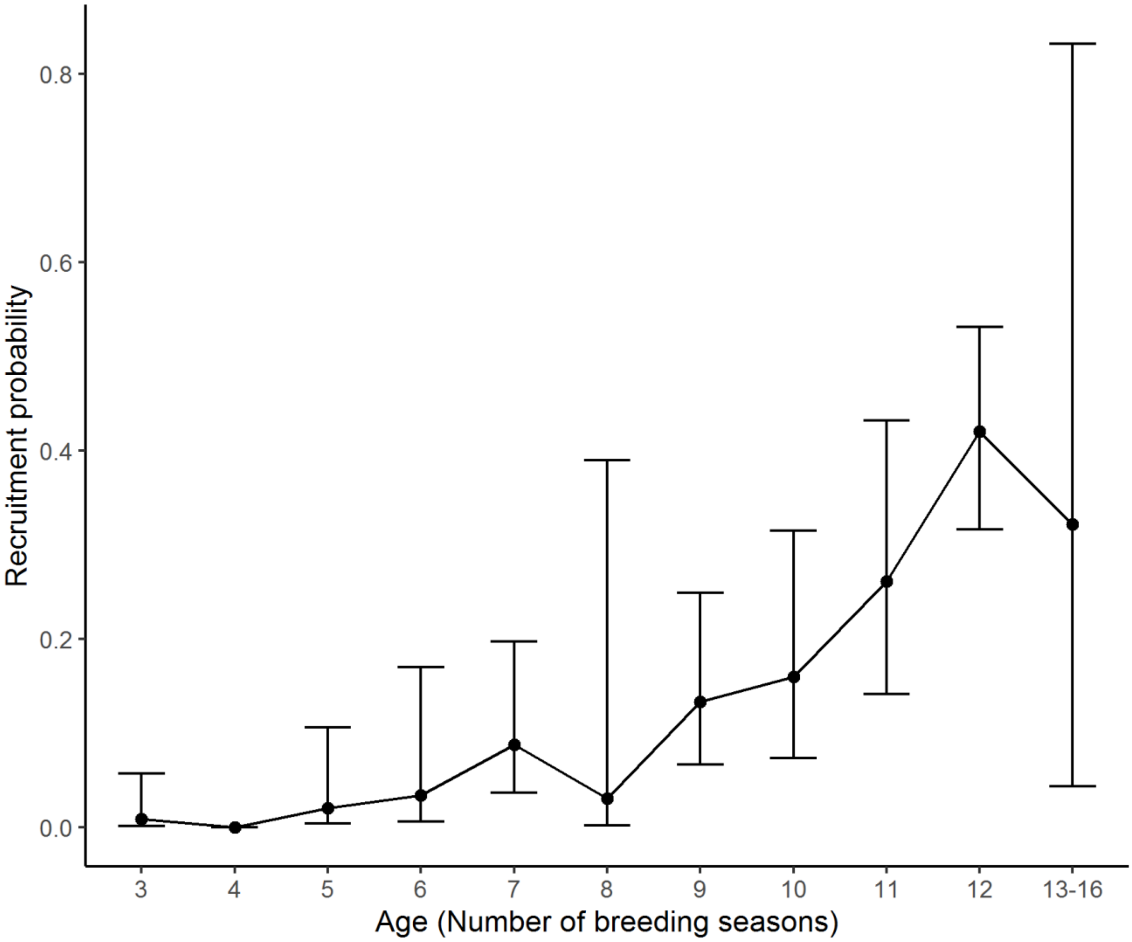


Figure 2.12 The probability of sooty terns recruiting to breed on Ascension Island for the first time as breeders by the number of breeding seasons after being ringed as chicks. Breeding seasons are a proxy for age, although breeding occurs every 9.6 months on Ascension Island. No individuals recruited before three breeding seasons had passed after fledging (approximately 2.4 years). Breeding seasons between 13 and 16 post fledge were grouped together given the limited data for these age ranges.

Table 2.5 Modelling of recruitment probability of sooty terns as first time breeders on Ascension Island between 2000 and 2015. n = 20 breeding seasons based on a 9.6-month breeding cycle. Chicks were ringed between 2000 and 2011 and recaptured until 2015.

Model	**Model structure**					**Deviance**	**AIC$_C$**	**ΔAIC$_C$**
	π	**Φ**	***β***	***p***	**k**			
Model 6	*C*	site	site	site**t**effort	11	11009.97	3886.51	0
Model 4	*C*	site	age	site**t**effort	21	11068.10	3926.90	40.39
Model 5[a]	*C*	site	age*site	site**t**effort	35	11023.05	3939.10	12.20
Model 2	*C*	site	site	*C*	10	11349.01	4003.54	64.44
Model 1	*C*	age	site	*C*	8	11391.16	4014.30	10.76

[a] Models that contained boundary parameters or were not fully parameterised and were therefore excluded from model selection. π is the initial state, Φ is survival, β is recruitment probability, *p* is recapture probability, and k is the model rank. *C* is constant, site is breeding site, *t* is time, and effort is re-trapping effort (man hours by site and time) that used an external covariate. AIC$_C$ is Akaike's information criterion (corrected for small sample size) and ΔAIC$_c$ is the difference between the lowest and highest AIC$_C$ values.

2.5 Discussion

Our results show a temporal shift in intra-population size and spatial structure of the breeding population of sooty terns on Ascension Island. This shift is the result of a compensatory change in breeding occupancy between the two breeding sites on the island between 1997 and 2015. While the population as a whole remained stable over this time period, the Mars Bay breeding site increased in population size by a staggering 337% while the Waterside population declined by 62% (Fig. 2.4). It was evident that this shift in population size was in part a result of movements of breeding birds between sites, together with recruitment favouring the growing population at Mars Bay (Fig. 2.11). There were also seasonal drivers of population size and body condition of breeding individuals, with more birds nesting in warmer months when they produce larger eggs than those nesting in cooler months (Fig. 2.6).

There was evidence for breeding site heterogeneity in the onset of breeding, the degree of breeding synchrony, and breeding density. The Waterside breeding site was always occupied first by returning breeders, and Mars Bay between two and 30 days afterwards. Mars Bay had significantly sparser nesting density, suggesting higher competition for nest sites at Waterside. It is well established in bird species that earlier breeders are usually more successful and in higher body condition (Verhulst & Nilsson 2008). It is possible that the disparity in breeding synchrony between sites could in part be caused by differences in breeding success, with years where site level success was similar resulting in more synchronous breeding. At the population scale there was evidence to suggest that breeding timing was influenced by breeding success in the previous breeding season (Fig. 2.8). Seasons of higher success resulted in longer lag times before the onset of breeding in the following season. It follows that a delay in onset could be caused by the additional investment required to rear young to independence.

In many organisms, including several bird species, studies have indicated that individuals leave a breeding area due to breeding failure (i.e. the ‘win-stay, lose-move’ strategy (Schmidt 2004) of their own breeding attempts or those of their neighbours (Danchin *et al.*

1998; Martinez-Abrain *et al.* 2003). Kokko *et al.* (2004) found movements between nest sites in common guillemots were linked to individual reproductive success but that nest sites were not always abandoned even when breeding attempts failed (i.e. those high quality sites that prevented eggs rolling into the sea). Similarly Switzer (1997) found that the breeding experience of territorial dragonflies *Perithemis tenera* dictated whether they switched breeding sites, with males that were not allowed to breed in field trials switching breeding sites in their subsequent breeding attempts regardless of site quality. Female greater sage-grouse *Centrocercus urophasianus* moved greater distances (5.2 km compared to 1.6 km) between breeding sites following breeding failures (Schroeder & Robb 2003). In an experimental manipulation, Tengmalm's owls *Aegolius funereus* moved nest holes following exposure to a caged predator (Hakkarainen *et al.* 2001). This behavioural response is expected when habitat quality is consistent from one breeding attempt to another, in that a failure in one breeding attempt would result in a failure in the following. The consistent increase in movement away from the Waterside breeding site, together with the declining population size suggests consistent breeding failures due to persistent factor/s that are responsible for such failures. The fact that birds continue to nest there and arrive there first suggests that they may be of higher body condition than later arriving individuals nesting at Mars Bay (Verhulst & Nilsson 2008). Fidelity to Waterside might be explained by the information barrier hypothesis (Forbes & Kaiser 1994). In long-lived seabird species individuals nest at less favourable breeding sites because the risk of moving sites is high (Forbes & Kaiser 1994). Given that high site fidelity is common amongst experienced breeders, for example in Cory's shearwaters (Mougin *et al.* 1999), these individuals could be arriving first and habitually nesting at Waterside, even though the other breeding site is empty and available. Prospecting behaviour, during which individuals use information from previous breeding seasons at other sites, has been shown to be less important for more experienced breeders, who tend to reply rely on individual experience (Switzer 1993). The strong effects of memory in our mark-recapture models suggest that there are non-physical costs of dispersing between breeding sites. Such costs could be associated with breeding in unfamiliar areas which would reduce local knowledge regarding predation and foraging benefits (Péron *et al.* 2010). Memory may also involve familiarity with conspecifics, reducing conflict through established hierarchies (Eason & Hannon 1994; Pshenichnikova *et al.* 2015). Site-based fidelity may also lead to kin clustering (Sonsthagen *et al.* 2010), giving rise to additional benefits such as social foraging (Brown & Brown 1996) and joint predator defence (Griesser & Ekman 2005).

Large areas of previously occupied habitat on the island are no longer in use (Fig. 2.4) since the population crash post-1960. The reasons for the present two breeding sites remaining occupied are unclear. Breeding site fidelity could have played a role in the occupancy of the two remaining breeding sites between the 1990s and the present day, given that fidelity was high at both sites, with breeding site memory a main factor in predicting the probability of future breeding site choice (Fig. 2.10). Some areas of the previous extent of breeding grounds for sooty terns on Ascension Island ceased to be occupied after eggs were consistently destroyed in successive breeding seasons to make way for the airport's runway in 1942 (Hughes 2014). Grosbois and Tavecchia (2003) showed that fidelity in black-headed gulls was higher in colonies that had not previously experienced environmental perturbation (e.g. drought), even when there were favourable subsequent settlement conditions. The high site faithfulness could be due to a combination of factors including a response to past experience, or the conspecific attraction phenomenon (Forbes & Kaiser 1994), where individuals are attracted to sites with a higher number of settlers. Grosbois and Tavecchia (2003) surmised that the observed greater fidelity at one of their three focal black-headed gull breeding sites was down to its elevated comparative breeding success and occupancy by nesting individuals. Gourlay-Larour *et al.* (2014) found breeding site fidelity was sex-biased in partially migratory common pochards *Aythya ferina*. Higher female site faithfulness was presumed to be a response to the increased investment in breeding output by females, with the quality of the breeding site positively influencing their breeding success.

Bird movements can indicate a response to changes in habitat quality, social and genetic structuring within the population may still prevail. For example, Francesiaz *et al.* (2017) found slender-billed gulls nested with familiar individuals despite moving breeding grounds. Sonsthagen *et al.* (2010) also found that group genetic structure was independent of breeding site fidelity in Pacific common eiders because of annual redistribution of breeding substrate.

The main causes of breeding failures on Ascension Island are thought to be predation, namely by introduced black rats and common mynas and endemic Ascension frigatebirds *Fregata aquila* (Hughes *et al.* 2012). Starvation of chicks has also been noted, although appears to vary seasonally (Ratcliffe *et al.* 1999; Hughes *et al.* 2008). The eradication of cats resulted in not only an increase in rat numbers (Hughes *et al.* 2019) but also in their longevity and thus increased reproductive activity since rats can survive for two sooty tern breeding seasons (Hughes *et al.* 2008). Although the two breeding sites are only 3 km apart, it is possible that one site is subject to higher predation than the other. Given the arid conditions of the two sooty tern breeding sites on Ascension Island (Hughes *et al.* 2008), there is little to sustain rat populations during non-breeding periods. Therefore, it is likely that they migrate to other areas of the island. For example Hughes (2014) found high numbers of rats on the lower slopes of Green Mountain where they feed on fruits and seed masts (S.B Weber pers. comm.). The Waterside breeding site is geographically closer to Green Mountain than Mars Bay (Fig. 2.1), and thus it is possible that rats inhabiting the mountain also exploit the sooty tern colonies for food during their breeding seasons, arriving at Waterside first. Rats are found throughout the island, although they are controlled more rigorously in areas of human habitation (Fig. 2.1) and are generally found in lower numbers at lower altitude (Hughes 2014). Given the conservation concern for the species (Hughes *et al.* 2017b), further work that builds on Hughes *et al.* (2019) is required to understand the interactions and extent of predation acting on the population. It is essential that each breeding site be considered separately given the differences in breeding timing and likely predation levels, especially where conservation interventions are proposed such as control or eradication of invasive species such as rats and common mynas that are major predators of seabird eggs on the island (Hughes *et al.* 2017a).

Both breeding timing and success in seabirds have been shown to vary with environmental conditions which have been primarily linked to indirect effects on prey availability (Spear *et al.* 2001; Frederiksen *et al.* 2008). The fact that less sooty terns tended to breed in cooler months with additional negative body condition consequences, suggests a paucity of food availability during these times. Previous reports of breeding failures due to starvation have also occurred in cooler months such as in February 1991 (Hughes *et al.* 2008), September 1997 (Ratcliffe *et al.* 1999), and November 2015 (LJHG pers. obs.), although chick starvation was also noted in June 2002 (Hughes *et al.* 2008). The lack of marked seasonality on the island, low primary productivity and patchy prey distribution in tropical oceans make such patterns of potential food scarcity difficult to predict (Weimerskirch 2007). Sooty terns rely on large predatory fish such as tuna pushing smaller prey to the surface on which they then feed (Schreiber *et al.* 2002), in so called ‘facilitated foraging’ (Maxwell & Morgan 2013). The distribution of such predatory and forage fish is related to SST (Jaquemet *et al.* 2007) as is sooty tern breeding performance that declines with warming oceans (Catry *et al.* 2013). Although Keogan *et al.* (2018) found very little evidence of temporal trends in phenotypic responses to SST by seabirds globally, Colchero (2008) reported that climate warming led to a delay in breeding timing of three months between 1950 and 2010 in sooty terns breeding on the Dry Tortugas, Florida. This change in breeding timing was thought to be due to alterations in prey abundance (Colchero 2008).

Although our multi-event models indicated high levels of breeding site fidelity, it is clear from the distances travelled by birds (i.e. 352.97 ± 9.48 m) within breeding sites and between nesting attempts that sooty terns are not faithful to specific nest locations on Ascension Island. In other seabird species nest site fidelity ranges from a few cm (e.g. common guillemots Kokko *et al.* 2004) to 300 km (e.g. slender-billed gulls Francesiaz *et al.* 2017). Other examples of changes in colony location between breeding seasons have been linked to changes in habitat suitability such as flooding in Caspian terns *Sterna caspia* (Cuthbert 1985). However, on Ascension Island there are few observable changes between breeding seasons in the habitats occupied. Of course, there may be differences in habitat quality perceived by birds which are not evident to the human researcher (Forbes & Kaiser 1994). Danchin *et al.* (1998) found local nest-site quality in black-legged kittiwakes was correlated with the abundance of tick parasites. Spatial variation in occupancy within breeding sites could be influenced by local parasite abundance, given that the re-use of breeding areas in subsequent years promotes parasitic infestation in black-legged kittiwakes (Boulinier & Danchin 1995), with older colonies having higher parasite loads (Danchin 1991).

Natal philopatry was high at the expanding breeding colony (Mars Bay) with the probability of recruitment over 80% (Fig. 2.11) for natal returners, and dispersal from the declining colony (i.e. Waterside to Mars Bay) was also higher than that in the opposite direction. This could be due to breeding timing, given that first time breeders tend to breed later than more experienced breeders (Becker *et al.* 2008; Zhang *et al.* 2015), and that Waterside is always occupied first by returning breeders. For example, Becker (2015) found that common terns *Sterna hirundo* bred 20 days later than more experienced breeders. It is also possible that tightly packed colonies may deter prospecting terns, especially those with a low number of single birds (Burger 1988). There was a significantly reduced breeding density of birds at Mars Bay compared with Waterside. Other research has also shown that recruits tend to favour less crowded areas (e.g. Kokko *et al.* 2004; Gauthier *et al.* 2010). Péron *et al.* (2010) found that breeding black-headed gulls used sub-optimal breeding sites before successfully recruiting into a preferred colony. On the other hand, information gathering prior to commencing to breed may also play a role in settlement decisions of naïve individuals (Switzer 1993). It follows that if Waterside is declining in breeder occupancy due to poor breeding success, for example, first-time breeders may be preferentially choosing the more productive site based on information gathered during prospecting. Indeed, prospecting behaviour in the breeding periods prior to breeding, whereby individuals obtain information such as breeding success to inform future movement decisions based upon site quality, is more frequently seen in first-time breeders than in more experienced breeders (Halley *et al.* 1995; Schjørring *et al.* 1999) .

Understanding life-history traits, such as age at first breeding and breeding probability, is key to explaining population dynamics, and this is particularly important in long-lived species where younger age classes can account for a large proportion of the total population size and have important consequences for reproductive output and demography (Sæther *et al.* 2013). Our multi-event model that included age (i.e. model 4 in Table 2.4) suggested a delayed breeding onset, as expected for a long-lived species (see Lebreton *et al.* 2003;

Becker & Bradley 2007; Aubry *et al.* 2009; Fay *et al.* 2015). Sooty terns breeding for the first time on Ascension Island tended to delay breeding until seven breeding seasons post-fledging (or until at least 5.6 years of age), with the highest probability of breeding at 12 seasons post-fledging (i.e. 9.6 years; Fig. 2.12). This latter finding concurs with findings of Hughes (2014) for the same population who estimated birds to be between 8 and 10 years of age which is slightly older than that found in other sooty tern populations, varying between 5 and 8 years of age (e.g. Seychelles: Feare & Doherty 2004, Johnson Atoll: Harrington 1974). There are costs associated with early breeding because although sooty terns are physiologically capable of breeding after just three breeding seasons since fledging (i.e. after 2.4 years on Ascension), few individuals do so at such an age with only three individuals at this age breeding apparently for the first time (see Fig. 2.12). Other attributes such as behavioural or social capacities may be equally important to render breeding efficient and to outweigh costs such as reduced breeding success or probability in the following year. For example, Pradel *et al.* (2012) found that breeder experience outweighed the age of birds in predicting the probability of breeding in greater flamingoes. It would be interesting to model breeding probability and experience beyond the first breeding attempt in sooty terns, although this would likely require increased mark-recapture efforts to acquire sufficient data for this purpose.

Planning the timing of field surveys, especially to predict population estimates, is crucial for effective population monitoring (Mitchell *et al.* 2004). Previous timing of surveys has been based on peak breeding occurring 40–60 days after first hatch dates where birds first arrive (Hughes *et al.* 2012). This is important, given that the largest numbers of breeding adults are present during this time, thus giving the most accurate population estimates. Our findings have implications for both predicting these timings, given that breeding success influences breeding onset, and that there is also variance in breeding synchrony between breeding sites. Thus, peak breeding at one site may not coincide with that at the other. Recapture effort increased the fit of all of our mark-recapture models, given there was heterogeneity in effort between breeding sites and seasons. This heterogeneity in recapture effort was in part due to the mistiming of field surveys with peak breeding timing and the disparity between breeding sites in the arrival times of birds. Previous monitoring of the sooty tern breeding population on the island was carried out by the Army Ornithological Society (AOS) during fieldwork lasting < one month in duration. Currently, seabird populations on Ascension Island (including Ascension frigatebirds) are monitored by the Ascension Island Government Conservation and Fisheries Department (AIGCFD), who have had a permanent presence on the island since 2002 (Hughes 2014), although ringing and recapture efforts are largely undertaken by the AOS. It is therefore important to gather information on the outcomes and success of breeding attempts at both breeding sites whenever possible, so that research efforts can be more accurately planned and executed. Overall recapture rates of marked individuals ringed as adults and chicks were low, and modelling changes over time (i.e. breeding seasons) using the mark-recapture dataset was limited by sparse data. Cole *et al.* (2014) estimated the number of recaptures per year and per site to apply fully time varying memory models to be between 30 to 250 recaptures for the more complex Pradel model and 20 to 165 recaptures for the AS model. Therefore, it is paramount that both ringing and recapture efforts are continued in order for more detailed analysis to be undertaken.

2.5.1 Conclusions

Long-term studies that include uniquely identifiable individuals are essential to answer questions in ecology and evolution that address life history, social structure, fitness and selection (Clutton-Brock & Sheldon 2010). They allow us to assess species' vulnerability to changes in environmental pressures, such as climate change and introduced predators. We have found evidence for a significant shift in the spatial structure of the breeding population of sooty terns on Ascension Island. The compensatory change in breeding occupancy between the two breeding sites was influenced by the movement and recruitment of individuals. Key differences in the breeding timing, synchrony, density and most likely success are evident between breeding sites, highlighting heterogeneities in the factors acting upon breeders which may be affecting the stability of the island ecosystem.

Chapter 3

A multiplex marker set for microsatellite typing and sexing of sooty terns *Onychoprion fuscatus*

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LJHG collected and analysed the data and wrote the manuscript. SJR and DAD assisted with writing the manuscript. DAD and GJH assisted with analysing the data.

3.1 Abstract

Seabirds have suffered dramatic population declines in recent decades with one such species being the sooty tern. An urgent call to re-assess their conservation status has been made given that some populations, such as the one on Ascension Island, South Atlantic, have declined by over 80% in three generations. Little is known about their population genetics, which would aid conservation management through understanding ecological processes and vulnerability to environmental change. We developed a multiplex microsatellite marker set for sooty terns including sex-typing markers to assist population genetics studies. Fifty microsatellite loci were isolated and tested in 23 individuals from Ascension Island. Thirty-one were polymorphic and displayed between four and 20 alleles. Three loci were Z-linked and two autosomal loci deviated from Hardy-Weinberg equilibrium. The remaining 26 autosomal loci together with three sex-typing makers were optimised in seven polymerase chain reaction (PCR) plexes. These 26 highly polymorphic markers will be useful for understanding genetic structure of the Ascension Island population and the species as a whole. Combining these with recently developed microsatellite markers isolated from Indian Ocean birds will allow for assessment of global population structure and genetic diversity.

3.1 Introduction

Sooty terns are long-lived pelagic seabirds distributed throughout the tropical oceans where their range covers in excess of 20,000 km^2 (BirdLife International 2017). They are obligate colonial breeders nesting in large numbers, with birds breeding on Ascension Island in the South Atlantic Ocean constituting 40% of the Atlantic population. The long-term study of demographics and life history (Ashmole 1963; Hughes *et al.* 2017b), make it an ideal study population in which to investigate genetic structure and diversity. Genetic diversity is fundamental for populations to adapt to environmental change (Frankham 2005). Declining and small populations often suffer from inbreeding depression and reduced genetic diversity making them vulnerable to extinction (Frankham 2005).

The sooty tern population on Ascension Island declined by 84% between 1942 and 2005 (Hughes *et al.* 2017b). A recent study of long-term population trends on Ascension Island prompted an urgent call for reclassification of their IUCN (International Union for Conservation of Nature) status from 'Least Concern' to 'Critically Endangered' (Hughes *et al.* 2017b). This decline mirrors that of seabirds globally with pelagic seabirds being the most threatened (Votier & Sherley 2017). A number of issues are thought to exert pressure on seabird populations including declining fish stocks, climate change, pollution and introduced predators at breeding grounds (Paleczny *et al.* 2015).

Since 2000 the breeding population on Ascension Island has occupied two main areas at Mars Bay and Waterside that are approximately 3 km apart (Fig. 1.1). Fine-scale DNA analyses would enable assessment of within-population genetic structuring and highlight potential barriers to gene flow. Microsatellite markers are an ideal tool with which to study demographic processes such as relatedness, inbreeding, genetic mixing mechanisms and genetic population structure due to features such as high levels of polymorphism and a large number of alleles (Zhan *et al.* 2017). Mutations can lead to non-amplifying null alleles but this can be estimated through null allele frequencies (Webster & Reichart 2005). In comparison with other methods such as single nucleotide polymorphisms (SNPs), which have increased in popularity in recent years, microsatellite markers are more powerful per locus and more cost-effective, requiring lower set-up costs (Zhan *et al.* 2017).

Despite their widespread distribution, such processes have not been investigated in detail in this species. Sixteen microsatellite loci, were recently isolated from the Indian Ocean population (Danckwerts *et al.* 2019) and given genetic differences have been documented between oceanic basins, combining these with markers derived from Atlantic Ocean birds would aid global-scale assessment of population structure. This would assist conservation management through understanding population ecology, evolutionary processes and vulnerability to environmental change.

3.2 Methods and Results

Genomic DNA was extracted from blood samples using an ammonium acetate precipitation method (Nicholls *et al.* 2000; Richardson *et al.* 2001). Microsatellite sequences were isolated from a single adult sooty tern (BTO ring number DE97026) from a blood sample collected on Ascension Island in May 2014 at Mars Bay (Fig. 1.1). Sooty terns are sexually monomorphic (Schreiber *et al.* 2002), but genetic sex-typing of this individual using three sex-typing markers revealed it was a male (sex markers: Z002A, Z002D, Dawson 2007 and Z43B, Dawson *et al.* 2016). DNA concentration was quantified using a fluorimeter (FluostarOptima, BMG LABTECH Ltd., Aylesbury, UK) and its quality assessed by electrophoresis. The library was created by digesting the DNA with the restriction enzyme MboI and enriching the MboI fragments for the dinucleotide microsatellite motifs (CA)n, (GA)n, (TC)n,(TG)n using magnetic beads in the hybridisation (Armour *et al.* 1994; Glenn & Schable 2005). An Illumina paired-end library was created using 1 µg of the repeat-enriched genomic DNA. The NEBNext Ultra DNA Library Prep Kit for Illumina (New England Biolabs Ltd. Hitchin, UK) protocol was followed and sequencing conducted using a MiSeq Benchtop Sequencer (Illumina Inc., San Diego, CA, USA). Sequencing was undertaken as two × 250 bp paired-end reads generating 1,292,242 sequences. These were trimmed for quality and Illumina adapters removed using Trimmomatic (Bolger *et al.* 2014) and paired reads aligned using FLASH [16]. SAULA/B-linker sequences (Armour *et al.* 1994) were removed and consensus sequences created with QDD (Meglecz *et al.* 2014). Finally suitable microsatellites were identified using MISA (Thiel *et al.*

2003). A total of 423 unique sequences were selected for potential primer design, based on a minimum of five tandem repeats and a flank of 20 bp on either side of the repeat region. These displayed five to 29 uninterrupted pure repeats (di, tri, tetra, pent and hex nucleotides) or possessed compound repeat regions (37 sequences). The lengths of the sequences obtained ranged from 196 to 457 bp in length. From the 423 sequences, those with at least eight tandem repeats were selected for primer design; primer sets were designed using PRIMER3 v 0.4.0 (Koressaar & Remm 2007; Untergasser *et al.* 2012). Specifications for primer selection were set at a length of 16 to 36 base pairs (optimum 20 bp), an optimal primer melting temperature of 59–61^{o}C (optimum 60°C), a maximum poly-X of three tandemly repeating nucleotides e.g. AAA, presence of a G/C clamp and the default settings for all other parameters. Fifty primer sets were designed. The 5' end of the forward primers was fluorescently labelled initially with HEX or 6-FAM. Uniqueness of each set of sequence primers was verified using BLAST software (Altschul *et al.* 1997).

Genotyping was carried out using DNA extracted from blood samples from 23 breeding birds from Mars Bay and Waterside (12 and 11 individuals, respectively) on Ascension Island (Fig. 1.1) during the December 2015 breeding period. Initially, each locus was amplified separately (singleplexed) in all individuals. All loci were PCR amplified using fluorescently labelled forward primers using either 6-FAM or HEX initially (A 1). QIAGEN's Multiplex PCR kit (QIAGEN, Manchester, UK) was used to perform PCRs following the manufacturer's protocol, but using a 2 µl reaction volume added to 1 µl of air-dried DNA (following Kenta *et al.* 2008). The same PCR profile was used to amplify each locus as follows: 95°C for 15 min, followed by 44 cycles of 94°C for 30 s, 56°C for 90 s, 72°C for 90 s and a final step of 72°C for 30 min. Three sex-typing markers (Z002A, Z002D (Dawson 2007) and Z43B (Dawson *et al.* 2016), were included to assign sex as little sexual dimorphism exists in sooty tern plumage (Schreiber *et al.* 2002; Reynolds *et al.* 2008). For genotyping, 1 µL of PCR product was diluted to a ratio of 1:80 H_2O and 1 µL of this solution was added to 9 µL formamide and 0.2 µL of 500-ROX size standard (Applied Biosystems, Warrington, UK). An ABI 3730 DNA Analyser was used to separate PCR products and alleles were scored using GENEMAPPER v 3.7 (Applied Biosystems, Foster City, CA, USA). Of the 50 primer sets tested, 14 either did not amplify or produced a non-specific product, five loci were monomorphic and three were Z-linked (the

13 males were heterozygous or homozygous but all 10 females were homozygotes with sexes identified using genetic sex-typing markers; see Appendix 3). Multiplexing was undertaken using the same QIAGEN Multiplex PCR Kit and profile as previously outlined (see Table 3.1).

To ensure allele frequencies were not biased by over-representation of genotypes through inclusion of related individuals (Anderson *et al.* 2010), pairwise relatedness was estimated using ML-Relate (Kalinowski *et al.* 2006), and confirmed individuals were unrelated with $r < 0.16$ (Mean ± SD = 0.01 ± 0.03). Observed and expected heterozygosities and predicted null allele frequencies were calculated in CERVUS v3.0.7 (Kalinowski *et al.* 2007). Departures from Hardy-Weinberg equilibrium and linkage disequilibrium were estimated using GENEPOP v 4.2 (Rousset 2008). To correct for multiple tests a false discovery rate control (Verhoeven *et al.* 2005) was applied to linkage disequilibrium *p*-values. The probability of identity, which estimates the likelihood that two unrelated individuals selected at random from the same population will have the same genotypes, was calculated using GENALEX v 6.5 (Peakall & Smouse 2006; Peakall & Smouse 2012). Two autosomal loci (Ofu28 and Ofu42) deviated from Hardy-Weinberg equilibrium (Appendix 3). They also showed high predicted null allele frequencies (> 10%) and, as a consequence, were not included in the final multiplex. All three Z-linked loci (Ofu27, Ofu37 and Ofu43) were polymorphic (Appendix 3) and did not deviate from Hardy-Weinberg equilibrium when assessed only in males. Although not included in the final multiplex, the three z-linked loci may be of utility for other studies. There was no evidence of significant linkage disequilibria between pairwise combinations of loci ($p > 0.05$). The 26 autosomal microsatellite loci, together with the three sex-typing markers, were combined into seven plexes by inclusion of the fluorescent dye NED (giving three dyes in total), to create a multiplex marker set using Multiplex Manager 1.2 (Holleley & Geerts 2009) and validated (Table 3.1). The number of alleles per locus of the multiplexed autosomal loci ranged from four to 20 (Table 3.1), with an average of 10 ± 5.6 (SD) loci. Mean (± SD) observed (H_O) and expected heterozygosities (H_E) were 0.82 ± 0.12 and 0.82 ± 0.09, respectively. The probability of identity for the 26 loci was 4.1×10^{-33}.

Table 3.1 Multiplex sets for sooty tern microsatellite genotyping including three sex-typing markers.

Locus	Clone name, NCBI accession number/ Reference	Repeat motif		Primer sequence (5'–3')	Multiplex / Fluoro-Label (F)	*n*	A	Observed (Expected) allele size range (bp)	H_O	H_E	P_{HWE}	Est null allele Freq.
Ofu1	Trn17616	CA$_{(17)}$	F	TGTTTAAGCAGTAAAGACAAAGCCTAC	7/NED	22	12	202-227	0.96	0.89	0.76	-0.05
	LT903723		R	GGTGCGTTTAGAGTGCTTCTTTAG				(211)				
Ofu2	Trn23851	AC$_{(15)}$	F	GGCTGTAGCGAGCAGTTAGG	2/HEX	22	8	189-359	0.78	0.80	0.74	0.02
	LT903724		R	GAAGCTTGGGTGCAGGTG				(209)				
Ofu3	Trn25452	CA$_{(16)}$	F	GGCTGTAGCGAGCAGTTAGG	5/6-FAM	23	10	144-166	0.78	0.80	0.43	0.01
	LT903725		R	GAAGCTTGGGTGCAGGTG				(170)				
Ofu4	Trn4256	AC$_{(18)}$	F	CCTGTTGCCAAGAAATAAATCTTAC	5/HEX	22	13	141-175	1.00	0.89	0.29	-0.07
	LT903726		R	TGAAGAAGCGTGGCTGTG				(150)				
Ofu5	Trn171	TG$_{(21)}$	F	TCCCTACTTGACTTTGGAAACATC	4/6-FAM	20	12	86-131	0.95	0.91	0.81	-0.04
	LT903727		R	TGTACAACACTGTTCCATCATGC				(103)				
Ofu6	Trn352	CA$_{(16)}$	F	GCGTTCGGCATCAAGTTAG	7/HEX	22	9	265-281	0.86	0.83	0.90	0.05
	LT903728		R	ATCCCTGCAAAGCACACAG				(282)				
Ofu7	Trn436	TG$_{(19)}$	F	TTGCTACAAACCTTGGTTATTGAC	4/NED	22	10	154-184	0.77	0.85	0.23	0.04
	LT903729		R	GCAACCTTAGCATTACCTAGCTG				(165)				
Ofu8	Trn640	GA$_{(15)}$	F	GGGTTACTGCTGGTCAGAGC	1/6-FAM	23	14	272-328	0.91	0.85	0.63	-0.06
	LT903730		R	GCTCTAGGCCAATTTCATCATC				(289)				
Ofu9	Trn643	TG$_{(20)}$	F	CTAAGCTGAAATTCCTGAACTGG	6/6-FAM	23	14	174-206	0.96	0.92	0.40	-0.03
	LT903731		R	CAACTACAGACATCCCACAAGC				(185)				
Ofu10	Trn16824	CTT$_{(26)}$	F	GGAAGGAGCATTCAGTCTGC	2/NED	20	17	132-210	1.00	0.95	0.91	-0.04
	LT903732		R	GATGCTCAGATGCTTGCTAGG				(167)				
Ofu11	Trn13992	TATC$_{(15)}$	F	AAAGTCTGTCACACATCCAACG	1/6-FAM	22	8	155-203	0.77	0.72	0.53	-0.05
	LT903733		R	CACGGTGCCAGTTAATAATGC				(203)				

Locus	Clone name, NCBI accession number/ Reference	Repeat motif		Primer sequence (5′–3′)	Multiplex / Fluoro-Label (F)	*n*	A	Observed (Expected) allele size range (bp)	H_O	H_E	P_{HWE}	Est null allele Freq.
Ofu12	Trn129	$CT_{(14)}$	F	TTAAGCAGAAAGCCAGAGTGG	3/6-FAM	22	9	300-330	0.73	0.80	0.14	0.04
	LT903734		R	CTTAGTGTGCTTGGTAAAGACTGAAC				(314)				
Ofu13	Ofu839	$TCCA_{(14)}$	F	GAGGCCACCCTTACACCTC	6/HEX	22	8	142-171	0.86	0.83	0.46	-0.04
	LT903735		R	AAATGAGCTTGGCTTTACGC				(169)				
Ofu14	Ofu897	$CA_{(14)}$	F	GATCTTTCCCAGTAGCACCTATG	4/HEX	19	7	350-365	0.79	0.82	0.63	-0.00
	LT903736		R	CCACCTGGCTGGATAACAG				(349)				
Ofu15	Trn191	$CA_{(14)}$	F	AAAGAGTCTCCACCTGAAGCAG	2/6-FAM	22	10	333-354	0.86	0.86	0.97	-0.02
	LT903737		R	AGCAATATCCCTGGCAGTACC				(340)				
Ofu16	Trn484	$CA_{(13)}$	F	TTTCCTCCTGAGACTTGCGTA	6/6-FAM	22	7	314-327	0.55	0.68	0.20	0.09
	LT903738		R	AAACCAAACTGGCATCAAATAAGT				(324)				
Ofu17	Trn715	$AC_{(12)}$	F	CACCTTATCAAGGGCAATGG	5/NED	23	10	185-207	0.74	0.87	0.11	0.08
	LT903739		R	TTGGATGGATAAAGCAAGCTG				(194)				
Ofu18	Trn269	$TC_{(12)}$	F	ATCCCTGTCACTCCCATGAC	1/HEX	22	5	298-306	0.64	0.76	0.25	0.08
	LT903740		R	TGCACATGGAAAGTTGCTTC				(303)				
Ofu19	Trn15	$AC_{(12)}$	F	TTAGCCCTTTACCCAAATGC	6/6-FAM	23	8	94-116	0.74	0.72	0.95	-0.03
	LT903741		R	ATTACGTCAGCCTCCTCCAG				(115)				
Ofu20	Trn551	$TTGG_{(11)}$	F	CCCAGTGACTCGCTTGCT	3/HEX	22	9	216-262	0.86	0.86	0.35	-0.00
	LT903742		R	CTGCAACAGCCTTTCAGTCA				(221)				
Ofu21	Trn121	$GT_{(11)}$	F	GGCTTAGAAATACTGCCTTTGC	5/6-FAM	22	20	269-321	1.00	0.95	0.36	0.04
	LT903743		R	CTGCTGGTCTGTAAACCATTTATC				(278)				
Ofu22	Trn652	$AC_{(11)}$	F	TTTGCAACAGAAACCTTATCCTG	6/NED	23	6	152-164	0.70	0.70	0.35	-0.00
	LT903744		R	TATATTGCCTCTGGCCGTTG				(162)				
Ofu23	Trn407	$CCAT_{(10)}$	F	CCTGCATATCCCAATATCATCC	1/HEX	20	10	142-183	0.80	0.86	0.53	0.02

Locus	Clone name, NCBI accession number/ Reference	Repeat motif	Primer sequence (5′–3′)		Multiplex / Fluoro-Label (F)	*n*	A	Observed (Expected) allele size range (bp)	H_O	H_E	P_{HWE}	Est null allele Freq.
	LT903745		R	GGGAGGTTCAGGTTGTAATGC				(171)				
Ofu24	Trn442	ATCT$_{(9)}$	F	ATGCATGGAAGCTGCTAACC	3/6-FAM	22	8	148-177	0.91	0.84	0.44	-0.05
	LT903746		R	ATCTGAGGTGGTCATCATTCTTAAC				(169)				
Ofu25	Trn126	TTTGT$_{(8)}$	F	TAGACCAGGCTGCTCAAAGC	5/HEX	22	10	221-226	0.73	0.73	0.42	0.00
	LT903747		R	TCCACCTCACCGTACTGGAT				(239)				
Ofu26	Trn825	AAAC$_{(8)}$	F	CCTGGGAATAAACAGGAAAGC	4/6-FAM	22	4	189-198	0.64	0.59	0.59	-0.05
	LT903748		R	ATCAGCCAAGGTTTGACCAC				(190)				
Z002A	Dawson (2007)	-	-	-	2/6-FAM	13M	1	249 (Z)	0	-	-	-
			-	-		10F	2	249 (Z) and 252 (W)	1.00	-	-	-
Z002D	Dawson (2007)	-	-	-	1/6-FAM	13M	1	127 (Z)	0	-	-	-
			-	-		10F	2	122 (W) and 127 (Z)	1.00	-	-	-
Z43B	Dawson et al. (2016)	-	-	-	7/6-FAM	13M	1	270 (Z)	0	-	-	-
			-	-		10F	2	266 (W) and 270 (Z)	1.00	-	-	-

NCBI is the National Center for Biotechnology Information. Primer sequence F is forward and R is reverse, https://www.ncbi.nlm.nih.gov/bioproject/PRJEB21955. *n* is the number of individuals tested and M is the number of males and F is the number of females identified using the sex-typing markers (Z002A, Z002B Dawson 2007 and Z43B Dawson *et al.* 2016). A is the number of alleles observed. H_O is the observed heterozygosity. H_E is the expected heterozygosity. P_{HWE} is the probability of deviation from Hardy–Weinberg equilibrium. Est null allele. Freq. is the estimated null allele frequency. The same PCR profile was used for all multiplexes as follows: 95°C for 15 min, followed by 44 cycles of 94°C for 30 s, 56°C for 90 s, 72°C for 90 s and a final step of 72°C for 30 min.

3.3 Conclusions

This multiplex set containing a large number of novel microsatellite loci together with the three sex-typing markers will be of great utility for fine- and large-scale population genetic structure analyses. More specifically, this multiplex set offers an effective and economical approach for investigating parentage assignment, relatedness and assisting conservation management plans for this colonial seabird. Combining this multiplex set with 16 microsatellite markers recently developed for sooty terns in the Indian Ocean (Danckwerts *et al.* 2019) would allow for robust global population genetic analysis of this species, given differences in genetic variance have been documented between Atlantic and Indo-Pacific populations (Avise *et al.* 2000). This is poignant given the recent urgent call for the reassessment of conservation status of this species (Hughes *et al.* 2017b). An assessment of population and global scale genetic structure and diversity would highlight vulnerability to environmental change and persistent population declines. Where evidence for genetic mixing occurs, conservation management which focuses on larger populations in isolation may be detrimental to the long-term resilience of the species as a whole.

3.3.1 Limitations

The present study was carried out independently of the study by Danckwerts *et al.* (2019) but ongoing discussions might result in collaborative testing of multiplex sets of primers on each research group’s study populations from the Atlantic and Indian Oceans. We did not have DNA available from allied species of seabirds from Ascension Island and the utility of our multiplex set for species such as brown noddies *Anous stolidus* and black noddies *A. minutus* still needs to be assessed.

Chapter 4

Spatio-temporal processes drive fine-scale genetic structure in an otherwise panmictic seabird population

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LJHG collected and analysed the data and wrote the manuscript. SJR, JPM, JPS, DAD, JKC, RCD and SBW assisted with writing the manuscript. DAD and HH assisted with data analysis.

4.1 Abstract

When and where animals breed can shape the genetic structure of populations, having consequences for the overall genetic diversity of species. The importance of such drivers of genetic diversity is amplified in island populations that have a more localised gene pool compared to continental populations. Studies of the spatial distribution of individuals, as a function of their relatedness, demonstrate the relative benefits to fitness with predictive outcomes that are conditional on the overall genetic diversity of the population. However, few studies have investigated the impact of breeding timing on genetic structure. We characterise the fine-scale population genetic structure of a geographically-isolated population of seabirds. Using microsatellite markers, we show evidence for largely transient effects of both local spatial and within-breeding season temporal processes, affecting genetic structure in an otherwise panmictic population. Localised spatial structure was evident with some individuals being more related to their nearest neighbours than the rest of the population. Earliest breeders had significantly different genetic structure from the latest breeders. Therefore, population genetic structure is shaped by both breeding timing and location. Our findings demonstrate the importance of investigating fine-scale genetic structure, providing new insights into how population genetic diversity is maintained within a locally structured seabird population.

4.2 Introduction

Population genetic structure is driven by a number of factors, including divergent selection, genetic drift and mutation (Garroway *et al.* 2013) with a lack of genetic differentiation or panmixia arising from random gene flow (Reudink *et al.* 2016). Although complete panmixia is rare, genetic differentiation is lowest in species with high dispersal capabilities, such as birds (Reudink *et al.* 2016), flying insects (Ward *et al.* 1992) and fish (White *et al.* 2011). In contrast, philopatric behaviour, and thus reduced dispersal, promotes inbreeding which may result in genetic differentiation between groups (Mayr 1963). For geographically isolated populations, genetic diversity is often lower than in mainland populations (Frankham 1997). For example, mainland populations of Kentish plovers *Charadrius alexandrinus* have high levels of gene flow and genetic panmixia, whereas those breeding on islands have lower genetic diversity and genetic differentiation from the mainland populations increases with increasing distance from the mainland (Küpper *et al.* 2012).

In addition to philopatry, genetic diversity may be affected by other factors such as land barriers and separation during the non-breeding season (Friesen *et al.* 2007a). Natal site fidelity over many generations may lead to kin groups (Ibarguchi *et al.* 2011), with benefits of nesting near genetic relatives including reduced aggression and increased predator vigilance (Griesser 2008). Fine-scale spatial genetic structure or isolation by distance (i.e. where similarities among genotypes decay with increasing distance (Wright 1943) has been recorded in a number of taxa including mammals (Innes *et al.* 2012), birds (Foerster *et al.* 2006), and fish (Planes & Fauvelot 2002).

Isolation over time may also result in heterogeneity in genetic structure (Hendry & Day 2005), whereby temporal barriers impede gene flow (Ribolli *et al.* 2017), giving rise to differentiation within a species occupying the same spatial location. For example, spawning time in rainbow smelt *Osmerus mordax* leads to genetic differentiation between early and late spawners to the same stream in eastern Canada (Coulson *et al.* 2006). Temporal genetic impacts on reproduction have been reported in invertebrates (Cooley *et al.* 2003), fish (Ribolli *et al.* 2017) and birds (Rolshausen *et al.* 2009), including seabirds (Friesen *et al.*

2007b). However, temporal effects on genetic structure are not common in the literature, especially in respect to within-breeding season effects (Braga-Silva & Galetti 2016).

Seabirds are an ideal study system to investigate fine-scale genetic structure given that many species exhibit philopatry (Schreiber & Burger 2001), despite their high dispersal capabilities. In fact, seabirds show highly variable levels of genetic structure at various spatial scales. For example, populations of Peruvian diving petrels *Pelecanoides garnotii* in South America are highly structured despite short distances between breeding sites, resulting in limited gene flow (Cristofari *et al.* 2019). In contrast, no genetic structuring was found in 13 colonies of grey-faced petrels *Pterodroma macroptera gouldi* nesting in New Zealand (Lawrence *et al.* 2014). In their meta-analysis, Friesen *et al.* (2007a) found evidence of genetic structure, at various geographical scales, in 40% of 53 species of seabirds. Previous research on seabirds has considered broad-scale variation in population genetics among geographically-isolated nesting colonies (Lawrence *et al.* 2014; Reudink *et al.* 2016). The usefulness of exploring within-population genetic mixing mechanisms for understanding species global gene flow and population dynamics was highlighted by Cristofari *et al.* (2015), who suggested that basic genetic features and processes may be obscured when analyses focus on larger geographic scales. Although their study did not consider temporal effects, they provided evidence for the importance of fine-scale spatial genetic heterogeneity, driven by variations in habitat quality in a panmictic king penguin *Aptenodytes patagonicus* colony in the Crozet Archipelago.

Sooty terns are one of the most numerous and globally distributed seabirds, occurring throughout the tropical oceans. However, little is known about their population genetic structure (but see Avise *et al.* 2000). Like many pelagic seabird species (Votier & Sherley 2017), sooty terns are in decline and a recent urgent call for the reassessment of their conservation status has been made (Hughes *et al.* 2017b). Factors such as declining fish stocks, climate change, pollution and introduced predators at breeding grounds (Reynolds *et al.* 2019) are thought to have contributed to such declines. We studied the population that breeds on Ascension Island in the South Atlantic which represents 40% of Atlantic sooty terns (Schreiber *et al.* 2002); the Ascension population has declined by 84% between 1942 and 2005 (Hughes *et al.* 2017b). We aimed to address the following research questions and associated hypotheses: 1) What is the current level of genetic diversity and is there evidence for inbreeding depression within the population? We hypothesise that the differences in breeding timing and other characteristics between the two breeding sites on Ascension Island together with the high propensity for site faithfulness in seabirds will lead to landscape scale partitioning between the breeding sites. Given the crash in population size in the 1950s this may also lead to evidence of reduced genetic structure; 2) What are the links between genetic structure and social organisation? We predict that the benefits of kin group social structuring will lead to spatial autocorrelation and evidence of genetic relatedness between neighbouring breeders which may be sex-biased; 3) Are there barriers to dispersal and genetic mixing in a) space and b) time? We hypothesise that temporal and spatial barriers in relation to breeding timing and social structure will lead to genetic clustering of genotypes within the population.

Given the recent declines in the Ascension Island population of sooty terns, a within-population approach will aid our understanding of local population dynamics, as well as genetic diversity and potential plasticity to environmental change. Few studies have sought to combine within-population genetic, spatial and temporal data to understand factors influencing the population persistence of a colonial seabird.

4.3 Materials and Methods

4.3.1 Study site and data collection

The study took place between 25th October 2015 and 26th January 2016 on Ascension, a 97 km^2 island in the South Atlantic (7°56′S, 14°22′W). Sooty terns on the island nest in spatially distinct colony clusters at two main breeding sites: Mars Bay and Waterside (Fig. 4.1). Population size at breeding grounds was estimated from breeding density and colony cluster area (see Hughes *et al.* (2008) for further details), to give an estimate of total population size of 194,407 ± 14,327 pairs (± 95% confidence intervals).

To assess spatial heterogeneity in genotypes we targeted breeding individuals along five 90 m transects placed at random within colony clusters, across both breeding grounds (Fig. 4.1). Temporal variation in genetic structure was assessed by monitoring breeders who initiated nests over a 42 day time period. Only areas with incubating individuals were included to reduce the risk of abandonment. Breeding adult terns were sampled along five 90 m transects with one transect per 1 ha of breeding area occupied. The 1 ha areas were chosen at random across sites by splitting each cluster occupied into roughly 1 ha areas and using random numbers to select sampling areas. Four sampling points were studied along each transect with ~ 20 m between each sampling point. Points were located at 0 m (the edge of the cluster), 30 m (accounting for ~ 10 m of the sampled area), 60 m and 90 m along the transect. Seventeen sampling points were monitored in total with one transect providing a single sampling point before eggs of birds in the remaining sampling points hatched. Where possible the nearest 15 nests to each sampling point were monitored totalling 266 nests. Between 10 and 30 individuals are required to compare genetic differences between populations (Trask *et al.* 2011; Hale *et al.* 2012). This informed the number of nests that were monitored at sampling points along transects so that comparisons at various spatial scales could be made. Nests were marked with numbered flagging tape tied around a nearby rock or a nest tag hammered into the loose substrate. Sooty terns typically lay one egg (Schreiber *et al.* 2002) which was marked with a number corresponding to that of the nest using a non-toxic permanent marker as a back-up should the nest label have been lost. Targeted birds were ringed with uniquely numbered British Trust for Ornithology (BTO) metal rings and marked with a non-toxic permanent marker on one side of the breast (which remained visible at a distance of 5 m for up to four weeks), preventing recapture of the same individuals. The location of each sampling point was recorded using a hand-held GPS unit (eTrex, Garmin, Hampshire, UK) accurate to ± 5 m. To increase nest location precision, each nest was manually recorded on a map and the triangular distances between each nest in relation to the sampling point were measured. These were later uploaded to ArcGIS 10.2(ESRI 2013) to obtain each nest's spatial coordinates. To estimate hatching date of eggs, nests were visited every three to six days. Blood samples were collected from 287 birds (including 77 pairs) at 210 nests. Approximately 100 µL of blood was taken by brachial venepuncture of each bird using a 27G syringe, and stored in 1 mL of 70% ethanol. Ad-hoc recoveries of recently deceased chicks were made and stored frozen (n = 7). DNA samples were extracted from chick brain tissue.

Blood sampling took place following approval for overseas fieldwork from the local review process of the Biomedical Ethical Review Sub-Committee (BERSC) of the University of Birmingham and under an Environmental Research Permit issued by the Ascension Island Government (AIG) (ERP-2015-13). All ringing and marking of birds were carried out under British Trust for Ornithology (BTO) ringing licence no. 6316 held by LJHG. None of the sampled birds abandoned breeding attempts during the study.

4.3.2 Genotyping

Genotyping used 26 highly polymorphic autosomal microsatellite markers (Garrett *et al.* 2017) together with three sex-typing markers (Dawson 2007; Dawson *et al.* 2016). The same protocols as those described by Garrett *et al.* (2017) were used to extract DNA from blood and tissue samples, conduct PCRs, and amplify and genotype samples.

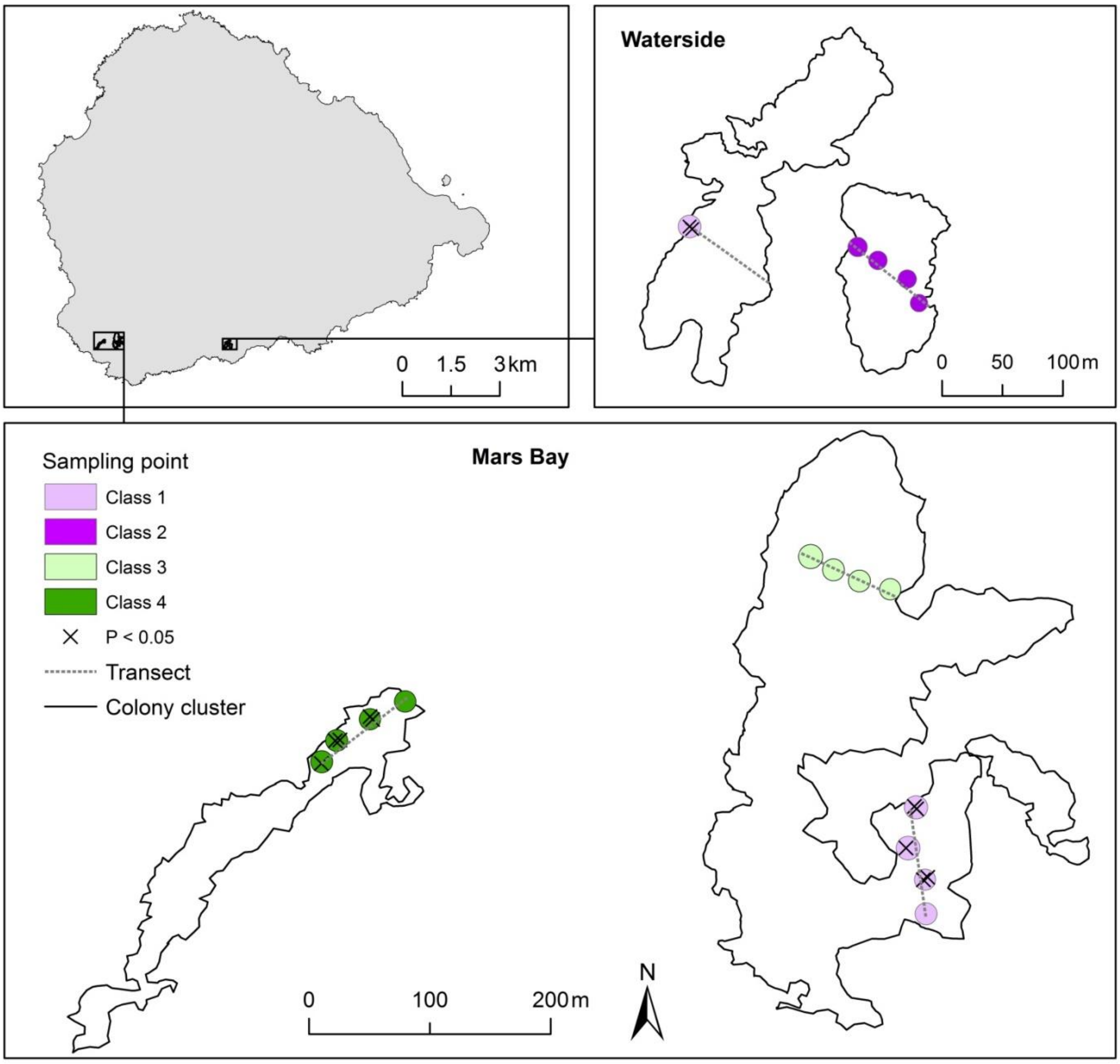


Figure 4.1 Locations of breeding grounds, nearest neighbour relatedness and breeding timing classes of sooty terns on Ascension Island. Inset map of Ascension Island (top left) shows the locations of the two sooty tern breeding grounds (Mars Bay and Waterside). The locations of 12 individuals significantly more genetically related to their four nearest neighbours than those selected at random from the population are shown within sampling points (marked with Xs). Sampling points are coloured by breeding timing classes with Class 1 being the earliest breeders and Class 4 the latest.

4.3.3 Statistical analysis

4.3.3.1 Genetic diversity and population structure

To test whether observed genotypic and allelic frequencies within the population differ from expected frequencies, deviations from Hardy-Weinberg Equilibrium (HWE) and Linkage Disequilibrium (LD) were assessed in GENEPOP v4.2 (Rousset 2008) using unrelated individuals (Anderson *et al.* 2010). Relatedness (*r*) values range from -1 to +1, with negative values between two individuals suggesting that they are less related on average than two randomly selected birds from the population. Non-relatives were selected using the program Friends and Family v21 (de Jager *et al.* 2017) with *r* set to < 0.24 (n = 219), assuming a half-sibling relatedness of *r* = 0.25. To correct for multiple tests a false discovery rate control (Verhoeven *et al.* 2005) was applied to LD and HWE *P*-values. Observed and expected heterozygosities were assessed using CERVUS v3.0.7 (Kalinowski *et al.* 2007). All markers tested were found to be in HWE except *Ofu06*, which displayed an excess of homozygotes. It also displayed a high estimated null allele frequency > 10% (Appendix 3). Therefore, this marker was excluded from subsequent analyses, giving a total of 25 markers. Genotyping error rate was assessed using two independent genotypes from the same sample (Bonin *et al.* 2004) with 50 individuals re-amplified from extracted DNA and genotyping error rate estimated using the program PEDANT v1.0 (Johnson & Haydon 2007). Missing alleles across all individuals for the 25 loci amounted to 0.32% with no one individual having more than 15% missing data (see Appendix 4). Therefore, all individuals were included in the analysis.

Population-level variation in genetic structure was tested using the program STRUCTURE v 2.3.4 (Pritchard *et al.* 2000). Clusters of individuals with similar variation are assigned to one of the n populations (*K*) identified using a burn-in of 100,000 iterations and 500,000 MCMC (Markov chain Monte Carlo) steps testing values of *K* from 1 to 10. The likelihood of different values of *K* was then assessed using posterior probabilities. To estimate this variation in the posterior probability, each value of *K* was assessed through 10 iterations. Pairwise relatives with an *r* > 0.24 were excluded from the analysis resulting in 219 individuals, due to the potential for *K* to be overestimated (Rodríguez-Ramilo & Wang 2012). Ten independent runs per *K* were performed to check for consistency across runs. Structure Harvester v 0.6.94 (Earl

& vonHoldt 2012) was used to calculate the most likely value of *K* using the Evanno *et al.* (2005) method. This uses Δ*K* based on the rate of change in the likelihood of data between successive *K* values. The 10 replicate runs of *K* were aligned in CLUMP v 1.1.2 (Jakobsson & Rosenberg 2007) and visualized using DISTRUCT v 1.1 (Rosenberg 2004). All *alpha* and F_{ST} values converged indicating the most likely value of *K* was observed (Appendix 5, Pritcharda *et al.* 2009). Given the high variability of the markers used which may influence identification of population structure (Botstein *et al.* 1980), we also performed STRUCTURE analyses using ten loci with the lowest polymorphic content (PIC) values. The PIC is a useful measure of genetic evaluation (Botstein *et al.* 1980). Runs were performed using the 219 unrelated individuals as well as the least related individuals (31 from Mars Bay and 25 from Waterside). Evidence for genetic clustering among sites was also evaluated via a principal coordinates analysis (PCoA) by plotting pairwise F_{ST} in GENALEX v 6.5 (Double *et al.* 2005). The F_{ST} differentiation and significance of the total inertia along each PCo axis were estimated using 10,000 bootstrap permutations in the program PCAGEN 1.2.2 (Goudet 1999).

Pairwise relatedness and individual inbreeding coefficients were used as measures of fine-scale genetic structure in subsequent analyses. The performance of four relatedness estimators was assessed with the R package 'related' (Pew *et al.* 2015) using all individuals including chicks (n = 294). Wang's estimator of relatedness (Wang 2002) had the best correlation coefficient and was used in subsequent analyses (Pearson's correlation coefficients [*r*] using: Li et al. = 0.9364; Lynch and Ritland = 0.8628, Queller and Goodnight = 0.9367; and Wang = 0.9375). All of the chicks genotyped (n =7) were correctly identified as offspring of their expected parents except for one which was unrelated to its expected paternal parent, suggesting extra-pair paternity. Chicks were only used to assess relatedness estimators and check the reliability of the markers and were excluded from all other analyses. Individual inbreeding coefficients were estimated using Ritland's method-of-moments estimator (MME) (Ritland 1996) in the R package 'related'. Observed inbreeding per individual was visualised by mapping a graduated colour ramp onto the colony using ArcGIS v10.2 (ESRI 2013).

4.3.3.2 Spatial genetic structure

In populations with some degree of kin-based philopatry and reduced dispersal, there may be evidence of genotypic spatial clustering. Genetic structure was therefore assessed at various spatial scales using all individuals excluding chicks. At the wider landscape scale, genetic differentiation between breeding grounds was calculated in GENALEX v 6.5 (Peakall & Smouse 2012) to estimate the pairwise G''_{ST} with the number of permutations and bootstraps set to 999. The G statistic was used given the commonly used F_{ST} can have limitations such as a reduced F_{ST} value when heterozygosity is high (Meirmans & Hedrick 2011) when using highly variable loci. To look for evidence of genetic isolation by distance, spatial autocorrelation analysis was performed in GENALEX v 6.5 (Peakall & Smouse 2006) on all adult genotypes together with their spatial location. Distances were restricted to 100 m to avoid over-weighting cross-transect comparisons (Cristofari *et al.* 2015). Correlogram significance was determined using the non-parametric heterogeneity test of Smouse *et al.* (2008) where the null hypothesis of a non-random distribution of genotypes in space is accepted when $P < 0.01$. Each sex was also analysed separately to examine sex-biased dispersal, with comparisons between sexes following Banks and Peakall (2012).

Heterogeneity tests in relatedness at transect - and sampling point- scales were conducted using permutations (10,000 simulations) to detect within- and between-transect and sampling point differences. These permutation tests used the same number of individuals from within, compared to between, sampling points, the latter of which were selected at random using 10,000 simulations to obtain the P value (Jacob *et al.* 2016). Fine-scale genetic spatial structure was analysed using the two-dimensional local spatial autocorrelation (2D LSA) statistics from the program GENALEX v 6.5 (Double *et al.* 2005). Given the four nearest neighbours are more likely to be an individual's direct neighbours surrounding a focal nest (LJHG pers. obs.), the number of neighbours was set to four. Local autocorrelation (*lr*) was inferred where $P < 0.05$ using permutation tests (100,000 simulations) to calculate significance. Locations of significant *lr* results were mapped onto the colony using ArcGIS v10.2.

4.3.3.3 Temporal genetic structure

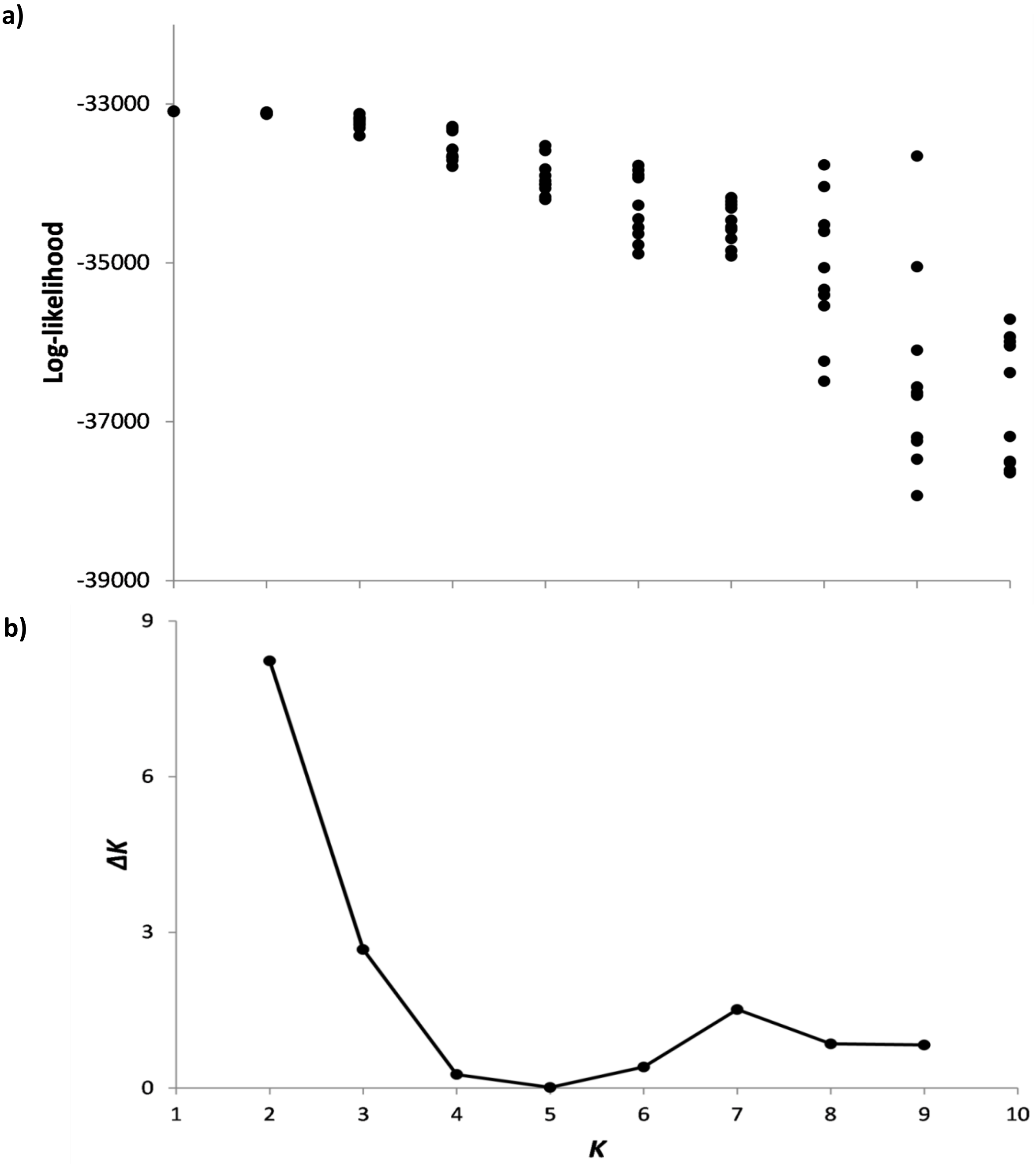
To assess within-breeding season temporal partitioning in genetic structure, breeding timing was estimated using hatching dates calculated as the number of days from the first reported hatching date (i.e. 24th September 2015) (AIGCFD pers. comm.), as laying dates were not always known. Evidence for a relationship between genetic structure and breeding timing was considered by assigning timing classes and as a linear relationship. For the former breeding pairs with known hatching dates (n = 203) were assigned a breeding timing class using a k means clustering algorithm in R (R Core Team 2019), resulting in four such clusters. Genetic differentiation between breeding timing classes was compared using G''_{ST} statistics in GENALEX v6.5 with permutations and bootstraps set to 999. Breeding timing classes were mapped onto the colony using ArcGIS v10.2. Inbreeding coefficients of individual birds were linearly regressed against hatching dates that had been Tukey transformed using the R package 'rcompanion' (Mangiafico 2017). Pairwise relatedness was also compared with the absolute difference (in days) between pairwise hatching dates using a Mantel test in GENALEX v6.5.

4.4 Results

4.4.1 Genetic diversity and population structure

The sooty tern population on Ascension Island has high genetic diversity with mean observed and expected heterozygosities of 0.80 ± 0.09 and 0.82 ± 0.09, respectively (Annex 2). The 25 microsatellite loci also had a high average number of alleles (17.36 ± 8.07 alleles per locus, range = 6 to 38). The log-likelihood of the number of populations declined as the number of populations increased (Fig. 4.2a) and overall average pairwise relatedness was low (mean = -0.007 ± 0.086, n = 43,071 pairs). The ΔK analysis also showed steep declines in the number of probable populations at $K > 2$ (Fig. 4.2b). STRUCTURE analysis indicated that all individuals were evenly split between populations from when K was greater than 1 (Fig. 4.2c, Appendix 6). The PCoA also demonstrated a lack of separation between the two sample sites on each axis with a cumulative total genetic variation of 37.1% explained by axes 1 and

2 (axis 1: 20.1%, F_{ST} = 0.002, P = 0.98; axis 2: 17.0%, F_{ST} = 0.003, P =0.87; Fig. 4.3). Individual inbreeding coefficients were also relatively low (mean = 0.006 ± 0.051, range: -0.09 to 0.23) and showed no obvious clustering when mapped onto the colony (Fig. 4.4).



c)

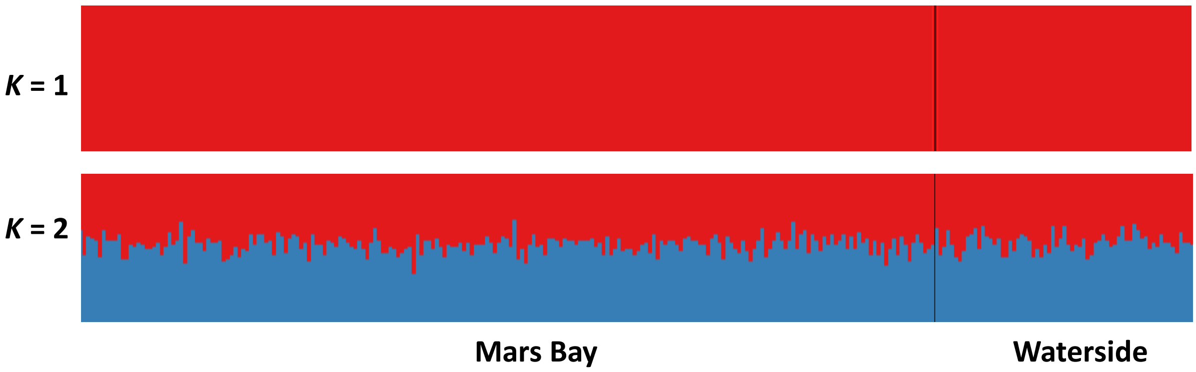


Figure 4.2 a) The individual log-likelihood values per run (10 runs per *K*) for each value of *K* (populations) showing convergence at *K* = 1. **b)** The most probable number of genetic clusters (*K*) evaluated by the Evanno *et al*. (2005) method using Δ*K* based on the rate of change in the log-probability of data between successive *K* values. **c)** Genetic structure plot of sooty terns genotyped using 25 microsatellite markers from the two breeding sites, Mars Bay (n = 217) and Waterside (n = 70), on Ascension Island for *K* = 1 and *K* = 2.

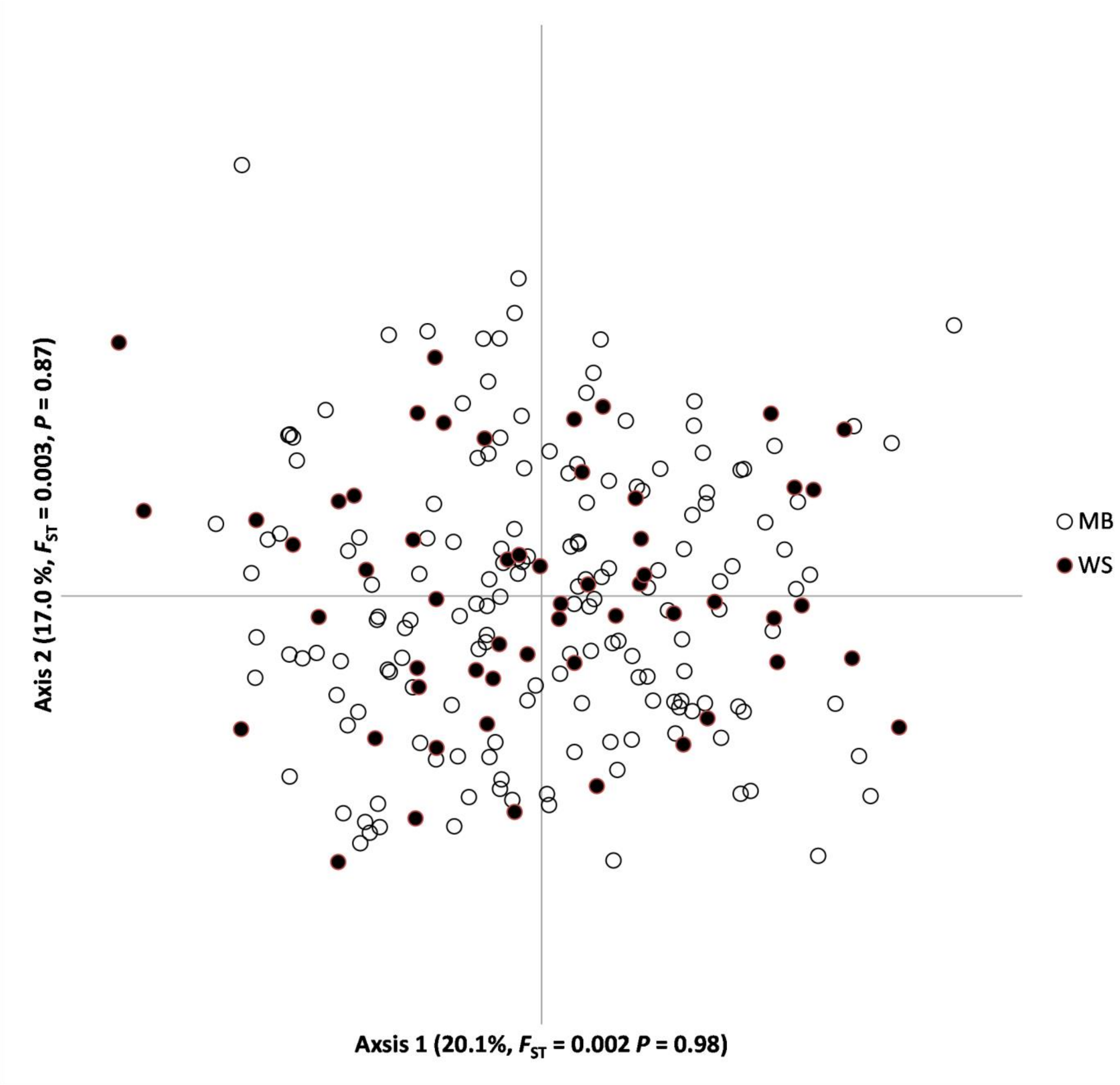


Figure 4.3 Plot showing the first two axes of the principal coordinates analyses (PCoA) accounting for 37.1% of the total F_{ST}-based genetic variation among sooty terns breeding at each study site on Ascension Island. Open circles are for Mars Bay (MB) and filled circles are for Waterside (WS). F_{ST} and P values indicate the amount and significance of genetic variation explained by each PCo axis.

4.4.2 Spatial genetic structure

We found varying degrees of genotypic structuring at different spatial scales but with more support for localised spatial genetic structure. There was no evidence of landscape-scale partitioning acting on the genetic structure of the population between the two main breeding grounds: $G''_{ST} = 0.004$, *P* = 0.89. Nor was there any distance-based structuring from autocorrelation analysis which detects isolation by distance (Omega = 28.1, *P* = 0.02, Fig. 4.5a), including between sexes (Omega = 12, *P* = 0.90, Fig 4.4b). Heterogeneity tests of relatedness either within (*r* = -0.007 ± 0.086) or between transects (*r* = -0.007 ± 0.086) showed no significant difference (*P* = 0.55). However, individuals located within sampling points were significantly more related to one another (*r* = -0.004 ± 0.090) than to individuals at other sampling points (*r* = -0.007 ± 0.086, *P* = 0.03). There was also evidence of fine-scale genetic structuring between neighbouring individuals, with the 2D LSA analysis yielding 12 individuals that were more related to their four nearest neighbours than those selected at random from the population ($P < 0.05$). These individuals were located within three sampling transects (Fig. 4.1).

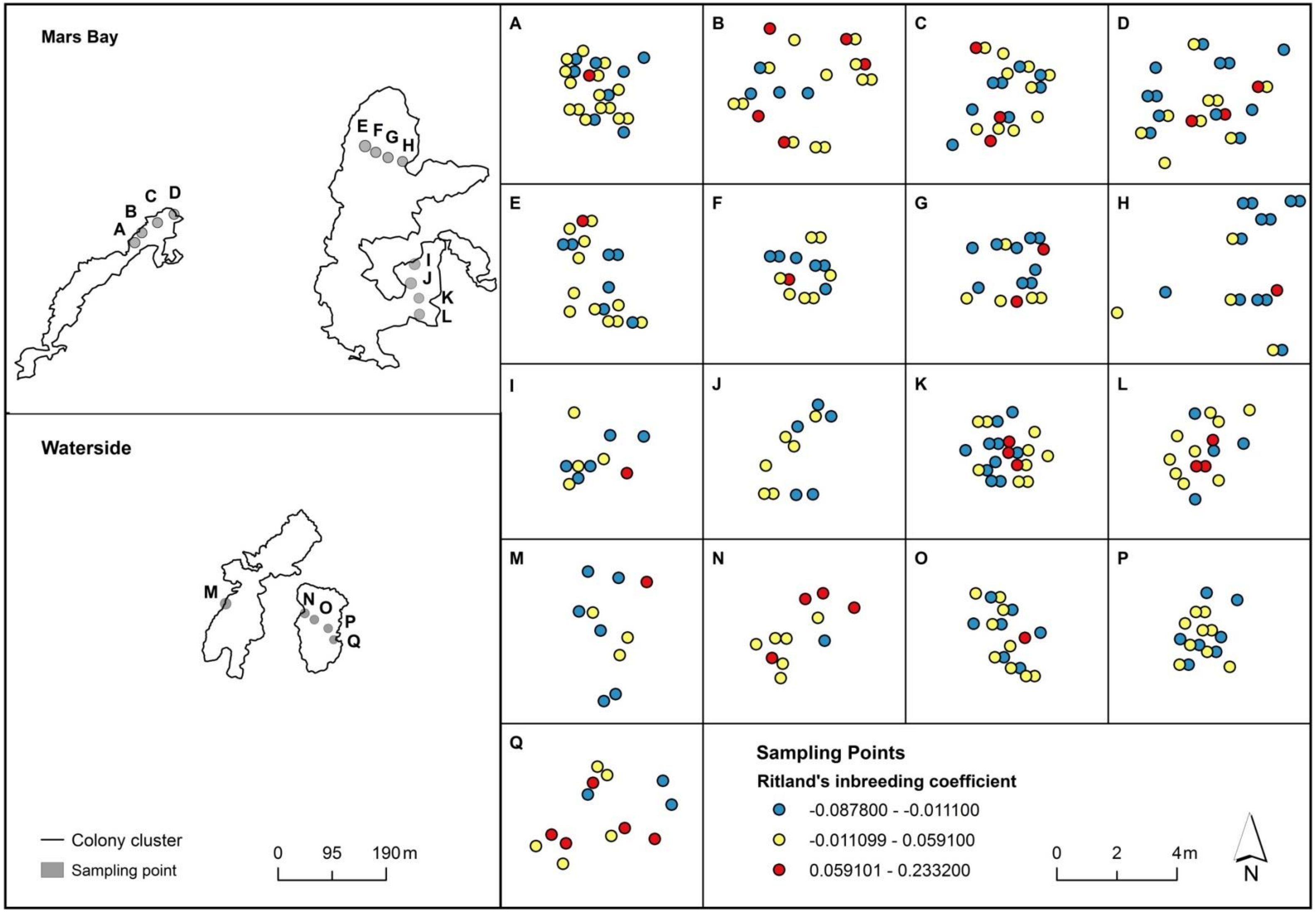

Mars Bay
A
B
C
D
E
F
G
H
I
J
K
L
Waterside
M
N
O
P
Q
Colony cluster
Sampling point
0
95
190 m
Sampling Points
Ritland's inbreeding coefficient
● -0.087800 - -0.011100
● -0.011099 - 0.059100
● 0.059101 - 0.233200
0
2
4 m
N

Figure 4.4 Spatial distribution of sampling points and individual inbreeding levels across two sooty tern breeding grounds (Mars Bay and Waterside) on Ascension Island. Left-hand maps show the two breeding grounds separately and the location of sampling points within colony clusters on Ascension Island during peak breeding (in January 2016). Right-hand boxes depict the spatial distribution of individuals nesting at each sampling point. Coloured points indicate Ritland's individual inbreeding coefficients. Where both sexes were sampled from the same nest, points have been offset by 30 cm for visualisation purposes.

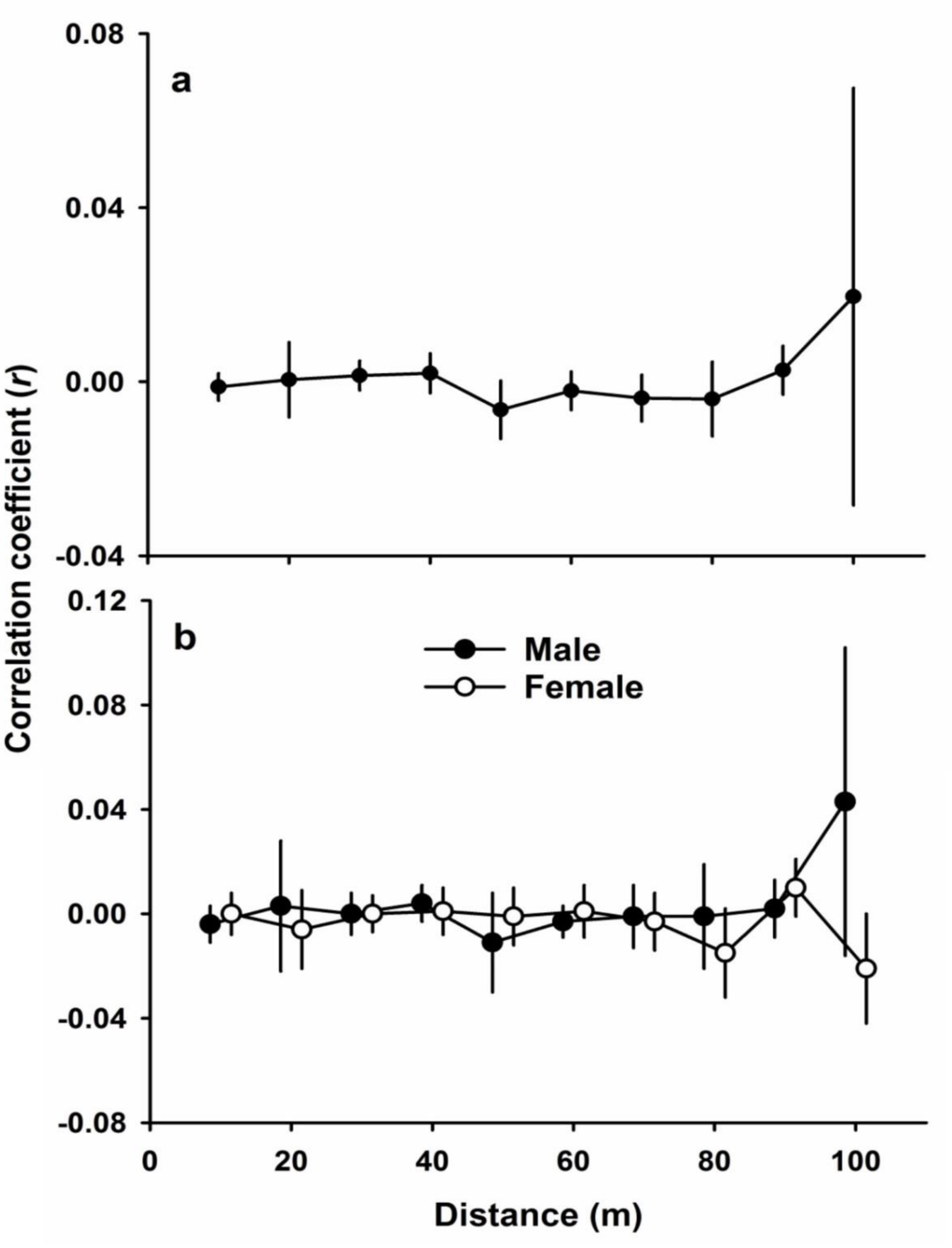


Figure 4.5 Genetic spatial autocorrelation analysis of sooty terns on Ascension Island **a)** Population level spatial correlogram. Solid line: Observed correlation coefficient (*r*) for each distance class, error bars: 95% confidence intervals determined by bootstrapping. **b)** Spatial correlogram displaying each sex separately. Error bars are 95% confidence intervals determined by bootstrapping.

4.4.3 Temporal genetic structure

There was within-breeding season temporal genetic partitioning at the population level. Pairwise comparisons of genetic similarity between breeding timing classes found significant differences only between the earliest and latest timing classes with 34 days between average hatching dates (Table 4.1). Interestingly, these breeding timing classes were located within the same three transects as the locations of individuals which were more related to their four nearest neighbours (Fig. 4.1). However, there was no support for temporal genetic effects as a linear association (breeding timing and individual inbreeding coefficients: $F_{1, 201}$ = 1.41, R^2 = 0.002, P = 0.24; pairwise relatedness estimates and absolute differences in breeding timing: Mantel R^2 = 0.0002, P = 0.24).

Table 4.1 Pairwise comparisons of sooty tern genetic differentiation between breeding timing classes on Ascension Island. Breeding pairs with known hatching dates (n = 203) were assigned a breeding timing class using a k means clustering algorithm, resulting in four clusters (Class 1: n = 53, Class 2: n = 37, Class 3: n = 48, Class 4: n = 65).

	Class 1	Class 2	Class 3	Class 4
Class 1		-0.011	-0.005	0.012
		0.916	0.781	**0.017**
		8	17	34
Class 2			-0.012	0.002
			0.923	0.432
			9	26
Class 3				0.007
				0.092
				17
Class 4				

Genetic differentiation is displayed using G''_{ST}. The G''_{ST} coefficient is shown followed by the *P* value and the number of days between average hatch times. Significant differences between classes are shown in bold text.

4.5 Discussion

Our results indicate local scale spatial and temporal genetic structure in an otherwise highly genetically diverse population. We found support for the importance of within-breeding season timing effects on genetic structure which parallels that found within other organisms, such as migratory fish species (Hendry & Day 2005; Coulson *et al.* 2006). The observed overall heterogeneity in both spatial and temporal effects on genetic structure, suggests a trade-off between these mechanisms. Together with processes, such as dispersal between populations, heterogeneities in spatial synchrony and temporal partitioning may contribute towards the maintenance of genetic diversity within the population.

4.5.1 Population panmixia

We hypothesised that the observed differences in breeding timing and other characteristics between the two breeding sites on Ascension Island (Chapter 2) together with the high propensity for site faithfulness in seabirds would lead to landscape scale partitioning between the breeding sites. We also predicted some evidence of reduced genetic diversity given the > 80% decline in population size in the 1950s from which the population has not recovered. However, our results showed high population genetic diversity, coupled with a lack of genetic differentiation between breeding colonies (i.e. Mars Bay and Waterside; Fig. 4.2, Fig. 4.3), suggesting that landscape-scale barriers to gene flow are not operational on the island. There was also no evidence of genetic isolation by distance (Fig. 4.5a) or sex-biased dispersal (Fig. 4.5b). Together with low levels of relatedness and inbreeding, our results suggest random breeding within the population. Given seabirds are long-lived species with high dispersal capabilities, there is also the potential for between-population gene flow (Bicknell *et al.* 2012). Non-breeding distributions of seabirds have been highlighted as key predictors of genetic structure and gene flow (Friesen *et al.* 2007a), with those staying close to their breeding grounds displaying greater genetic structure. In terns (Sternidae), philopatry usually occurs once breeders have undertaken their first breeding attempts (Palestis 2014), with natal dispersal often considerably exceeding adult breeding dispersal (Lebreton *et al.* 2003). Pre-breeder dispersal in Leach's storm-petrels *Oceanodroma leucorhoa* demonstrates such a mechanism for genetic mixing between subpopulations and the persistence of isolated populations despite increased rates of predation (Bicknell *et al.* 2014). Evidence of introgression in the Ascension Island sooty tern population includes: (i) a retrap of a bird ringed as a juvenile off the coast of Brazil that subsequently bred on Ascension Island (Hughes *et al.* 2010), (ii) a pre-breeding bird originally from Ascension Island recovered in Abidjan, West Africa, and (iii) recoveries of juvenile birds from the Dry Tortugas, Florida, USA that were made in the Gulf of Guinea off West Africa (Robertson 1969). Therefore, it is likely that before breeding for the first time, birds fledged from Ascension Island and the Dry Tortugas may forage together in the Gulf of Guinea. Preliminary genetic analyses on the differentiation between populations also revealed similarities within but not between ocean basins, with differences observed between the Atlantic and Indo-Pacific populations (Avise *et al.* 2000). The relatively recent global scale population expansion, within the last 100,000 years, is also likely to influence contemporary genetic diversity (Peck & Congdon 2004). Thus, inter-population dispersal could be a key process for maintaining genetic diversity within the Ascension Island population and indeed within the species as a whole.

4.5.2 Fine-scale spatial genetic structure

We predicted that the benefits of kin group social structuring would lead to spatial autocorrelation and that there would be some evidence of genetic relatedness between neighbouring breeders which may be sex-biased. Indeed, at finer scales there was evidence of genetic structuring both spatially and temporally. Individuals within sampling points (within < 5 m of each other) were more related to one another than those located at other sampling points. Localised spatial structure was also evident in 12 individuals that were more related to their nearest neighbours than the rest of the population (Fig. 4.1). A shared decision on the movement of groups of individuals in space is likely to evolve where conflicts between group members are low relative to group cohesion benefits (Conradt & Roper 2010). The benefits of nesting near genetic relatives include reduced aggression and increased vigilance against predators (Griesser 2008), reduced nest site competition (Sonsthagen *et al.* 2010) and infanticide avoidance (Hatchwell 2010).

4.5.3 Temporal genetic structure

We hypothesised that temporal and spatial barriers in relation to breeding timing would lead to genetic clustering of genotypes within the population. We found evidence of genetic structuring related to intragroup breeding synchrony with earliest breeders having significantly different genetic structure from those breeding over one month later (Table 4.1). The coordination of group movement in time is likely to evolve where the conflicts between group members are relatively high (although not higher than group cohesion benefits (Conradt & Roper 2010). For example, if group members differ in their previous breeding season success rates, their optimum return times for the following season will also differ, given the higher offspring investment levels for successful individuals. An extreme example of this is black-browed albatrosses *Thalassarche melanophris* that breed at South Georgia. They delay breeding by up to four years following successful fledging of young, whereas around half of breeders failing during incubation return to breed the following year (Prince *et al.* 1994). Competition for nest sites was also thought to be a driver in the genetic divergence of two breeding populations of band-rumped storm petrels *Oceanodroma castro* that breed on the same colony in the Galapagos Islands but at different times of the year (six months apart) (Smith & Friesen 2007). Timing-related genetic mechanisms show high heritability (Ribolli *et al.* 2017) and may arise due to high competition for resources such as space, food and mates (Braga-Silva & Galetti 2016). Indeed, Casagrande *et al.* (2006) suggested that the relatively high genetic differentiation between early and late breeding Eurasian kestrels *Falco tinnunculus,* breeding one month apart in close proximity, may be a result of variable food supply and weather conditions. Differences in population-level genetic structure according to breeding timing have also been observed in a salmonid fish *Oncorhynchus* sp. with differences in arrival times of as little as two weeks (Hendry & Day 2005). However, few studies have investigated within-breeding season effects on genetic structure in birds (but see Casagrande *et al.* 2006).

4.5.4 Heterogeneity in spatial and temporal synchrony

Temporal and spatial synchronies are not always independent (Ribolli *et al.* 2017) and the earliest and latest breeding birds in our study matched spatially with those that showed higher genetic relatedness to their nearest neighbours (Fig. 4.1). However, a trade-off in collective movement between space and time may also occur, where individual benefits are disparate (Conradt & Roper 2010). For example, an individual's optimum breeding time may be different from that of the group in which it is contained. This is likely as sooty terns have a low rate of re-nesting if the initial attempt fails (Ashmole 1963), because of the large investment of energy and time in a breeding attempt. Thus, heterogeneity in breeding success in both space and time may give rise to transient movement behaviours, where genetic mixing occurs across a gradient, resulting in only local scale genetic structuring.

Information exchange between individuals can also be important in determining a species' spatial and temporal resource use (Danchin *et al.* 2004). Local reproductive outcome rather than individual breeding success has been shown to influence whether returning breeders maintain group cohesion in the future in colonially nesting black-legged kittiwakes (Boulinier *et al.* 2008). Thus, information on group-level breeding success may determine with whom individuals nest the following season. Francesiaz *et al.* (2017) found social connections in slender-billed gulls were maintained temporally, despite breeding site fidelity being low, with colony fidelity dependent on breeding success in the previous season.

4.5.5 Genetic adaptability

High levels of genetic diversity are thought to enhance species recovery after experiencing extreme climatic conditions. For example, Reusch *et al.* (2005) found that increased genotypic diversity in eelgrass *Zostera marina* led to higher plant density and biomass production after exposure to near lethal temperatures. Populations of yellow warblers *Setophaga petechia* with the least genomic variation were also predicted to be most vulnerable to extinction under projected climate change scenarios and indeed are already experiencing population declines (Bay *et al.* 2018). High genetic diversity and thus population persistence is likely to be a result of a combination of multiple factors (Fig. 4.6). In species subject to high environmental variability, such as extreme weather events, variable prey abundance and predation, competition for both space and food is often high, which has been demonstrated in some seabird species (Durant *et al.* 2012). Possible adaptive strategies to combat such stressors may include spatial and temporal structure, as well as dispersal between breeding populations, which leads to high genetic diversity (Fig. 4.6). However, although high genetic diversity and life-history traits such as longevity promote plasticity to a changeable environment, with single season breeding failures having little effect on population persistence, recurrent breeding failures and low adult survival due to low food availability for example, will result in population declines (Cury *et al.* 2011). Anthropogenic impacts through overfishing, climate change, introduction of invasive species (Paleczny *et al.* 2015), egg harvesting (Feare & Lesperance 2002) and other disturbance at nesting grounds (Grémillet & Boulinier 2009) increase pressure on such a population (Fig. 4.6).

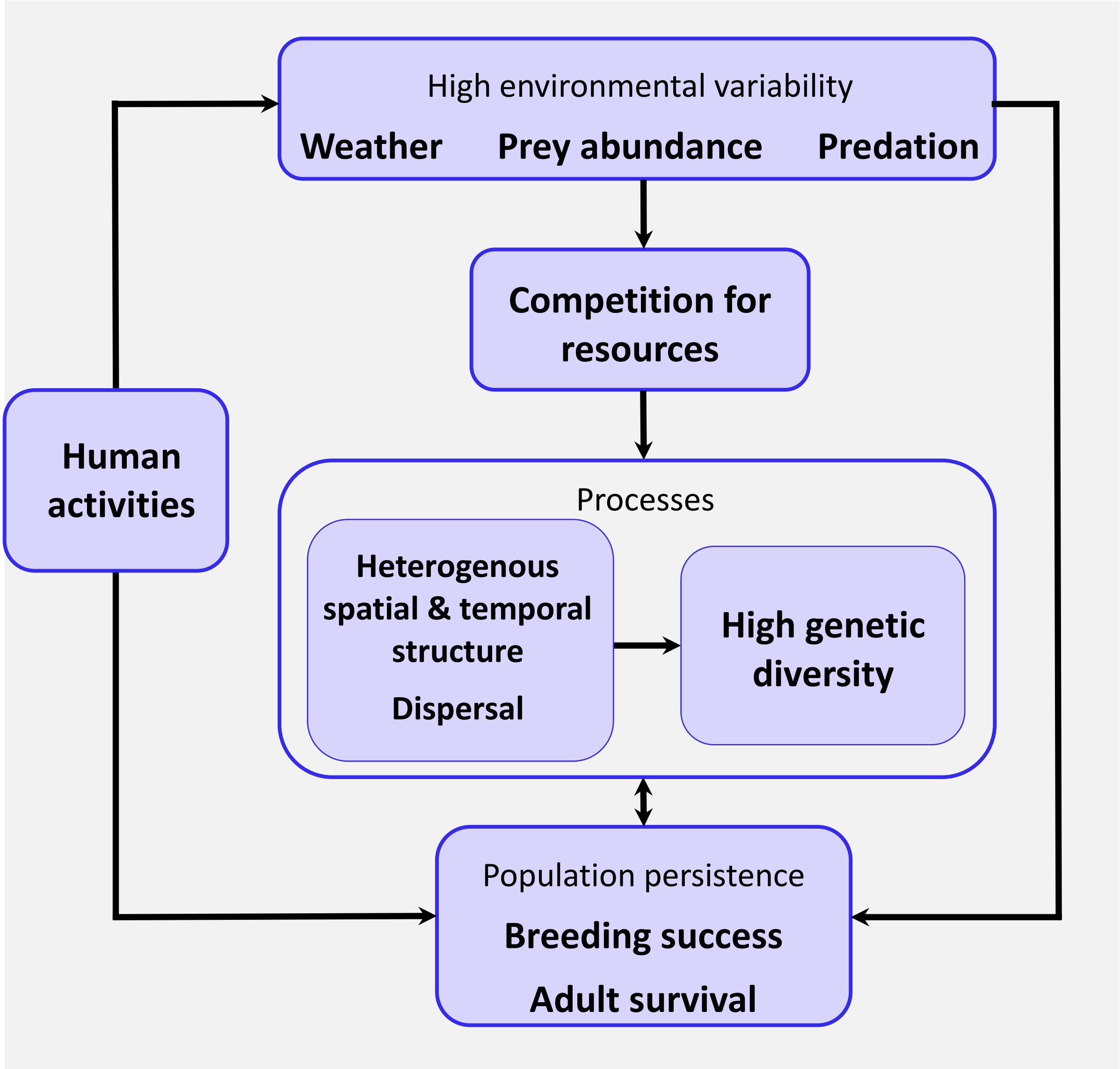


Figure 4.6 Potential factors influencing the evolutionary strategies and population persistence of sooty terns on Ascension Island and their interactions. A highly variable natural environment often leads to increased competition for space and food. Possible adaptive strategies to enable increased genetic plasticity and thus population persistence may include heterogeneity in fine-scale spatial and temporal structure, and within- and between-population dispersal. Human activities increase the severity of environmental stressors (e.g. through climate change, overfishing and introduced predators) and limit population persistence through direct impacts on breeding success and survival (such as via egg harvesting).

4.5.6 Conclusions

Our findings indicate spatio-temporal processes underlie local-scale genetic structure in an otherwise panmictic seabird population. Local-scale structure could be dependent on factors such as breeding success, information exchange and competition for resources. Heterogeneity in the benefits individuals stand to gain from collective group structure in space and time are likely to maintain genetic diversity and gene flow within the population, given genetic structure was only evident at fine scales. These processes, together with the potential for juvenile dispersal between populations, may lead to gene flow at a scale that mitigates philopatry and avoids inbreeding, thereby increasing the likelihood of population persistence over time through adaptability to environmental change. Future studies investigating population structure would benefit from assessing within-population processes and the inclusion of spatio-temporal parameters to enhance our understanding of a population's ecology and evolution, and the maintenance of population genetic structure.

Chapter 5

Cost-effective and non-invasive field methods for studying colonially breeding seabirds with highly mobile young

Lucy J.H. Garrett, Julia P. Myatt, Jon P. Sadler, and S. James Reynolds

LJHG collected and analysed the data and wrote the manuscript. SJR, JPM, JPS and JKC assisted with writing the manuscript.

5.1 Abstract

Obtaining estimates of reproductive success for large seabird colonies can be challenging, especially for those with highly mobile (precocial) young. Identification of individual chicks is needed for accurate survival estimates to be made. Previous methods for estimating daily survival rates and reproductive success are often intrusive, expensive and can have detrimental effects on survivorship. We build on previous techniques to develop a set of non-invasive and cost-effective marking and monitoring techniques to study breeding behaviour and breeding success in a colonial seabird. These include methods for marking nests, adults and chicks which have no observable behavioural or physical impacts.

5.2 Introduction

For researchers monitoring population ecology and behaviour it is often essential to identify individuals. In colonially nesting species this can prove logistically challenging given the sheer size and density of aggregating individuals (Cuthbert & Southern 1975; Walsh *et al.* 1995; Schreiber & Burger 2001). Around 98% of seabird species are colonial breeders (Lack 1968), yet in-depth descriptions of field-based monitoring methods typically go unreported (Calvo & Furness 1992). For example, authors may state that nests were individually marked but not provide detail as to how (e.g. Pakanen *et al.* 2014; Sommerfeld *et al.* 2015; McLeay *et al.* 2017). Further challenges are presented when young are highly mobile and leave the nest (Arnold *et al.* 2011), meaning that nests cannot simply be re-visited by researchers to monitor chick survival. Morphological features may also negate the use of adult marking methods, for example the tarsi of chicks are too large to accommodate adult metal or plastic rings in some species of waterfowl (Anseriformes) and rails (Rallidae) (Arnold *et al.* 2011), and terns (Laridae) (Ricklefs 1979). Negative effects of marking techniques for monitoring birds have been noted (see review by Calvo and Furness 1992), although often studies do not assess the impacts of marking methods employed (Vandenabeele *et al.* 2011). We describe several non-invasive and cost-effective methods for marking and monitoring nest sites, adults and precocial chicks in a colonial seabird, the sooty tern. Sooty terns nest in large colonies and both parents share incubation and chick rearing duties (Dinsmore 1972). Chicks are highly mobile and leave the nest after a few days when they gather in social groups or crèches, while both parents forage at sea (Ashmole 1963).

5.2.1 Marking methods

5.2.1.1 Nest sites

Methods for marking nests are usually dictated by the nesting substrate. For dense rocky substrates methods include cattle tags (Cuthbert & Southern 1975), painted pebbles with contrasting numbers (Coast 2016) and numbered metal disks attached with wire (Trefry *et al.* 2013). These methods can prove expensive, time consuming to prepare and impractical if for large sample sizes. Painting numbers directly onto rocky substrates has been used for razorbill *Alca torda* nests (Diamond 2013), although there may be environmental and visual concerns from marking directly onto the substrate. Nests located on soft substrates such as soil or sand can be marked using wooden stakes with painted numbers (Feare 1976b; Diamond 2013; Fern *et al.* 2016) and tongue depressors/lollipop sticks (Diamond 2013; Ness & Klaver 2016). However, some species have been observed to remove certain types of markers. For example sooty terns on Ascension Island pull out and discard tongue depressors (B.J. Hughes pers. comm). Nest flags, consisting of a nylon triangle attached to a thin flexible pole, have also been used to mark Arctic tern *Sterna paradisaea* and common tern (Diamond 2013).

5.2.1.2 Adults

There are a multitude of well-established methods for marking adult birds (see summary by Calvo and Furness (1992), the most commonly employed one being metal or coloured plastic rings engraved with unique alpha numeric codes. Whilst these are long-lasting with most remaining for the lifetime of the birds, metal rings are not very effective for viewing at a distance, and both are obscured when birds are sitting on nests or closely brooding chicks. The need for an additional non-permanent marking method may arise where both members of the nesting pair need to be identified. Methods for quickly assessing whether a bird currently on a nest has been previously captured include dyes and markers. These have had mixed impacts on the behaviour and reproductive success of marked individuals. For example, dyes can lead to excessive preening of the dyed area and changes in social organisation (Calvo & Furness 1992). In mourning doves *Zenaida macroura* yellow dye applied to the head caused a breakdown of pair bonds and altered male courtship by reducing cooing frequency (Frankel & Baskett 1963). However, other studies found no impact of colour dying plumage. For example paint-marking pens on cliff swallows *Petrochelidon pyrrhonota,* (Brown & Brown 1988) and dyes used on Canada Geese *Branta canadensis* (Raveling 1969). Other temporary marking techniques include imping, where feathers or coloured tape are secured to the cut shaft of a feather but this is time consuming (Marion & Shamis 1977) and Silvy *et al.* (2012) note that painting the feathers is a more effective technique in terms of visibility. Hair dye was applied to wing and tail feathers of whiskered terns *Chlidonias hybrida* (Ledwoń & Neubauer 2017), although no assessment was made of the behavioural consequences of this.

5.2.1.3 Chicks

In some species conventional ringing methods cannot be used on chicks due to morphological constraints where tarsi are proportionally larger compared to adults thus adult rings are too small in diameter for use on chicks. The post-guard period, where chicks are no longer brooded by adults and move away from their nests, presents a particular issue for identification. Several methods have been employed to both mark and monitor precocial chicks with varying impacts on their behaviour and survival.

5.2.1.4 Marking approaches

Methods that physically mark chicks have included Tipex® on the head or bill tip (e.g. Arctic and common terns, Robertson *et al.* 2016; black guillemots *Cepphus grille*, Cook *et al.* 2000), yellow paint (e.g. sooty terns, Feare 1976a) and marker pen (e.g. herring gulls *Larus argentatus,* Crisologo and Bonter 2017; merlins *Falco columbarius,* Wright 2003). Although most researchers have reported no effects on behaviour and survival, drastically changing the chicks colour, in the case of yellow paint, did increase predation rate (Calvo & Furness 1992). These types of marks do not distinguish between individuals and are usually used in conjunction with another method or for small numbers, such as to tell nestlings apart (Crisologo & Bonter 2017).

Numbered cattle ear tags are a way for distinguishing between a larger number of individuals and have been glued to the backs of ring-billed gull *Larus delawarensis* chicks (Cuthbert & Southern 1975). Although there were no observed effects on chick predation rates, there were issues with cattle tag retention when chicks sought shelter under crevices, making this method more suited species nesting in open terrain. Nape tags, which consist of safety pins with rings or beads attached, are inserted into the skin behind the neck, and have been used to identify precocial waterbird chicks (Arnold *et al.* 2011). Although there were no effects on parent-offspring relationships nor chick survival, tag loss exceeded 20% near to fledgling and this is also an intrusive procedure.

A non-invasive marking technique designed for chick identificaton was developed by Willsteed and Fetterolf (1986) in the form of a numbered Velcro^{TM} leg flag. The tag was trialled on precocial ring-billed gull chicks and fitted around the upper leg (i.e. tibia). The authors found no impacts of the tags on survival with high tag retention rates. However, the tags were also used on herring and great black-backed gulls *Larus marinus* where there was low tag retention and abscess growth from tag restriction as chicks grew (Cavanagh & Griffin 1993). They suggest that this method is suitable for short-term studies but frequent visits are required to adjust tags to prevent their loss or tissue abrasion.

5.2.1.5 Monitoring survival

The most predominantly employed technique for monitoring precocial chick survival is fencing off areas to contain chicks so that they can be easily located. Although this method is widely accepted it can affect the natural crèching behaviour of chicks as well as having detrimental impacts on survivorship of the fenced individuals. For example Stienen and Brenninkmeijer (1999) fenced sandwich tern S*terna sandvicensis* chicks that resulted in increased kleptoparasitism by black-headed gulls. Once chicks were able to be led away from their nest sites by their parents the rate of gull robbery declined. Nisbet and Drury (1972) noted that fencing caused fatalities in common and roseate terns as well as injuries and feather damage from collisions with the fencing. Other changes in behaviour included disrupted feeding when adults landed outside of the fence to feed chicks with. This also led to kleptoparasitism by other adult terns and increased food wastage from fish being dropped the wrong side of the fence. Other researchers installed shade cloth around the base of enclosures to prevent injury, they note from observations that rates of kleptoparasitism and predation were similar to those outside the fenced areas (McLeay *et al.* 2017). Gilbert and Servello (2005) also found no effects of enclosures on black tern *Chlidonias niger* chick provisioning rates nor any differences in nesting success of whiskered terns between fenced and unfenced areas.

Other monitoring methods include radio-tags that are either glued to the body or secured subdermally, which is costly, requires training and ethical approval (Whittier & Leslie 2005). There can also be issues with retention rates. For example Whittier and Leslie (2005) glued radio-tags to the backs of least tern *Sternula antillarum* chicks but some tags needed to be re-attached up to six times and chicks needed to be recaptured twice per day to check for signs of tag loss. Grant (2002) attached radio tags to Eurasian curlew *Numenius arquata* chicks, again, initially using glue but following tag loss they attached them to an open Darvic style ring with tape. This was placed around the leg and chicks were captured every three days to be weighed. The authors found no effect of the tags on chick weight gain. Radio tags rely on the location of chicks to be determined using an antennae and receiver, allowing estimates of survival for example. To detect mortality Ackerman *et al.* (2014) used radio tags containing thermistor switches to monitor changes in body temperature of Forster's tern *Sterna forsteri* chicks. The tag emits a pulse rate corresponding to the chick's body temperature that enables researchers to detect abnormal signatures, indicating whether chicks are likely to still be alive. Radio tags were sutured to the backs of chicks so that body temperature could be continuously recorded. Amundson and Arnold (2010) also sutured radio tags to the backs of mallard *Anas platyrhynchos* ducklings, which had a significant effect on survival. Ducklings with radio tags had average daily survival rates of 0.04 compared with unmarked ducklings of 0.22 and ringed ducklings of 0.14 in the same breeding period. Subcutaneous suturing has also resulted in bill entanglement in harlequin ducks *Histrionicus histrionicus* (Bond & Esler 2008). There are also a range of reported deleterious effects of radio tags on adult birds such as lower food consumption (Pietz *et al.* 1993), impeded locomotion (Enstipp *et al.* 2015), nest desertion (Garrettson & Rohwer 1998; Robert *et al.* 2006), lower breeding success and reduced adult survival (Lameris & Kleyheeg 2017).

5.2.1.6 Permits and ethics

Prior to capturing, marking and carrying out any procedures on animals, the appropriate permits and permissions must be obtained by the relevant granting body. Land-owner and government permissions must be sought in order for any field research to be undertaken at a particular location. Capturing and handling wild animals is regulated in most countries, for example in the UK and EU under The Wildlife and Countryside Act 1981, The EU Birds and Habitats Directives. Licences for ringing birds required by those undertaking ringing activities (e.g. in the UK licences are granted by The BTO and in the U.S by the Bird Banding Laboratory, U.S. Geological Survey, Department of the Interior, Laurel, Maryland 20708-4037, or the Canadian Bird Banding Office, Canadian Wildlife Service, Ottawa, Ontario, Canada KIA OH3) with any ringing activities recorded and details submitted to the licensing bodies. Other procedures such as marking feathers and the use of radio tags may require additional licences, such as a special methods licence from the BTO in the UK, and more invasive procedures such as suturing or nape tags require a Home Office licence in the UK under the Animals (Scientific Procedures) Act 1986. In addition, most institutions require that researchers submit health and safety proformas and additional approval from the relevant granting body for working with animals in research. All research should question the need to capture and mark animals, especially where invasive procedures are involved, and aim to limit detrimental effects to animal health, behaviour, reproduction and movement (Silvy *et al.* 2012).

In this study we develop and describe non-invasive methods for marking nest sites, adult sooty terns and newly hatched chicks to fledging age. These methods can be used where individuals need to be distinguished from one another, for example to study animal behaviour, individual breeding success and mark-recapture purposes.

5.3 Methods

5.3.1 Study area and species

The reproductive success of sooty terns was monitored on Ascension Island, South Atlantic (7°56’S, 14°22’W between 25th October 2015 and 9th March 2016. Sooty terns nest at two main breeding sites (Mars Bay and Waterside; Fig. 1.1) and the estimated total population size was: 194,407 ± 14,327 pairs (± 95% Confidence Intervals). Breeding sooty terns were only monitored during the incubation period, a minimum of seven days after egg laying, in order to minimise the risk of abandonment, which is more likely during the early settlement period (LJHG pers. obs.). Breeding pairs were sampled along five 90 m transects placed at random between each colony. Four sampling points were studied along each transect. Points were located at 0, 30, 60 and 90 m along each transect. A total of 17 points were surveyed (one transect only had one point due to the rest of the cluster hatching before nests could be surveyed). Where possible the closest 15 nests to each sampling point were monitored in roughly a 3 m^2 area (total nests monitored = 266). Sooty terns usually lay one egg per nest and are unlikely to relay should their breeding attempt fail (Ashmole 1963).

5.3.2 Nests

Sooty tern nests, which consist of bare ground or a shallow scrape sometimes with a few placed stones (Hughes 2014), were marked with white plastic gardening tags with the stem cut off (Fig. 5.1). Holes were punched in the neck of the tags with a standard hole punch to allow roofing nails (mechanical galvanised spring head nails, 65mm long) to be pushed through to secure the tags in soft substrate. On hard substrate, tags were secured to a small rock found in the vicinity of the nest site with coloured flagging tape. Tags were numbered with black permanent Sharpie^{TM} marker pen. Tags were placed within 5 cm of the nest and were visible from 5 to 10 m. All markers were retrieved for future re-use.

Figure 5.1 Nest tag made from white plastic gardening label with the stem cut off and a hole made using a hole punch. Tag width is 60 mm. (Photo: L.J.H. Garrett).

5.3.3 Eggs

Marking eggs allows identification of nests should nest markers be removed. We used non-toxic permanent Sharpie^{TM} marker pen for marking eggs, which has been successfully used in other studies with no adverse effects (e.g. Frederick & Collopy 1989; Brooks *et al.* 2014). We used dark blue (n = 60), black (n = 201) and purple (n = 5) coloured fine tipped non-toxic marker pens. We assessed the nesting pair's reaction to numbered eggs and also the longevity of the marks.

5.3.4 Adult birds

Incubating adults were captured using a telescopic long-handled, rubber net fish landing net (Agility trout net, Shakespeare, UK, 80 x 12 x 10cm; Fig. 5.2a). Unique BTO metal rings were used to identify individual adults. Permanent non-toxic Sharpie^{TM} marker pen on the side of the breast (Fig. 5.2b) was used to reduce disturbance to the breeding colony by enabling rapid assessment of whether incubating adults had already been sampled. Sooty terns share incubation and change over approximately every four to seven days on Ascension Island (Ashmole 1963). A small (approximately 2 cm × 2 cm) patch of colour was applied to the white feathers on one side of the breast which were visible from 5 to 10 m. The first bird marked with blue pen (n = 1) became highly agitated, looking at the coloured patch and excessively preening the marked feathers. Subsequent use of green pen resulted in no such behaviour (n = 421).This may have been due to the green pen being of similar colour to the bird's faecal deposits, which were regularly observed staining the body plumage. Blue pen could have been too similar to their black plumage markings, which has been found to affect social dominance. For example experimentally dying the heads of Gouldian finches *Erythrura gouldiae* to mimic the black morph altered dominance hierarchies (Pryke & Griffith 2006). We assessed the effects of marking sooty terns by monitoring the behaviour of birds immediately after release. We recorded any signs of behaviour that were different from those expected under normal ringing and handling conditions when birds were not marked with permanent marker (which were familiar from ringing and re-trapping efforts carried out by the same researcher during the previous breeding season in May 2014 and the present study period, n = > 500 individuals). These included: excessive levels of agitation and preening of the marked area and an extended period before the bird returned to its nest.

Figure 5.2 a) LJH Garrett about to capture an incubating adult sooty tern with a fish landing net on Ascension Island, 2015. (Photo: K. Mullin). **b)** Adult sooty tern marked with green permanent marker on the breast to distinguish sampled individuals and prevent recapture during the 2015-2016 breeding season on Ascension Island. (Photo: L.J.H. Garrett).

5.3.5 Chicks

As newly hatched chicks’ tarsi were unable to accommodate conventional rings (tarsus circumference was too thick and length too short), temporary, flexible leg flags were used. They were constructed using 6 mm lengths of biodegradable plastic drinking straw (5 mm diameter) and PVC insulating tape (19mm wide, colour: green and yellow stripe; Fig. 5.3a). A lengthways slit was then cut in each straw, unravelled and placed in the centre of a 60 mm long piece of coloured insulating tape that had been cut in half lengthways (to approximately 10 mm width) (Fig. 5.3a, b). Leg flags were pre-cut and prepared to minimise chick handling time. The nest number was written in fine-tipped black Sharpie^{TM} permanent marker on both sides of the leg flag prior to attachment. Chicks were captured every three to six days until approximately 45 days of age (when they could fly and were considered fledged) by directly searching for individuals. Upon capture chicks were weighed using a Pesola (± 1 g, Pesola®, Light-Line, Switzerland) and white cotton drawstring bag, total head length (from base of skull to bill tip) and minimum tarsus length (Redfern & Clark 2001) using Vernier dial calipers (± 0.1 mm, dialMax, Wiha, Switzerland) were recorded, and their GPS location taken using a hand-held GPS (eTrex, Garmin, Hampshire, UK) accurate to ± 5 m. Once chick’s tarsi were able accommodate them (assessed by holding a ring to the leg to check the length was long enough and then placing the band over the leg to check if it was able to move freely up and down the leg), temporary leg flags were replaced with orange coloured polymethylmethacrylate leg bands (Interrex-Rings, Lodz, Poland) with two contrastingly coloured letters: AA, AB, AC etc. As part of a larger study, we also captured and marked any non-focal chick ‘friends’ from unknown nests that were found within two body lengths of focal chicks. We use the term friends to refer to those that chicks were associating with henceforth given that it is a more relatable term across disciplines and for consistency throughout. These chicks were ringed with Interrex blue or green coloured rings to distinguish them from focal chicks. The location of non-focal chick friends was recorded on subsequent visits, although they were not recaptured after initial ringing (to reduce processing time). Sooty tern chicks fledge at approximately 60 days post-hatch, and given that tern chick survival increases closer to fledging (Nisbet & Drury 1972), we ringed chicks with metal BTO rings (on the opposite leg to the colour ring) when they were > 35 days old.

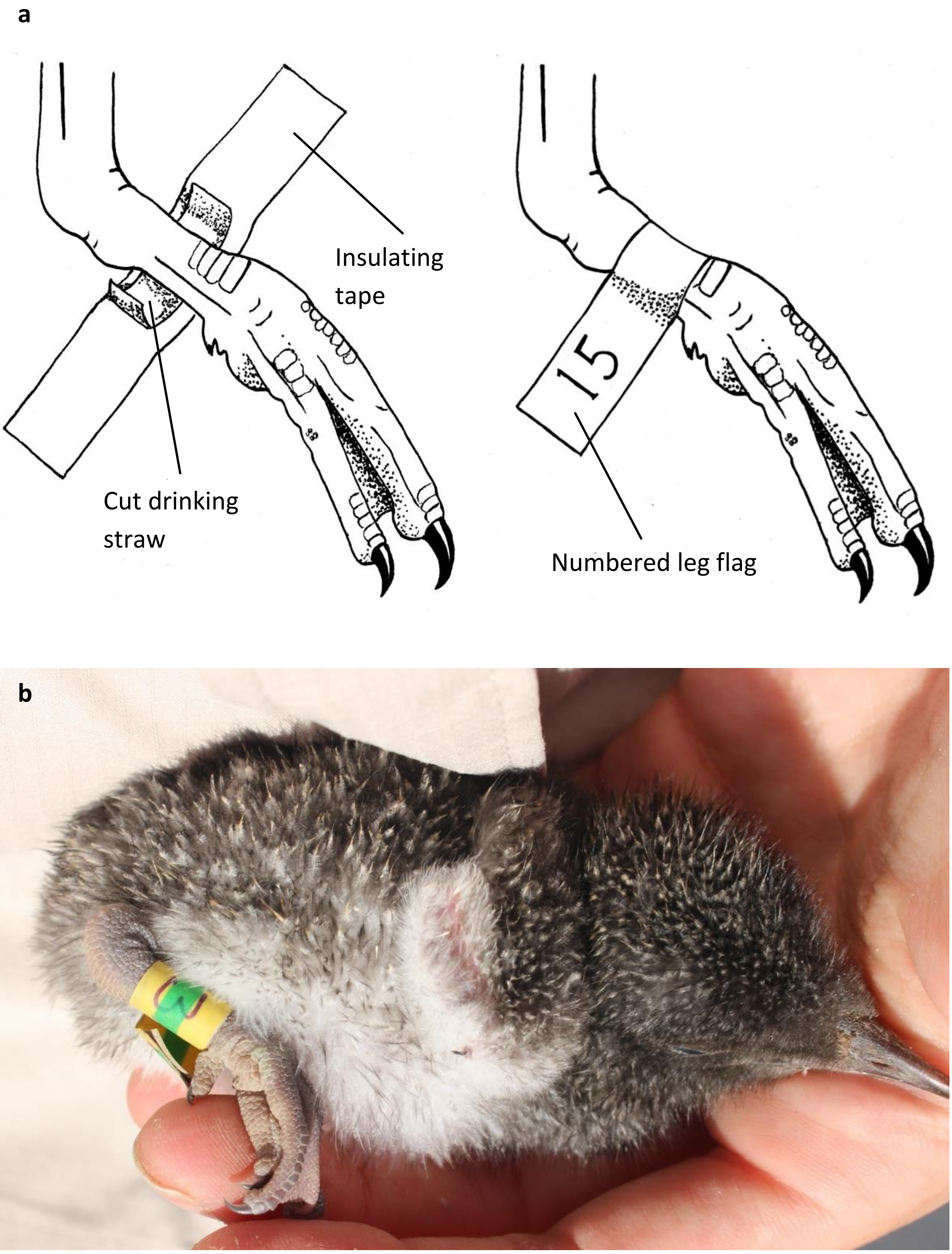


Figure 5.3 a) Diagram of temporary leg flag design. **b)** Sooty tern chick approximately four days old with temporary leg flag fitted during the 2015-2016 breeding season on Ascension Island. (Diagram and photo: L.J.H. Garrett).

We recorded the age at which tags could be changed for plastic rings as well as the tarsus length, although it should be noted that the width of the tarsus also determines whether a plastic ring can be accommodated. We assessed the effects of marking chicks by observing their behaviour immediately after tags were applied and whenever they were recaptured for signs of agitation, impeded mobility, and physical effects of the marker to the leg, for example abrasion, contusion, oedema. We assessed the effects of marking and monitoring on survivorship by comparing the local densities of tagged birds to non-tagged birds. It was not possible to measure quantitatively tagged and non-tagged chick survival given that un-marked birds were highly mobile and were not individually identifiable.

5.3.6 Data analysis

We analysed the ranging behaviour and movements of chicks during crèching stages by calculating the maximum distance travelled by chicks from their original nest sites. We also modelled the effects of age on chick movement. To assess the likely turnover of chick friends from unknown nests we calculated the cumulative number of rings issued and compared this to the total number of ringed friends from unknown nests remaining alive in the population over time. Chick friends from unknown nests were not included in any other statistical analyses given that they were captured at varying ages and their initial nest location was unknown, potentially biasing sampling effort.

We estimated nesting success using the Mayfield method (Mayfield 1961; Mayfield 1975). Our chick movement data fitted a Poisson error distribution and we adjusted for overdispersion by fitting a Quasi-Poisson General Additive Model (GAM) where the variance is given by the dispersion parameter multiplied by the mean (Zuur *et al.* 2009). Individual ID was included as a random effect to account for multiple captures of the same birds. The GAM analyses were performed in R version 3.6.0 REF for R and the packages ‘AER’ (Kleiber *et al.* 2008), ‘mgcv’ (Wood 2011) and ‘ggplot2’ (Wickham 2016) for visualization.

5.4 Results

5.4.1 Nests

None of the 266 nest tags used during the study were lost. Some tags that were attached to rocks were moved slightly (presumably by one of the nesting pair) from their original position, but as eggs were marked, the correct nest was easily identified.

5.4.2 Eggs

We did not observe any impacts of marking eggs on the bird's behaviour. Different coloured pens had different longevity in terms of readability. Purple pen faded within five days and became completely illegible, whereas black and dark blue pen remained legible until hatching (> 20 days) and in some cases for over a month after the hatch date, where eggs failed to hatch but were still tended by adults (>30 days).

5.4.3 Adult birds

Marking 422 adult birds with permanent marker pen on the breast enabled us to capture 106 breeding pairs without disturbing birds that had already been captured. All monitored breeding birds returned to their nests after handling and none abandoned their nesting attempt in the days that followed. Breeding attempts that failed during incubation were either due to depredated eggs or failed to hatch with an adult still incubating the egg. Marks were still visible after > 20 days.

5.4.4 Chicks

A total of 124 chicks were fitted with temporary leg flags and a further seven chicks were ringed initially with plastic colour rings given their tarsi were able to accommodate them. Temporary leg flag loss was relatively low (4%), with five flags found in-tact (closed) at nest sites, presumably having slipped off over the foot. This was likely related to tarsus size, as those that fell off had smaller mean tarsus length upon application than those that stayed on (Table 5.1). However, the minimum size that tags remained on was smaller than the minimum length that they fell off. Mean tarsus length at which temporary leg flags were exchanged for plastic colour rings or those focal chicks that could accommodate colour rings after hatching was 19.2 ± 0.1 mm with the average age being > 6 days old (Table 5.1). One chick retained its temporary leg flag for 31 days as it remained undetected due to late season vegetation growth in the nest site vicinity. There were no observable behavioural or physical impacts of the leg flags or plastic rings on any of the chicks.

Table 5.1 Mean tarsus length of focal sooty tern focal chicks on application of temporary leg flags by those that subsequently were lost and those that remained intact during the 2015-2016 breeding season on Ascension Island. Mean tarsus length and age of chicks at the time temporary leg flags were changed or large enough for plastic rings is also given.

Variable	Mean ± SD	Min.	Max.	n
Tarsus length when flag retained (mm)	17.0 ± 0.9	14.7	19.0	119
Tarsus length when flag lost (mm)	16.1 ± 0.4	15.7	16.8	5
Tarsus length when plastic ring accommodated (mm)	19.2 ± 0.1	16.8	-	94
Age of chick when plastic ring accommodated (days)	6.1 ± 0.4	1.0	-	94

Chicks moved away from the nest site at four days old (n = 98). The average maximum distance chicks aged ≥ four days old travelled from their nest site was 5.4 ± 5.5 m and the maximum distance travelled from a nest was 25.9 m (Fig. 5.4). However, distance travelled varied with age, with chicks found further from their nest sites with increasing age. Distance travelled and individual id were significant effects in the GAM analysis, accounting for 49% of the model deviance (adjusted r^2 = 42%; Fig. 5.5). The significant effect of individual suggests there was variation between individuals. Overall, the average distance travelled from nest sites by age class remained within 10 m (Table 5.2).

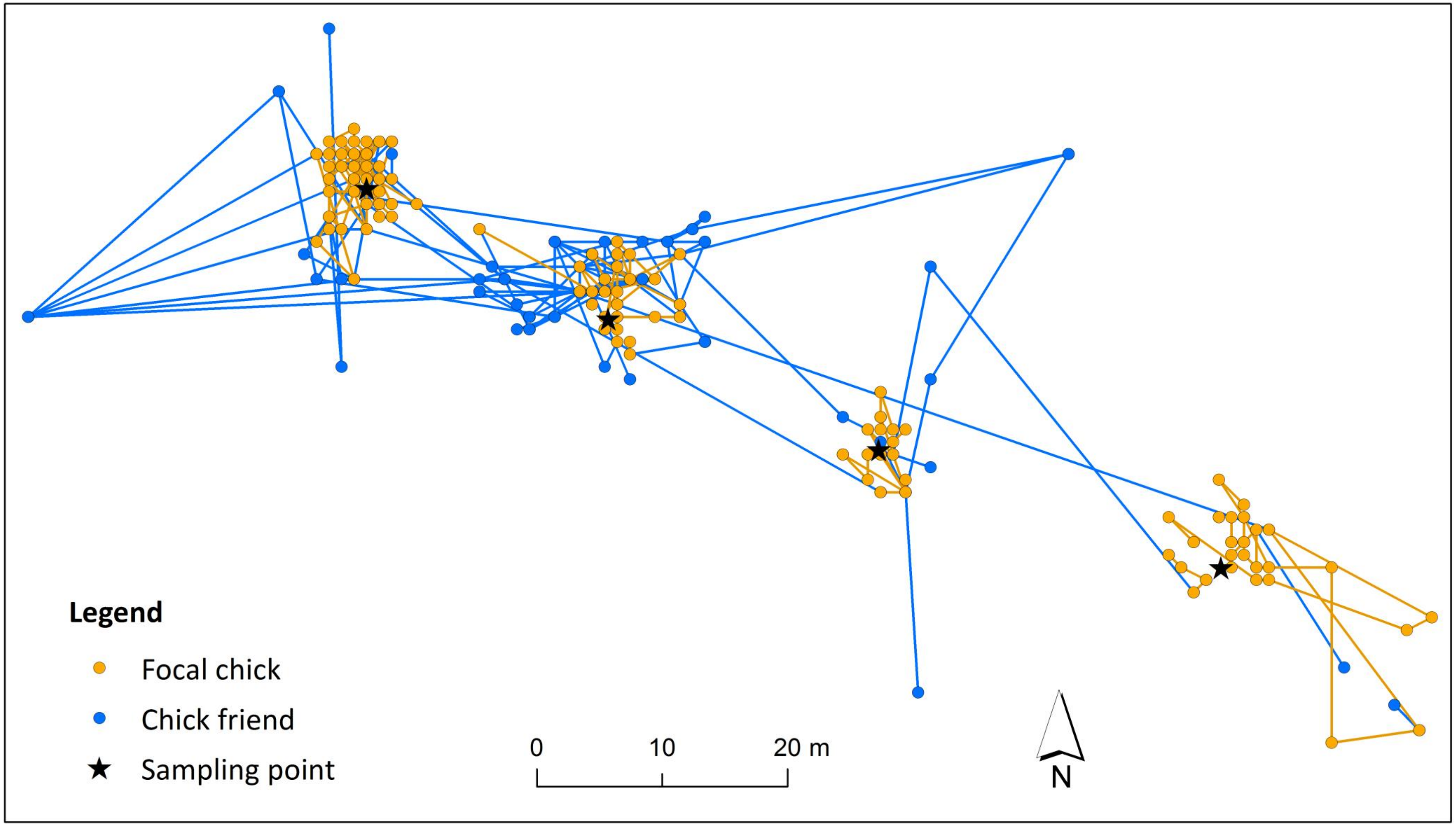


Figure 5.4 An example of sooty tern chick movement behaviour from four sampling points along one transect during the 2015-2016 breeding season on Ascension Island. Points represent sightings of focal chicks (from known nests) and chick friends from unknown nests. Lines between points represent movement between captures. Stars represent the centre of sampling points.

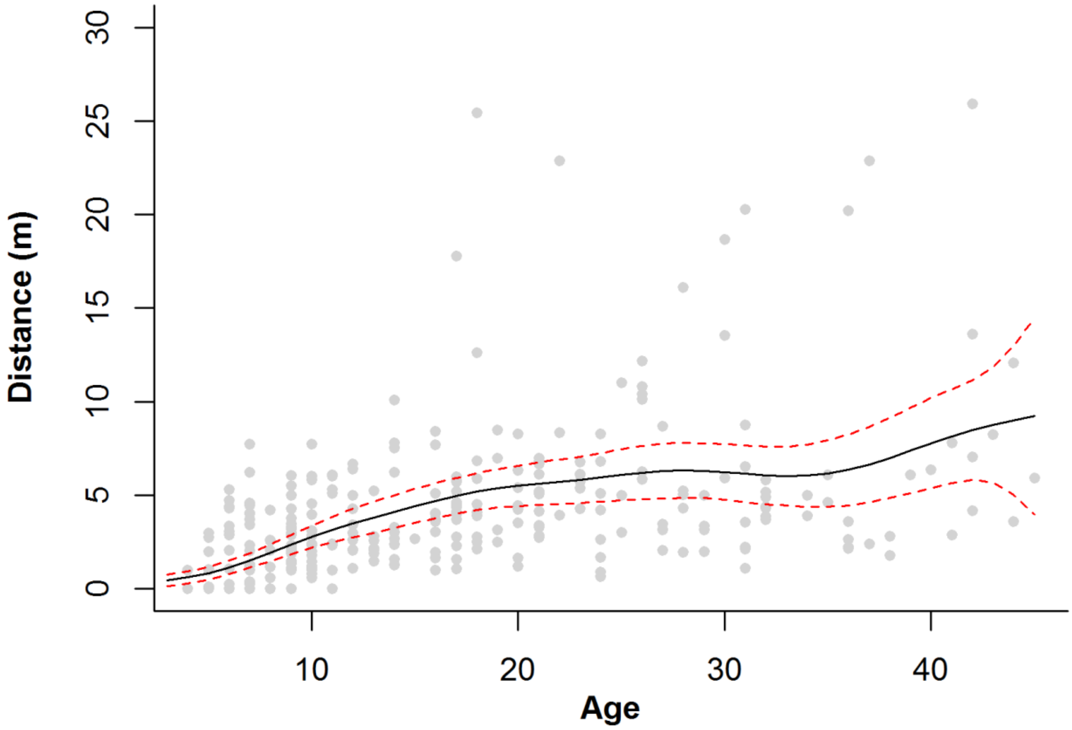


Figure 5.5 Distances travelled by sooty tern chicks from their original nest sites by age during the 2015-2016 breeding season on Ascension Island. The solid line is the GAM model fit, and the dashed red lines are the 95% pointwise confidence bands. Grey points are the raw data.

Table 5.2. Mean distance travelled by focal sooty tern chicks from their original nest sites by age class on Ascension Island during the 2015-2016 breeding season.

Age class (days)	Mean distance (± 1 SD) (m)	n
4-10	1.5 ± 1.8	115
11-15	3.3 ± 2.2	59
16-20	5 ± 3.8	63
21-25	6.4 ± 4.4	30
26-30	6.2 ± 5.1	26
31-35	6.2 ± 6.7	14
35-45	8.9 ± 6.6	11

Based on numbers of chicks of similar size in the vicinity of marked chicks, survival was representative of un-marked chicks. In general survival was low with only 18 focal chicks reaching fledging age. Daily survival rate (including pre incubation stage) was 0.97, with a total survival probability of 0.15 fledglings per nestling. Causes of death were often difficult to determine, although Ascension Island frigate birds were witnessed depredating un-marked chicks, and there was also evidence of predation by black rats on corpses (see Hughes 2014) for detecting rat predation). Starvation was also a likely cause of death in some cases, with chicks found with no evidence of predation but with poor muscle scores and protruding keels. Although it could be possible that some chicks went undetected, large areas were searched throughout the nesting grounds.

The total number of ringed chick friends from unknown nests was 285. The average group size was 5.29 ± 7.24 (range: one to 35) and the average number of friends from outside of the sampling points was 3.52 ± 6.30 (range: zero to 31). The average number of focal friends was 0.78 ± 1.24 (range: zero to five). The number of friends ringed from unknown nests continued until focal chicks reached fledging age, with the peak number of friends from unknown nests ringed between 15 and 17 days of hatching (Fig. 5.6). However, the number of friends from unknown nests that were still present in the population differed markedly from the number of rings issued after approximately20 days, when mortality increased.

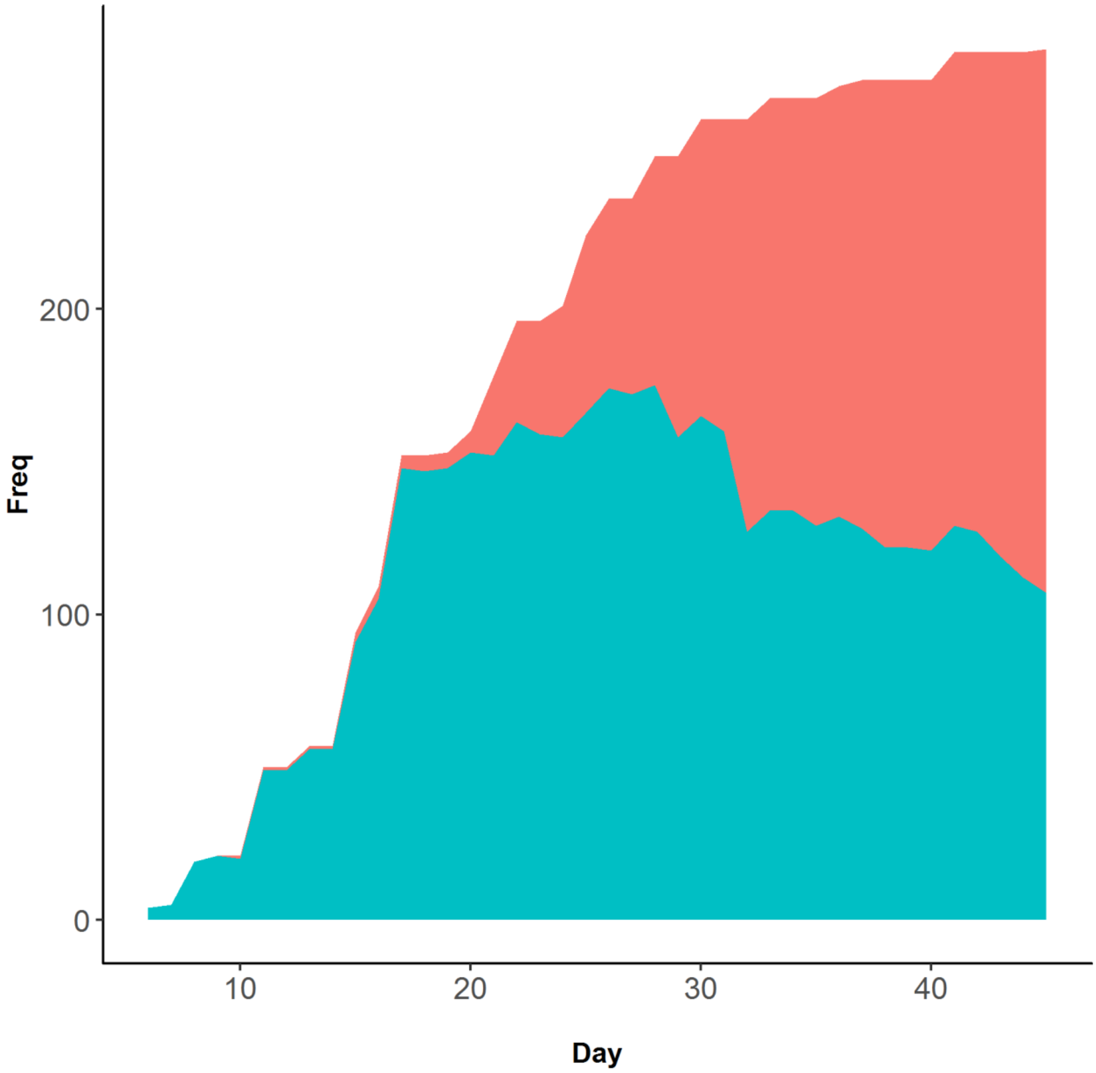


Figure 5.6 Frequency plot showing the cumulative number of ringed sooty tern chick friends from unknown nests (red) and the number of ringed friends still alive from unknown nests (blue) by the number of days post hatch at the sampling point location where they were first ringed. Data were collected during the 2015-2016 breeding season on Ascension Island.

5.5 Discussion

Our marking and monitoring methods were successful in estimating breeding success to fledging of a precocial seabird nesting in dense aggregations with no observable behavioural or physical impacts. Previous studies have stated the need for methods such as fencing to study species with precocial offspring (Brooks *et al.* 2014), but they often come at a cost, with adverse impacts such as kleptoparasitism (Nisbet & Drury 1972; Stienen & Brenninkmeijer 1999), injury (Nisbet & Drury 1972; Shealer & Jeffrey 2000) and limiting feeding behaviour (Nisbet & Drury 1972). Other methods such as tracking devices can be expensive and also negatively affect feeding, breeding success and survival (Lameris & Kleyheeg 2017). Our study showed that chicks can be monitored with minimal human disturbance (we checked chicks every three to five days) whereas the use of radio tags required checking chicks twice per day in some cases (Whittier & Leslie 2005).

5.5.1 Nests and eggs

Marking eggs with permanent marker pen was highly effective for identification purposes, as noted in previous studies (Brooks *et al.* 2014). However, we found that the colour of the mark impacted the longevity of identification marks. Both dark blue and black were the most effective lasting > 30 days, whereas purple marker pen became illegible in a short space of time (< five days). This was most likely due to the hot climate causing for example photodegeneration of marks through prolonged exposure to direct sunlight. Our nest markers were inexpensive to make and easy to install and re-use, with all nests being relocated. Compared to other methods such as painting directly on the substrate (Diamond 2013), or hammering in large stakes (Fern *et al.* 2016), the environment impacts (e.g. chemical deposition and substrate disturbance) and logistical effort required were low.

5.5.2 Adults

Marking the breast with permanent marker pen allowed easy identification of individuals on subsequent visits and prevented unnecessary additional disturbance to incubating adults that had been previously captured. Some birds had also been ringed during previous mark-recapture efforts and thus merely sighting a metal ring would not have precluded that the individual had been sampled during the present study. Although temporary, marks lasted for > 20 days which is probably due to plumage not being regularly exposed to sea water given sooty terns are not diving birds.

5.5.3 Chicks

We found that chicks moved away from their nests at approximately four days post-hatch. The average age that temporary leg flags could be replaced with lettered plastic rings was six days old. Therefore, the development of an effective marking method to enable identification of individuals before they leave the nest is crucial, given adult sized rings can only be used after they have left the nest. Our temporary leg flags remained in-tact for up to 31 days with no observed physical or behavioural effects. Other temporary leg flag designs have resulted in constriction of the leg as the chicks grow (Cavanagh & Griffin 1993), but ours allowed for growth whilst remaining in place. Tag loss was low with 5 out of 124 tags slipping off over the foot, which could be prevented by ensuring that insulating tape closes closely around the leg. Directly searching for chicks as opposed to other methods for monitoring precocial chicks such as fencing, allowed chicks to perform natural movement and aggregating behaviours with no observed changes to predation risk. We checked areas for chicks every three to five days, and most chicks remained within 5.4 ± 5.5 m of the nest, although some did travel up to 26 m. Chick movement increased with age (Fig. 5.5), although remained on average within 10 m of the nest at the upper age range (35-35 days post-hatch).

Once chicks had left the nest they formed social aggregations with an average group size of 5.29 ± 7.24 and groups of up to 35 individuals in some cases. Focal chicks formed associations with chicks from outside of sampling areas (i.e. >3 m^2) traveling up to 26 m from the nest, and on average 85% of groups were made up of friends from unknown nests . There was also a high group turnover as indicated by the increasing number of rings issued to friends from unknown nests, whilst those that remained alive declined (Fig. 5.6). Methods that restrict chick movement could have detrimental impacts on chick social behaviour by reducing their ability to form social groups of optimum group size, something that has previously been overlooked in the literature. Often chicks (both marked and unmarked) were found huddling under dried vegetation and rocky overhangs, most likely as a predator avoidance strategy. Chicks that are confined to an area with insufficient cover may increase competition and aggression. It could also alter predation risk wither decreasing it by predator exclusion, or increasing it by reducing chicks feeling ability (Stienen & Brenninkmeijer 1999). Survival rates appeared representative of the population, and in general were low (0.15 fledglings per nestling) especially compared with previous estimates for this (0.31 fledglings per nestling (Hughes 2014) and 0.44 ± 0.21 fledglings per nestling for other sooty tern populations (Schreiber *et al.* 2002). Causes of chick failure included predation from endemic Ascension frigatebirds and black rats. It is unlikely, given the location of temporary leg flags and plastic rings, that marking chicks increased visibility to aerial (Ascension frigatebirds) or ground dwelling (black rats) predators given that chicks < six days old (whilst wearing leg flags) and whilst huddling under cover mainly had their legs tucked under the body. Plastic rings often became coated in faecal deposits, reducing visibility. Starvation, indicating limited food resource availability, was also noted and could have exacerbated predation levels of malnourished chicks that may be more vulnerable to predation (Scopel & Diamond 2017). Chick ranging behaviour may vary depending on mortality rates, for example chicks may travel further distances to form groups with those that remain alive in breeding seasons with high levels of mortality. Further work is needed to investigate the influence of factors such as predation rate on chick movement behaviour and social group formation.

5.5.4 Conclusions

We present several cost-effective and non-invasive methods for monitoring seabird breeding success, especially those with precocial young. Our findings indicate that chicks are highly mobile travelling up to 26 m from the nest, forming groups of up to 35 individuals and a high friend turnover, with new friends from unknown nests accrued up until fledging age. Our chick marking and monitoring methods had no observed physical or behavioural effects on chick movement or predation levels. We encourage other researchers who have developed field methods in this area to publish them in detail as they could be extremely useful for other researchers working with free-living nesting birds. In doing so we can continually improve field practices and work towards the development of the most efficient and least invasive methods to the species targeted.

Chapter 6

Friends with benefits: The importance of chick sociality for survivorship in a precocial seabird

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LJHG collected and analysed the data and wrote the manuscript. SJR, JPM, JPS and JKC assisted with writing the manuscript.

6.1 Abstract

Species with socially aggregating young, that form crèches, are found through-out the animal kingdom. For many taxa, an individual's social environment can have fundamental consequences for key ecological and evolutionary processes. However, the social structure of offspring tends to be overlooked, with any consequences of offspring sociality only included as a function of adult reproductive success. Offspring benefit from reduced adult aggression, predator protection and increased thermoregulation. Here, we combine a network approach with likelihood estimates for daily survival to explore the social structure of precocial seabird chicks. Our findings indicate that chick associations or 'friendships' change over time, with the benefits of maintaining social connections being age-dependent and 'de-friending' occurring when the costs of such relationships outweigh any potential benefits to survival. We show that chick sociality, together with age and habitat cover, have important consequences for their daily survivorship, and ultimately how it might shape the breeding success of colonially breeding species.

6.2 Introduction

Individual variation in sociality can have important fitness consequences through mechanisms such as the transmission of information, the spread of diseases, and predator avoidance (reviewed by Krause *et al.* 2007), and is thus subject to selection (Ohtsuki *et al.* 2006). The study of offspring social structure, i.e. animals undergoing growth and development, however, has been relatively overlooked (but see (Berman 1982; Nuñez *et al.* 2014). Consequences of offspring social structure, are often only accounted for indirectly as measures of adult breeding success and are often excluded from social network analyses on the assumption that their networks mirror those of their parents (Sundaresan *et al.* 2007). In species with dependent young that exhibit high levels of sociality during early life stages, have long maturation times and exhibit social learning, social structure may have important survival and fitness consequences (Stanton & Mann 2012). For example, network structure of crab spiderlings *Diaea ergandros* containing non-relatives experienced disrupted group dynamics and exhibit reduced overall survival compared with those containing more closely related young (Ruch *et al.* 2014). In great tits nestling social dynamics affects adult food provision, and thus fitness outcomes, with females providing more food to broods that display higher cooperation and network connectivity (Royle *et al.* 2012). Survival of male bottlenose dolphin *Tursiops sp.* calves (pre-weaning) was also affected by social network structure, with calves that had stronger associations with weaned juvenile males (> 3-4 years old and pre-sexual maturity < 10 years old) having lower survival, presumably linked to increased stress (Stanton & Mann 2012).

Offspring social aggregations (also known as crèches), are defined as offspring that are left alone while parents forage, containing both kin and non-kin from multiple parental pairings. Offspring aggregations are found in birds (Davis 1982; Evans 1984; Seddon & van Heezik 1993), reptiles (Magnusson 1980) and mammals (Levy & Bernadsky 1990). The benefits of forming such aggregations include reduced adult aggression directed towards offspring of other pairs (Tourenq *et al.* 1995; Le Bohec *et al.* 2005) and predation (Tourenq *et al.* 1995; Le Bohec *et al.* 2005; Wilson 2009), and increased thermoregulation (Evans 1984; Black *et al.* 2016). Conversely Velando (2001) found no evident benefits to European shag *Phalacrocorax* *aristotelis* offspring during post-fledging when they aggregate and are provisioned by adults for up to one month. Rather they suggested that crèching behaviour acts as a social hub, facilitating information transfer on the location of foraging grounds (via the information centre hypothesis (Ward & Zahavi 1973) and opportunities for pair formation in this species. A similar suggestion has been proposed by Dentressangle *et al.* (2008) for Dalmatian pelicans *Pelecanus crispus* in which social rank and competitive skill development are likely outcomes of such group formation.

The structure of social networks during development also provides valuable insights to life-stage determined survival. For example, Turner *et al.* (2017) investigated the change in social structure from early life to adulthood independence in the spotted hyena *Crocuta crocuta*. Offspring social dominance and sex had consequences for social development and network position as adults, with females having more social connections than males. High-ranking females initiated more aggressive acts and received more affiliative acts than did females of other rank, with rank thought to affect reproductive success. Velando (2000) also found offspring development had an important impact on social rank, with chicks that hatched and joined crèches earlier benefiting from higher dominance that resulting in them suffering fewer fish thefts than their lower ranking associates.

Seabirds are an ideal species to investigate offspring social dynamics as they are long-lived, have long maturation times and a number of species have offspring that form large social groups. Half of the 14 families of waterbirds have socially aggregating offspring, although most studies have primarily focused on penguins Sphensciformes (see Wilson 2009), pelicans Pelecaniformes (Evans 1984) and gulls Laridae (Chokri *et al.* 2011). Few studies have directly assessed the influence of social structure on fitness and survival (but see (Silk *et al.* 2009; Frère *et al.* 2010b; Lehmann *et al.* 2015), and few have combined social structure with ecological (e.g. habitat types) and demographic (e.g. breeding density) parameters to examine how they impact survival. Cohort size, as determined by the total number of offspring produced, has a positive effect on offspring survival in some studies (reviewed by Maness & Anderson 2013), indicating that social structure might play an important role in species with socially aggregating young.

Here, we describe the social environment of sooty tern chicks through an examination of their social connections (hereafter ‘friends’), how these vary over time, whether these friendships are stable, and the impact of connectedness on daily survival during the stage when chicks are able to form associations until fledging. To do this, we explore the variation in chick friends together with friendship stability (using lagged association rates) over time. We then use social network analysis (SNA) to measure chick sociality, specifically using weighted degree (the number and strength of associations) to input into survival models along with other factors thought to influence chick survival (e.g. age, population size, nest density and habitat cover). Specifically, we have three main study questions: 1) Does offspring social group size vary with age? 2) Are offspring friendships stable over time? 3) What are the impacts of offspring social structure on survival? Thus, we provide a multi-faceted approach to explore the social environment of a wild seabird species that aggregates in large breeding colonies and that also forms social aggregations during offspring development. The overarching aim is to understand the importance of sociality early in life and how it might ultimately shape the breeding success of colonially breeding species.

6.3 Methods

6.3.1 Study system

We monitored sooty tern chick social structure and survival on Ascension Island, South Atlantic (7°56’S, 14°22’W), a 97 km^2 volcanic island, between 25th October 2015 and 9th March 2016. Sooty terns usually lay one egg per nest and are unlikely to relay should their breeding attempt fail (Ashmole 1963). Both parents share incubation and chick rearing (Dinsmore 1972). Sooty terns are semi-precocial and after hatching chicks are brooded by alternate parents for several days before they are left alone while both parents forage at sea (Ashmole 1963). It is at this time that they leave their nests and participate in aggregating behaviour. Fledging occurs approximately 60 days post-hatch. Sooty terns nest at two main breeding sites on the Ascension Island (Mars Bay and Waterside; Fig. 1.1) which is designated an Important Bird Area (IBA) (‘Wideawake Fairs’ IBA SH009) (BirdLife

International 2019). At the time of study estimated total population size was 194,407 ± 14,327 pairs (± 95% confidence intervals). In order to minimise the risk of abandonment which is more likely during the early settlement period (LJHG pers. obs.), we monitored sooty terns a minimum of seven days after egg laying and prior to hatching. Breeding pairs were sampled along five 90 m transects placed at random between study sites. Four sampling points were studied along each transect. Points were located at 0, 30, 60 and 90 m along each transect. In total 17 points were surveyed (one transect only had one point due to the rest of the cluster hatching before nests could be surveyed). Where possible the closest 15 nests (hereafter 'focal nests') to each sampling point were monitored in roughly a 3 m^2 area (total nests monitored = 265).

6.3.2 Field observations

Adults were captured using handheld fish landing nets, ringed with British Trust for Ornithology (BTO) rings and morphometrics including body mass, wing length, tarsus, gonys and total head length, were taken to assess adult fitness. Where possible both breeding adults were captured at a nest. As sooty terns are sexually monomorphic sex was confirmed using microsatellite sexing for individuals where blood samples were taken (n = 287), see Chapter 4. At hatching focal chicks (from focal nests) were marked with temporary leg flags until they were large enough to accommodate plastic rings (see Chapter 5). Focal chicks were given orange polymethylmethacrylate leg bands (Interrex-Rings, Lodz, Poland) (Fig. 6.1a).

To study chick social structure we visited chicks every three to six days, when focal chicks were captured along with any 'friends', which included chicks from unknown nest locations, who were within two body lengths of them. Morphometrics were recorded of focal chicks to calculate growth rate. Chick friends from unknown nests were fitted with green or blue Interrex leg bands to distinguish them from focal chicks (Fig. 6.1a) but morphometrics were not taken from them to reduce processing time. Friends from unknown nests were not captured on subsequent visits, but were recorded as present or absent. On first capture we estimated the age and hatch dates of non-focal chicks using plumage stages as given by Hughes (2014). For detailed methods see Chapter 5. Chick habitat cover, either under the cover of overhanging rocks, in rock crevices, under vegetation or open ground was also recorded (Fig. 6.1b) together with their GPS location using a hand-held GPS (eTrex, Garmin, Hampshire, UK) accurate to ± 5 m. Chicks were monitored until they were able to fly. Chicks were considered dead if a carcass was recovered or they had not been seen alive after two visits.

Figure 6.1 a) A focal (monitored from incubation) sooty tern chick on Ascension Island ringed with an orange Interrex ring captured with a chick friend (from unknown nest location) ringed with a blue Interrex ring. (Photo: L.J.H.Garrett). **b)** Chicks found under habitat cover guarded by parents during the 2015-2015 breeding season on Ascension Island. (Photo: K. Mullin).

6.3.3 Data analysis

We collated data on factors which we hypothesised a priori may have an impact on the daily survival rates of chicks until fledging (Table 6.1).

6.3.3.1 Temporal variation in chick friends

To model whether the number of friends varied with the age of focal chicks, we fitted a generalised linear mixed model (GLMM) using the 'glmmTMB' package (Brooks *et al.* 2017) using the Tweedie family in R (R Core Team 2019). To account for the effects of chick availability we calculated the proportion of chick friends by the number of ringed chicks that were alive (and thus available to be friends with). This included non-focal and focal chicks while controlling for transect given that chicks can move between sampling points within transects (Chapter 5). We then used the percentage of friends by total chicks alive to input to the model. Thus, a percentage of 100% indicates that focal chicks were associating with all available chicks in the area at a given age. We assigned individual ID as a random effect to account for variation between individuals and fitted a quadratic function of age given the distribution of raw data. The relationship of the number of friends by age was also modelled in the same way as described above but using a negative binomial parameterization with the nbinom2 family (see Appendix 7 for outputs).

We also estimated the number of chicks that went missing (presumed dead) by age of both focal and non-focal chicks. The frequency of dead chicks was square-root transformed to meet the model assumptions, which were checked using residual plots and a global validation of model assumptions test using the R package 'gvlma' (Peña & Slate 2006). We fitted a linear model and a quadratic term given the spread of the raw data.

6.3.3.2 Friendship stability

We examined the stability of friendships over time using lagged association rates. The lagged association rate measures the change in associations between individuals over time and is calculated by the probability that two individuals will be observed together τ units of time later, given that at least one individual is observed (Whitehead 2008). Here τ was defined as the time between observation days (3 to 6 days apart), with a lagged association rate of 0.5 when $\tau = 1$ equating to a 50% chance of observing the same individuals together on the next observation day. We also calculated the lagged identification rate, or death rate (Whitehead 2008) to establish whether rates of disassociation followed the same trend as individuals being lost from the population. Lagged association rates and Jack-knife errors, used to obtain confidence intervals by removing one observation day for each resampling, were calculated in the R package 'asnipe' (Farine 2013) following (Whitehead 2008). Lagged association rates were then compared to what would be expected by chance using a null model. This was created using 1,000 random permutations performed with swaps between groups within observation days. Thus, the number of individuals and the number of groups that were observed on each observation day were retained, but swaps of individuals between groups were allowed. As sampling transects were visited on different days, this did not result in non-feasible random associations between individuals.

Table 6.1 Description of variables used to model daily survival rate of focal sooty tern chicks until fledging on Ascension Island in 2015-2016. Reasons and predictions for variable inclusion in the models are also outlined. Variables in bold type were selected for input to MARK after checking for co-correlation (see section 6.3.3 for further details).

Variable name	Description
Pop	Population size of colony cluster at the nest site location, calculated as total area × no. nests per m^2. The number of chicks present in an area may impact predator encounter rate (Smith & Wilson 2010). We predict that chick survival will increase with population size given increased predator detection through the many eyes hypothesis.
Tran	Individual transect ID (n = 5). Included to account for potential variation in habitat parameters or other location based differences.
Volume	Egg volume, calculated using the following Hoyt (1978): $\text{Volume} = K_v \cdot LB^2$ Where L = Length, B = Breadth, K_v = volume coefficient (which is a function of egg shape). K_v was taken as 0.51 from Hoyt (1979). To convert to cm^3 we divided the answer by 1,000 (Sorensen *et al.* 2009). For nests with missing egg volumes (n = 2), we used mean-cantering

	to standardise the missing values without affecting the population mean. Minias *et al.* (2013) found egg size and hatch date were the best predictors of chick survival in whiskered terns, with larger eggs and earlier hatching dates increasing success rates.
Degree	Mean weighted degree or the expected total association rate per individual calculated using social network analysis in the R package ‘asnipe’ using the simple ratio index (SRI) (Farine 2013). We predicted a positive effect of weighted degree on chick survival given the benefits associated with group association, such as predator evasion (Dall *et al.* 2005)and social learning (Templeton *et al.* 2011).
Group	The absolute number of individuals observed in each group of associating chicks. This measure accounts for demographic processes that may be acting upon survival.
Growth	Chick growth rate, estimated for each chick as the linear regression coefficients of body mass on age (adjusted $r^2 = 0.77$, $n = 412$, $p < 0.0001$). Growth rate reflects parental foraging success and also food abundance, which may vary temporally.
Cover	Percentage of times captured found using habitat cover, such as rock crevices or vegetation. We predicted that habitat cover would reduce detection by predators and increase survival.
Date	Date taken as the number of days after the first day of the breeding season, taken as 4th December 2015. Timing of lay dates is a good predictor of reproductive success, with earlier nesting birds having higher reproductive success (Ramos 2002; Antolos *et al.* 2006).
Age	Age was taken from hatching date as day 1. Several studies have found a positive relationship with chick age and survival (see meta-analysis by Colwell *et al.* 2007).
Precip	Precipitation as measured by daily rainfall (mm) measured at the airhead (see Fig. 2.1) (supplied by Met Office, Ascension Island Base, British Forces South Atlantic Islands). Adverse weather may reduce chick survival through lowering body condition of chicks and adults (Tulp & Schekkerman 2006).
Area	Area of colony cluster at the nest site location (m^2), calculated using ArcGIS 10.2 (ESRI 2013). Linked to population size (see above).
Density	Nest density at each sampling point per m^2. Coulson and White (1960) found that neighbour density affected synchrony in kittiwakes *Rissa tridactyla* and more synchronous breeders had higher reproductive success (Darling 1938).
Site	Breeding site: Mars Bay or Waterside (Fig. 1.1).

Bodycon	An index of adult body condition, calculated by combining wing length, headbill and gonys in a PCA (Forero *et al.* 2001). PC1 had the highest correlation with the various variables accounting for 58% of the variance. We then extracted the residuals from the linear regression of body mass on PC1 scores (adjusted $r^2 = 0.17$, $n = 417$, $P < 0.0001$). We used random numbers to select one parent for nests where both parents were captured and measured. Parental body condition had a positive effect on northern lapwing *Vanellus vanellus* chick survival (Blomqvist *et al.* 1997).
Dist	Distance of nest site location to the edge of the colony cluster (m), calculated in ArcGIS 10.2 (ESRI 2013). The centre-periphery hypothesis is based largely on the assumption that predation will be greater on the edge of a colony than in the centre (Hamilton 1971). Colony position in relation to the centre-periphery gradient has been found to influence breeding success in several colonial bird species (Götmark & Andersson 1984; Antolos *et al.* 2006; Minias *et al.* 2013).

6.3.3.3 Daily survival estimates

To estimate daily survival rates of focal chicks we used the nest-survival model (Dinsmore & Dinsmore 2007) in the program MARK (White & Burnham 1999). Chicks were considered successful (i.e. fledged) when they reached 45 days old, as this is when they could fly and thus difficult to catch (LJHG pers. obs.). We only included data from chicks that were at least four days old) at which stage they could form friendships. We used multi-colinearity tests to check for co-correlation between variables excluding temporal predictors (age, date and precipitation) and sequentially removed covariates with the highest variance inflation factor (IF), greater than 3 (Zuur *et al.* 2010) in the R package 'usdm' (Naimi 2015). This left six remaining predictors which were input to MARK (Table 6.1). We also included group size (which was co-correlated with degree) to account for potential demographic processes that may underlie survival. We used a hierarchical modelling approach to select the most parsimonious model (Hood & Dinsmore 2007) using AIC$_c$ model selection (Burnham & Anderson 2002). First, we assessed sources of temporal variation by constructing models with constant daily survival, a linear time trend and a quadratic time trend for both age and date separately. We also set daily rainfall as a temporal predictor of survival. We combined age and date into an additive model to test the hypothesis that they performed better than they had separately. To the temporal model which performed best we then added each covariate singly (Smith & Wilson 2010). We also used ΔAIC*c* to distinguish which of social (degree) or demographic (group size) effects best explained daily survival; the variable that performed best was taken forwards. From those models that had a higher ΔAIC_c than the best temporal model alone we combined them into additive models. Competing models that had $\Delta AIC_c \leq 2.0$ were considered as the most parsimonious models explaining daily survival rate. We also ran a global model including all covariates. Models that contained covariates with β-estimates whose confidence intervals crossed zero, indicating a weak effect (Barber-Meyer *et al.* 2008), were excluded.

6.4 Results

Of the 265 sooty tern nests monitored, 98 chicks survived to four days post-hatch. Only 18 nests produced chicks that reached fledging age (i.e. 45 days).

6.4.1 Temporal trends in chick friends

The number of chick friends when controlling for the number of possible friends varied with chick age (Table 6.2). There was high variation in the percentage of friends at all age ranges (Fig. 6.2). However, there was a significant quadratic effect of age in the model (Table 6.2). As chicks aged they formed larger groups (Fig. 6.2). At approximately 28 days of age the percentage of friends peaked and then declined as chicks approached fledging. This relationship was similar to the absolute number of friends by chick age (Appendix 7).

Table 6.2 Results of a negative binomial zero-inflated mixed model (glmmTMB package, R Version 3.4.2) examining the percentage of chick friends controlling for chick availability by sooty tern chick age. The model included a quadratic function of age and chick ID as a random effect. P: * < 0.001.

Predictor	Coeff.	SE	Z	*P*
Intercept	-1.61	0.37	-3.00	< 0.001*
Age	0.21	0.03	6.57	< 0.001*
Age^2	-0.00	0.00	-4.68	< 0.001*
Zero-inflation model	-1.68	0.40	-4.17	< 0.001*

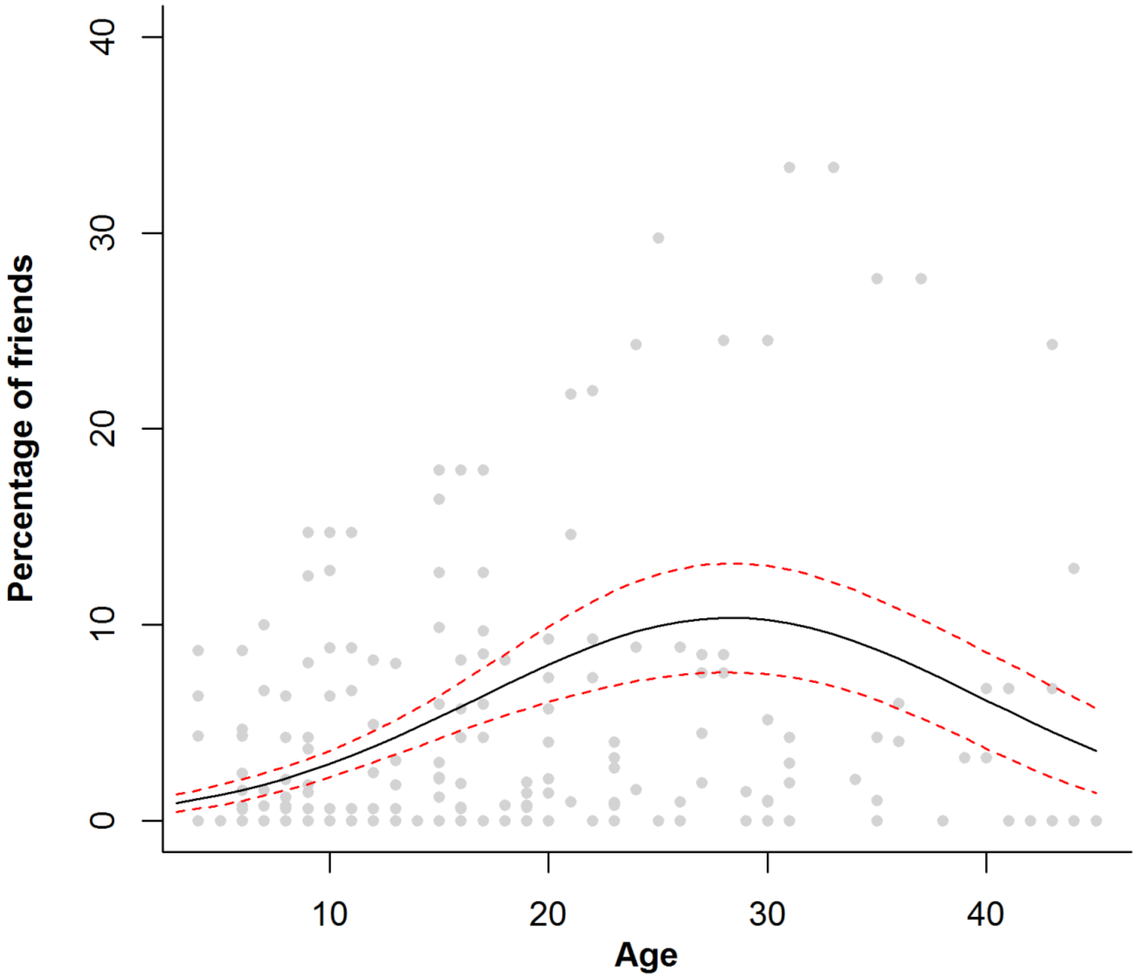

Figure 6.2 The percentage of focal sooty tern chick friends in relation to the total number of chicks alive by age on Ascension Island in 2015-2016. A percentage of 100% indicates that

focal chicks are associating with all available chicks in the area. Grey dots represent the raw data. The solid black line is the prediction curve from a zero-inflated mixed model regressing the number of friends against chick age with a quadratic function of age. Dashed red lines are the 95% confidence intervals. The random effect is not included in the model for visualization purposes. n = 297 observations.

There was a significant positive effect of age on the frequency of chicks that were assumed dead ($F_{1,39}$ = 3.69, R^2 = 0.12, P = 0.03; Fig. 6.3). The number of chicks that went missing peaked between ages 20 to 30 days with a significant quadratic effect of age in the model (Table 6.3, Fig. 6.3). The average number of deaths per day between 4 and 19 days was 4.1 (± 2.3, n = 70 total deaths) increasing to 14.5 (± 10.3, n = 145 total deaths) between 21 and 30 days and declining between 31 and 45 days (mean = 3.7 ± 2.9, n = 56 total deaths).

Table 6.3 Results of a linear model examining the square-root of the frequency of dead sooty tern chicks by age. The model included a quadratic function of age. *P*: * < 0.05; ** < 0.01; *** < 0.001.

Predictor	**Coeff.**	**SE**	**t**	***P***
Intercept	0.38	0.76	0.51	0.62
Age	0.19	0.07	2.70	0.01*
Age^2	-0.00	0.00	-2.70	0.01*

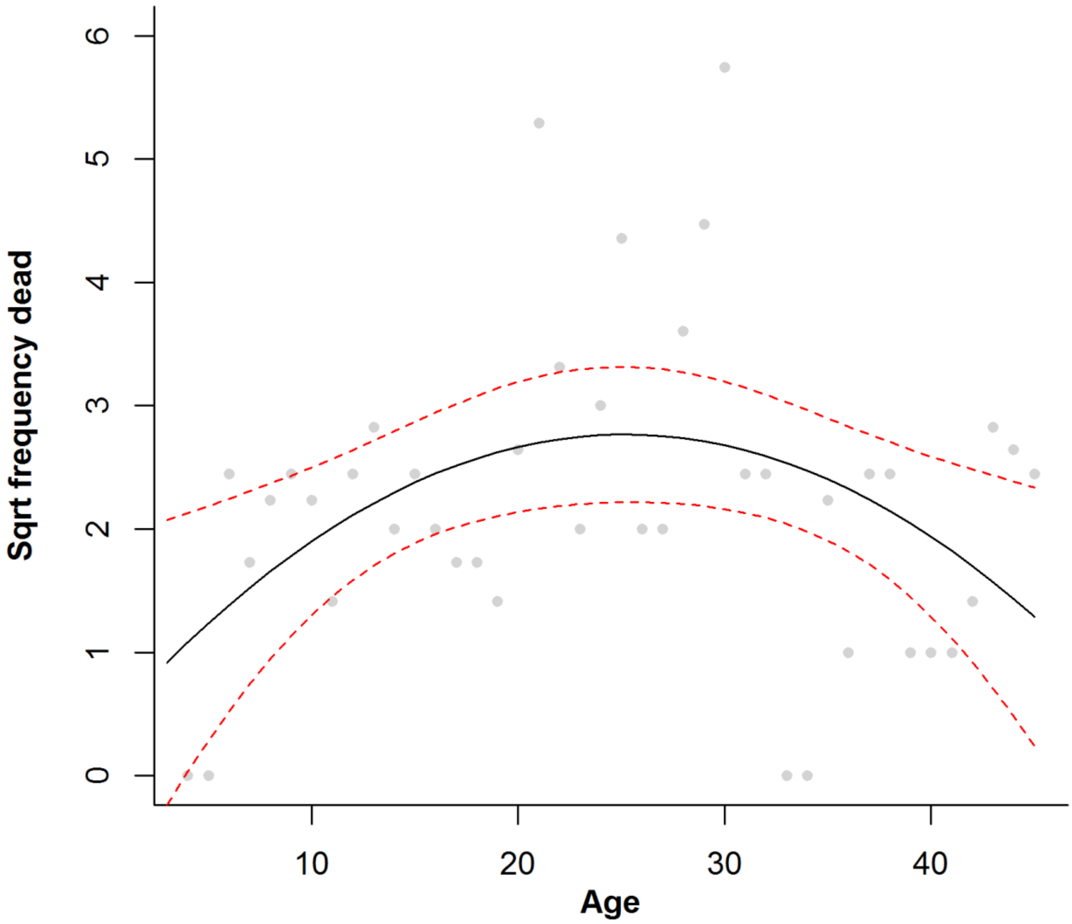

Figure 6.3 The square-root of the frequency of focal and non-focal sooty tern chicks that went missing (presumed dead) between the ages of > 3 days old and prior to fledging at 45 days old by age on Ascension Island in 2015-2016. Grey dots represent the raw data. The solid black line is the prediction curve from a linear model with a quadratic function of age. Dashed red lines are the 95% confidence intervals. n = 271 individuals.

6.4.2 Friendship stability

The stability of friendships over time was higher than what would be expected by chance (Fig. 6.4). Chicks initially retained around 50% of their associates, with the number of associates then declining in line with the lagged identification rate as individuals were lost from the population (and therefore were no longer available to associate with). At observation point five the rate of disassociation appeared greater than the lagged identification rate, indicating a breakdown in group stability. When converted to chick age this increased disassociation occurred between 19 and 34 days of age.

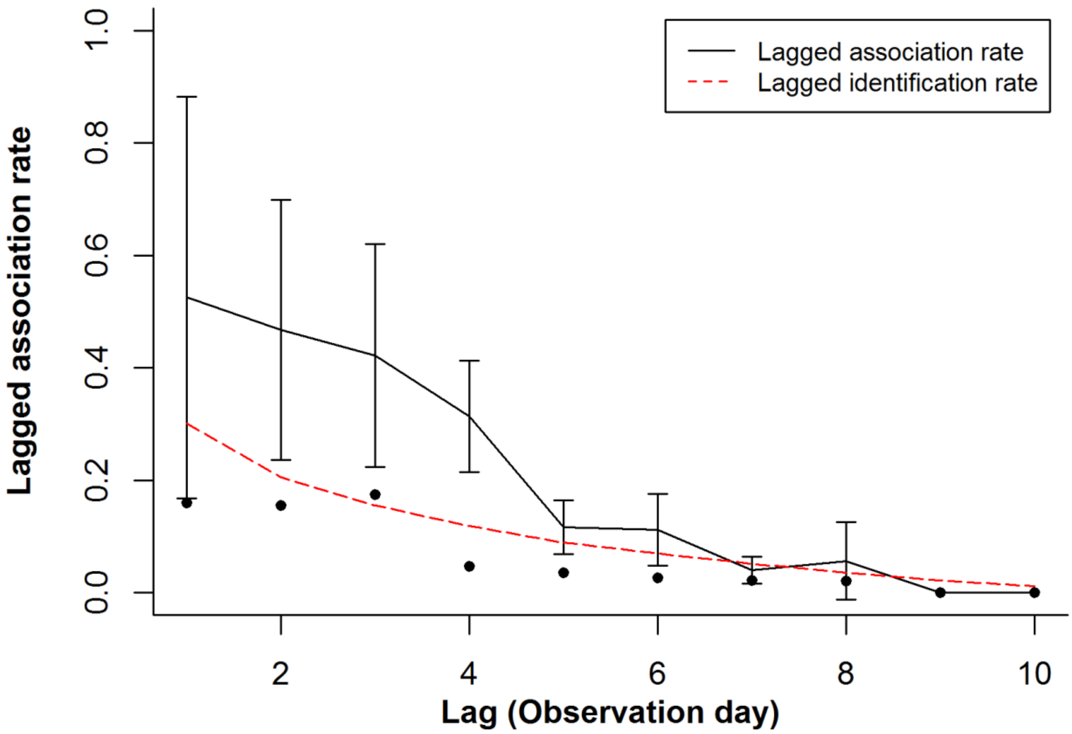

Figure 6.4 Lagged association rates of friends of focal sooty tern chicks between observation days (three to six days apart) on Ascension Island in 2015-2016. The solid line indicates the lagged association rate at each observation day with error bars (SE) obtained by jack-knifing. Points indicate the random association rate while the dotted red line is the lagged identification rate or the rate of loss of individuals from the population (i.e. death rate).

6.4.3 Daily survival

Daily survival of sooty tern chicks varied temporally and was a function of chick age with a quadratic trend (Age = -0.43, SE = 0.07, 95% CI = -0.57 – -0.29; Age^2 = 0.01, SE = 0.004, 95% CI = 0.007 – 0.015), indicating that daily survival rates initially declined with age but then increased closer to fledging. The best approximating model, after excluding models with β - estimate 95% confidence intervals containing zero, included mean degree (Table 6.3) with daily survival increasing with higher numbers of friends (Degree = 0.10, SE = 0.03, 95% CI = 0.04–0.15; Fig. 6.5). The frequency of occasions on which chicks were found using habitat cover was also included in the top-ranking model (Table 6.3), having a positive effect on daily survival, albeit a relatively weak one (Cover = 0.01, SE = 0.004, 95% CI = 0.003–0.02).

Table 6.3 Daily survival models of sooty tern chicks until fledging at 45 days of age in the 2015-2016 breeding season on Ascension Island. The most parsimonious model is in bold.

Model	AIC_C	ΔAIC_C	W_i	*k*	Deviance
Age + Age^2 + Degree + Cover + Pop[a]	339.32	0.00	0.22	6	327.27
Age + Age^2 + Degree + Cover	**339.32**	**0.00**	**0.22**	**5**	**329.29**
Age + Age^2 + Tran+ Degree + Cover + Pop[a]	339.52	0.20	0.20	9	321.43
Age + Age^2 + Tran+ Degree + Cover[a]	339.52	0.20	0.20	9	321.43
Age + Age^2 + Tran + Degree[a]	340.79	1.48	0.10	8	324.71
Global model[a]	343.24	3.92	0.03	11	321.11
Age + Age^2 + Degree	343.79	4.47	0.02	4	335.77
Age + Age^2 + Group	345.65	6.33	0.01	4	337.62
Age + Age^2 + Cover	351.81	12.50	0.00	4	343.79
Age + Age^2 + Tran[a]	354.62	15.29	0.00	7	340.56
Age + Age^2 + Pop	357.32	18.00	0.00	4	349.30
Age + Age^2	359.60	20.28	0.00	3	353.58
Age + Age^2 + Volume	359.77	20.45	0.00	4	351.75
Age + Age^2 + Date + $Date^2$	360.60	21.27	0.00	5	350.56
Age + Age^2 + Growth	361.55	22.23	0.00	4	353.53
Date + $Date^2$	340.00	50.67	0.00	3	383.98
Precip	412.40	73.08	0.00	2	408.39
Age	413.84	73.52	0.00	2	408.83
Constant survival	413.44	74.12	0.00	1	411.44
Date	414.93	75.61	0.00	2	410.92

Akaike's information criterion with small-sample bias adjustment (AIC_C), the difference between the lowest AIC_C and AIC_c (ΔAIC_c), the model weight (W_i) and the number of variables (*k*), are shown. The global model contains all variables measured. [a]The 95% CI for the β estimates of one or more parameter in these models contained zero and were therefore excluded from model selection.

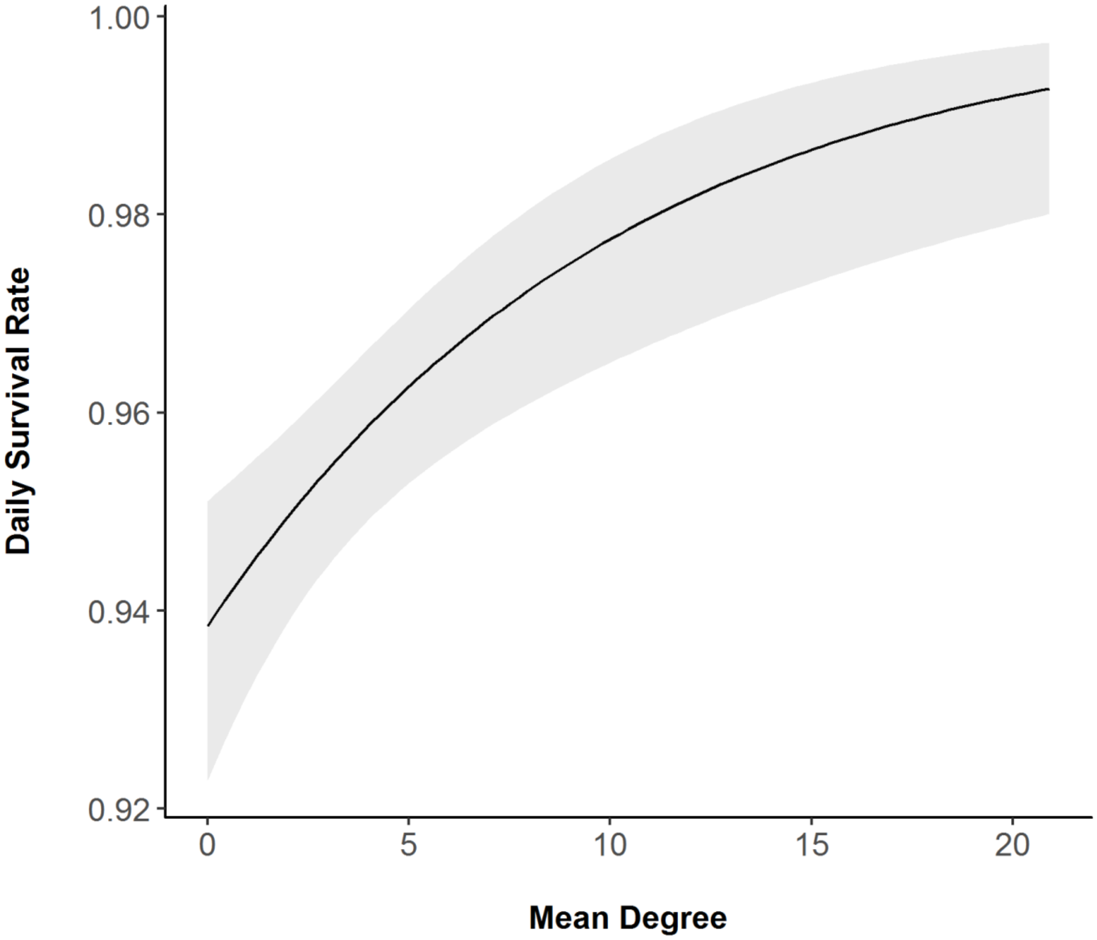

Figure 6.5 Chick daily survival rates of sooty terns on Ascension Island in 2015-2016 as a function of mean weighted degree as estimated in MARK. Mean weighted degree (the expected total association rate per individual) was calculated using social network analysis.

6.5 Discussion

The importance of social interactions for individual survival and fitness has been highlighted in previous work on animal societies, including humans (Krause *et al.* 2007). However, research in the field of offspring social networks is limited (Nuñez *et al.* 2014), with offspring often being excluded altogether from analyses (see Barocas *et al.* 2011). Our study is the first to explore offspring social connectedness in an aggregating seabird. The key findings from our study are that: 1) the number of chick friends or associates varied with age, with a peak in the percentage of friends out of possible associates occurring approximately 28 days old, before declining closer to fledging; 2) friendships were stable until between 19 and 34 days old when the rate of de-friending was greater than the loss of individuals from the population; 3) association strength had a positive effect on chick daily survival rates.

Although there was high variation in the number of chick associates, the peak followed by a decline in the percentage of friends that chicks associate with suggests a period of heightened vulnerability (Fig. 6.2, Appendix 7). This was also supported by a similar trend in the number of chicks that went missing from the population (presumed dead) which peaked between 20 and 30 days of age (Fig. 6.3). Predator avoidance has been proposed as a key factor underlying crèche formation (Chokri *et al.* 2011). Besnard *et al.* (2002) used an evolutionary stable strategy (ESS) modelling approach to suggest that even where no antipredator behaviour is observed, crèching behaviour in gulls Laridae invades when the breeding site becomes under intense pressure from terrestrial predators. The main predators on Ascension Island include endemic Ascension frigatebirds and introduced black rats (Hughes 2014). Ascension frigatebirds predominantly depredate newly hatched up to seven day old chicks (Ashmole 1963), but can take chicks up to 25 days old (LJHG pers. obs.). Therefore it is likely that most chick predation from frigatebirds occurred prior to forming social groups. Indeed the highest rates of mortality in the Ascension Island sooty tern population were recorded in the first few days after hatching (LJHG pers. obs.; Hughes 2014). Brooding by adults may increase predation risk through attraction, given adult plumage is more visible than their camouflaged chicks in many waterbird species (Colwell *et al.* 2007). Introduced rats on Ascension Island have been observed to take chicks at any age, and will depredate fledglings (Hughes 2014). Since the eradication of feral cats in 2004, they have become more prolific predators on the island (Hughes *et al.* 2008; Hughes *et al.* 2019). The causes of chick mortality were often difficult to determine, especially as decomposition happens in just a few days should a carcass be recovered, but frigatebird and rat predation together with starvation were all observed during the breeding season (Chapter 5). It is likely that chick aggregating behaviour is a form of anti-predator defence through mechanisms such as collective detection and dilution effects (Bednekoff & Lima 1998).

Other drivers of group stability include information exchange (Iñiguez *et al.* 2014), kinship (Frère *et al.* 2010b) and habitat structure (Titcomb *et al.* 2015). We observed group social stability over time, with over half of chicks' previous associates remaining stable between the initial observation and the first time lag (three to six days later) (Fig. 6.4). This indicates that some relationships between individuals are maintained over and above what would be expected by chance and that retaining familiar friends confers some benefits. The decline in friendship stability was in line with the lagged identification or death rate (Fig. 6.4), suggesting an underlying demographic effect driving disassociations, i.e. as individuals are lost from the population they are no longer available to associate with (Whitehead 2008). However, after five time lags (between 19 and 28 days post-hatch) the rate of disassociation exceeded the rate of loss of individuals from the population. This break-down in friendship stability or de-friending occurred at the same age range as detected declines in chick friends (i.e. from approximately 28 days onwards; Fig. 6.2). This suggests that the costs of remaining in large groups (e.g. competition for space) outweigh the benefits (e.g. decreased predation risk due to dilution effect). Lusseau *et al.* (2003) attributed temporary stability in group social structure of bottlenose dolphins *Tursiops truncates* in New Zealand to ecological constraints in the form of unstable food resources. In unstable environments individuals in social groups may rely on information exchange to maximise fitness, with more stable groups allowing greater cooperation between individuals by reducing intraspecific aggression and competition ('dear enemy' phenomenon (Jaeger 1981). For example in groups of sea trout *Salmo trutta* consisting of more familiar individuals there were fewer changes in social rank resulting in fitness benefits from increased food intake, presumably from a reduction in stress (Höjesjö *et al.* 1998). For sooty tern chicks predation risk could drive the need for not only an increase in the number of associates but an increase in the stability of social groups, thereby stabilising social hierarchy. Such group cohesion may be critical for an individual’s fitness (Iñiguez *et al.* 2014). However, there may also be a trade-off between group cohesion and group size where the competitive costs of increasing group size outweigh the benefits of group cohesion (Dávid-Barrett & Dunbar 2012). In sooty tern chicks associated costs may include competition for space that provides the best protection against predators. By associating with familiar individuals to propagate more stable social bonds, effects of competition may be mediated (Trigosso-Venario *et al.* 2002; Sueur *et al.* 2011). Such trade-offs are more common in species where sociality underlies non-foraging fitness-related issues – namely predation risk (Dunbar & Shultz 2010). Competition for space and a decline in predation risk as chicks age may reduce the benefits derived from group stability, eventually resulting in a breakdown of social structure at approximately 25 days post-hatch.

Overall, chick association strength was an important predictor of their daily survival rates, indicating that having a greater number of friends confers fitness benefits. Nuñez *et al.* (2014) found that connectedness in juvenile feral horses *Equus caballus* promoted their survival rates and was a better predictor of foal survival than other classic survivorship measures such as body mass. The mechanisms by which social connectedness results in increased survival are unclear, although they have been related to the ability to cope with environmental and social stressors (Lehmann *et al.* 2015). For example, social connectedness reduced aggression through increased cooperation during the mating season in Barbary macaques *Macaca sylvanus* (Berghänel *et al.* 2011). Increased social learning through social connectedness may be a mechanism by which fitness benefits arise (Templeton *et al.* 2011). Such learning could include inadvertent information transfer about predation risk through observation of fleeing behaviour (Dall *et al.* 2005) or simply of who remains alive (Welton *et al.* 2003). There may also be advantages from protection by adults returning with food that remained close to chicks and chick aggregations following feeding (LJHG pers. obs.; Fig. 6.1b). During this time adults issued alarm calls on the approach of predators (frigatebirds) and humans with chicks responding by running for cover (LJHG pers. obs.). Thus, being in a larger group would increase the likelihood of an attending vigilant adult compared with solitary behaviour. We also found the use of habitat cover by chicks to have a positive impact their daily survival. Given the climatic conditions on Ascension Island - low rainfall and high temperatures that vary little seasonally (Ashmole & Ashmole 2000) - it seems likely that the use of cover may be a predator evasion strategy rather than providing endothermic benefits. This further supports earlier arguments about predation risk being the primary driver of chick survival.

Our daily survivorship model had a strong temporal element with the quadratic function of age on survival mirroring the observed temporal changes in the number of associates with age. When chicks are responsible largely for their own movement decisions and able to move away from the nest, survival was initially high and then decreased with age before increasing again closer to fledging. However, most studies have found a positive association between survival and chick age (e.g. Dinsmore & Knopf 2005; Colwell *et al.* 2007; Smith & Wilson 2010). Age-dependent survival has been noted in other precocial species with eight of 10 studies that reported the causes of chick mortality listing predation as the primary cause (Colwell *et al.* 2007). In snowy plovers *Charadrius alexandrinus nivosus* increased survival closer to fledging was linked to increased adult independence and decreased vulnerability to avian predators (Colwell *et al.* 2007). Ruthrauff and McCaffery (2005) found that older and larger western sandpiper *Calidris mauri* chicks were able to evade predators through their increased mobility and spatial dispersion. In Chapter 5 we found that sooty tern chicks on Ascension Island travelled greater distances with age with mobility increasing the most within the first 20 days post-hatching, although on average chicks remained within 10 m of their original nest.

The distribution and spacing of nesting adults may have consequences for the availability of individuals chicks can associate with, especially as chicks remain relatively close to their original nest site (Chapter 5). Our survival model indicated that both group and population size of the colony cluster had a positive effect on daily survival (Table 6.3), although they were excluded from the final model. Therefore, the number of terns that decide to nest in a given breeding season together with the location and density of breeders, the latter of which has been found to impact breeding synchrony (Coulson & White 1960), may impose constraints on a chick’s social environment at the time of nest placement. Further investigation into the effects of spatial distribution and timing of colony clusters on chick aggregating behaviour would shed light on this theory.

Further work is also needed to better understand predator targeting strategies to disentangling the drivers of chick social group size and how these change with chick age. For example, sparrowhawks *Accipiter nisus* targeted sparser redshank *Tringa totanus* flocks than those containing more tightly packed individuals (Quinn & Cresswell 2006). Furthermore, knowing more about longer-term outcomes of social connectedness in seabird species would allow us to examine its importance to pre-breeding survival and subsequent recruitment to the breeding population. For example, male song sparrows *Melospiza melodia* were more likely to establish neighbouring territories with associates formed at fledging (Templeton *et al.* 2011). Similarly, for male long-tailed manakins *Chiroxiphia linearis* early life connections predicted later life success, in terms of the opportunity to reproduce, with males that had increased levels of connectivity achieving higher ranking positions approximately five years later (McDonald 2007).

6.5.1 Conclusions

The direct fitness benefits of sociality are rarely explored (Wey *et al.* 2008), and even fewer studies have explored the importance of offspring social connectedness (but see Nuñez *et al.* 2014). Our study shows that an individual's social environment is an important predictor of survivorship and should be included in survivorship models of socially aggregating species. Furthermore, we highlight that offspring social strategies change temporally and present evidence of predation risk likely driving such temporal patterns. We found that social stability varied with age and that de-friending was a probable response to the likely decrease in predation risk and to the increase in the costs such as competition for space associated with aggregating behaviour. Thus, an individual's number and strength of social connections can have strong fitness consequences in species with socially aggregating young.

Chapter 7

General Discussion

The focus of this PhD project was to investigate trends in the spatial, temporal and genetic colony structure of a highly social seabird population breeding on Ascension Island in the South Atlantic. To achieve this we combined long-term demographic data with measures of genetic relatedness and individual social behaviour. We utilised an extensive mark-recapture database collected over two decades together with additional field research undertaken as part of this PhD. Our findings suggested that the sooty tern population has undergone significant temporal changes in size and spatial distribution at the intra-population scale, suggesting an ecosystem shift at the two breeding sites (Chapter 2). Breeding timing was affected by breeding success, with more successful breeders returning earlier. There was also asynchrony in breeding timing between sites. Multi-even models showed the importance of memory and site fidelity in the probability of within-population breeder dispersal.

Adult breeder site fidelity was not supported by our genetic analysis of within-population gene flow and an absence of population structure at the island and intra-population scales (Chapters 3 and 4). There was however, evidence for genetic variation between early and late breeders indicating within-breeding season temporal partitioning. This suggests that heterogeneities in breeding timing are important in shaping both the population and genetic structure.

Chick survival was lower at the breeding site at which population size declined compared to the one where it increased (Chapter 5), adding support for potential heterogeneity in habitat conditions. The social environment of chicks played a key role in their daily survival (Chapter 6) with those which had a higher number of connections (friends) being more likely to reach fledging age. This has consequences for population-level processes such as recruitment and population dynamics. A breakdown in social structure caused by extrinsic factors such as increased predation has the potential to disrupt intra-population stability further. This has parallels with the importance of making friends in human children, with the formation and retention of friendships supporting positive developmental outcomes (e.g. increased cognitive ability) (Hartup 1996). The observed variation in chick social group formation behaviour can inform how selection may act on certain behavioural strategies and phenotypes. This is the first study to examine social structure in relation to survival of precocial seabird chicks, and highlights the importance of early-life social structure in the study of animal behaviour and evolution.

7.1 Population trends

Our aim was to evaluate the stability of breeding timing, synchrony and success at different spatial and temporal scales and how these relate to trends in population size. Given the population has remained relatively stable since the crash in population size in the 1950s (Hughes *et al.* 2012) and that seabirds show high breeding site fidelity, we predicted site-level population size would remain relatively stable over time. However, our results suggested otherwise, with dramatic shifts in breeding population size between sites. We also found consistent differences in site-level characteristics (e.g. timing and density), with birds at one site breeding earlier and at higher densities than those at the other. We predicted that breeding outcome would influence arrival time in the following season, and that breeder site faithfulness would be evident from the presence of memory in our mark-recapture dataset. We found support for our hypothesis that breeding outcome would have carry-over effects on breeding timing the following season (Fig. 2.8). Following breeding success birds returned later than in seasons of reduced success.

Unstable populations are more likely to experience extinction events or the dispersal of breeders to other breeding locations (Cuervo & Møller 2017). Following a crash in population size of 84% between 1942 and 2013, the extent and geographic location of the Ascension Island breeding population of sooty terns has altered and from the 1990's the population has occupied two breeding sites on the island (Fig. 1.1). A reduction in population size at one site (Waterside) and a compensatory increase at the other (i.e. Mars Bay) were supported by the higher likelihood of individuals to move from Waterside to Mars Bay (211: 0.74 ± 0.036 cf. Mars Bay to Waterside [122]: 0.55 ± 0.057) in our multi-event models (Fig. 2.10). Strong influence of model memory in our dataset was evident with breeders preferring to stay at the same site in consecutive breeding events (Fig. 2.8). There was however, a clear difference in recruitment rates, with higher recruitment of first-time breeders at Mars Bay (Fig. 2.9b, Fig. 2.11). The movement of breeders between breeding seasons is generally related to their breeding success in the previous season based on the 'win-stay, lose-move' strategy (Schmidt 2004). For example, Kim *et al.* (2007) found breeding dispersal was higher in blue-footed booby *Sula nebouxii* pairs that had changed mates after a breeding failure than successful breeders. Possible drivers of the surmised changes in habitat conditions on Ascension Island are differences in predation risk between breeding sites. Predation is the primary limiting factor for some seabird breeding populations causing dramatic declines in breeding success (Lavers *et al.* 2010) and even resulting in complete abandonment of breeding grounds with breeders dispersing to other locations (Scopel & Diamond 2017). Introduced predators, namely black rats and common mynas have increased significantly on Ascension Island in recent years (Hughes *et al.* 2019). Following the removal of feral cats in 2003, rat populations have seen not only an increase in numbers but also longevity (Hughes *et al.* 2008). The geographical proximity to potential rat refuges when sooty terns are not breeding, such as Green Mountain (Hughes 2014), could be responsible for the disparity in habitat quality (i.e. breeding success potential) between breeding sites, with Waterside being closer to Green Mountain. The question then arises as to why sooty terns continue to breed at the lower quality site? Therefore, some individuals appear to go against the win-stay, lose-move strategy. Naves *et al.* (2006) found the likelihood of breeder dispersal was dependant on the timing of failure in black-legged kittiwakes, with later failures having higher mate and breeding site fidelity. Matthiopoulos *et al.* (2005) used spatially explicit models to show that site fidelity in colonial species slows down the growth and movement of colonies, with density dependence and competition between colonies preventing occupancy of all available breeding habitat. Breeding site fidelity is higher in more experienced breeders (Mougin *et al.* 1999; Kim *et al.* 2007). The fact that first-time breeder recruitment was higher at Mars Bay regardless of fledging site, suggests a lack of natal site philopatry (Chapter 2). Recruiting breeders may have assessed site quality, in terms of breeding success, by visiting breeding sites prior to breeding for the first-time. For example, Votier *et al.* (2011) observed juvenile pre-breeding northern gannets visiting breeding colonies in the years prior to breeding, presumably to assess breeding success. This is consistent with an ecological trap (Grémillet & Boulinier 2009) where breeders continue to use poor quality sites (i.e. those with low breeding success). For example, in west coast colonies of South African cape gannets *Morus capensis* breeders continued to use poor quality sites over a 10 year period (Distiller *et al.* 2012).

Our study provides estimates of within-population breeder dispersal, recruitment probabilities and juvenile survival estimates that will be important for future population forecasting and predicting responses to future environmental conditions such as climate warming.

7.2 Genetic population structure

We aimed to examine the links between genetic structure and social organisation, levels of inbreeding depression and potential barriers to gene flow. We predicted that given site-level differences in breeding timing, population density and site faithfulness of seabirds in general, there would be genetic differences between breeding sites and evidence of potentially sex-biased spatial autocorrelation from kin group organisation. We found no support for landscape scale effects on population genetic structure, nor evidence of spatial autocorrelation. In contrast, we found high levels of population panmixia indicating random breeding. However, there was evidence for fine-scale population spatial and temporal structure.

Nest and breeding site fidelity is high in seabird species (Lebreton *et al.* 2003; Palestis 2014). Reduced dispersal, especially in geographically isolated island populations, promotes inbreeding which may result in genetic differentiation from mainland or other isolated populations (Mayr 1963). However, evidence for genetic structure and inbreeding is variable in seabirds (Milot *et al.* 2008). For example, population genetic structure was evident in Peruvian diving petrels *Pelecanoides garnotii* (Cristofari *et al.* 2019) while no evidence of genetic structure was found in populations of grey-faced petrels nesting in New Zealand (Lawrence *et al.* 2014). Our analysis of sooty tern genetic structure breeding on Ascension Island revealed high levels of genetic diversity within the population and low levels of relatedness suggesting population-level panmixia, or random mating (Chapter 4).

Although we found evidence of memory and site faithfulness in our multi-event models, the probability of dispersing between breeding sites was also high (Chapter 2), although this does not necessarily preclude kin group structure because individuals may be moving in social groups. To this effect, we did find some evidence of fine-scale spatial and temporal genetic structuring. Birds nesting within sampling points showed higher relatedness compared to between-point relatedness, and there was also some evidence of higher relatedness between some immediate neighbours (Fig. 4.1). Our findings of evidence for temporal genetic structure, with earlier breeders genetically different from later arriving breeders, are paralleled by those found in salmonid fish which displayed differences in arrival times of as little as two weeks (Hendry & Day 2005). To the best of our knowledge, few studies have investigated within-breeding season effects on population genetic structure in birds. High variability in egg-laying timing (i.e. 40–60 days between the first and last egg laid across the two breeding sites) has been recorded in sooty terns breeding on Ascension Island (Ashmole 1963; Hughes 2014) compared to those breeding elsewhere. For example, egg laying by sooty terns is completed in nine days on the Seychelles (Feare 1976b) and 21 days on the Dry Tortugas (Colchero 2008). Such disparity within breeding season between arrival times could lead to breeders and potential pairs being prevented from coming into contact with one another.

Plasticity in the response of organisms to changes in environmental factors such as climate warming may increase the likelihood of population persistence (Cuervo & Møller 2017). High levels of genetic diversity are thought to enhance the ability of species recover after experiencing extreme climatic conditions. For example, Reusch *et al.* (2005) found that increased genetic diversity in eelgrass led to higher plant density and biomass production after exposure to near lethal temperatures. Plastic responses to climate warming were recorded by Colchero (2008) in sooty terns breeding on the Dry Tortugas, Florida, although levels of population genetic diversity are unknown. Climate warming, which was surmised to cause alterations in prey abundance, led to a delay in breeding timing of three months between 1950 and 2010. A subsequent increase in nest predation by aerial predators also led to a shift in nest location to habitat with greater habitat cover (Colchero *et al.* 2010).

Evidence of genetic structuring at fine spatial and temporal scales in the sooty tern population on Ascension Island could be a result of individual and group-level processes. As shown in Chapter 2 breeding success may be a driver of temporal mismatches in breeding timing, given the likely heterogeneities in breeding success between sites (see also Chapter 6). However, differences in the benefits that individuals stand to gain from maintaining collective group structure may result in within-population dispersal that, coupled with likely immigration from other populations, maintains genetic diversity and gene flow within this highly panmictic population.

7.3 Social behaviour and population ecology

We aimed to assess factors influencing contemporary reproductive success as measured by daily survival rates of chicks to fledging. Given the benefits of sociality for survival and reproductive success we predicted that there would be a positive influence of social group structure on chick survival to fledging. In agreement with our predictions sociality and the tendency of chicks to connect with other individuals promoted daily survival until fledging (Chapter 6). Few studies have focused on offspring sociality and its consequences for survival (but see Nuñez *et al.* (2014). Our findings indicate a peak in the number of friends at 28 days old which might suggest a period of increased vulnerability to predation. This increase in social group size together with habitat cover having a positive effect on chick survival (Table 6.3) is suggestive of predator evasion strategies. Hughes (2014) highlighted predation as a major cause of chick mortality in the same population. The cause of chick mortality can be difficult to ascertain. Evidence of consumption by rats and crabs can be determined from carcasses, if found, although the initial cause of death could still be due to other causes, such as starvation. There may also be interactions between predation risk and food shortages (Scopel & Diamond 2017), with food limitation weakening chicks that are then more likely to be depredated.

The distribution and spacing of breeding adults may have consequences for the availability of other chicks with which chicks can associate given chicks remain relatively close to their original nest site (Chapter 5). Our survival model indicated that population size of the colony cluster had a positive effect on chick daily survival (Table 6.3), although it was excluded from the final model. This supports previous research that has found at lower population densities and smaller group sizes breeding success is reduced by processes such as increased predation (Sutherland 1996). This scenario has further reaching conservation implications given that a lower number of connections may reduce offspring survival, thereby potentially reducing fitness outcomes. For example, Archie *et al.* (2006) found high levels of relatedness within social groups of African elephants *Loxodonta africana*, increased cooperation and reproductive success. Thus, the breakdown of social networks through removal of individual elephants by poaching has the potential to reduce both population size and fitness of the remaining group members.

We also noted starvation as a cause of chick mortality (Chapter 5) indicating that chicks might have been food-limited during the study. Indeed, a significant dietary shift in prey composition in recent years has been documented in the Ascension Island population (Reynolds *et al.* 2019). This shift from predominantly teleost fish to prey of lower nutritional value including squid is a cause for conservation concern. Such dietary pressures may have acted to exasperate the detrimental impacts of predation on breeding success. Indeed, breeding success of black-legged kittiwakes was reduced in years of low food availability due to the combined effect of food shortage and an increase in egg predation by great black-backed gulls that was also caused by food shortages (Regehr & Montevecchi 1997). The proposed designation of a marine protected area (MPA) encompassing at least 50% of Ascension Island’s exclusive economic zone (approximately 320 km radius from the island) would likely benefit breeding sooty terns. Preliminary tracking data suggest a range of 256 km from the island during breeding (AIG 2018).

Further research is required to investigate the ranging ability of rats to establish whether they travel between breeding sites and whether there are differences in rat refuges between breeding sites when terns are not breeding. Optimal foraging theory (Stephens & Krebs 1986) predicts that predator decisions on moving between prey patches (e.g. breeding sites) are based upon a cost-benefit threshold between energy gain (i.e. from higher prey abundance at the alternative patch) and the time and energy it takes to reach that patch.

Consistent breeding failures may lead to the complete abandonment of breeding colonies. For example, five years of complete breeding failures at an Arctic tern colony at the Gulf of Maine resulted in permanent abandonment of 90% of the colony (Scopel & Diamond 2017). The authors also found a threshold of 25% depredation at which point resulted in the breeding failure of the colony, regardless of food availability.

7.4 Application to other species and study systems

Throughout this thesis we have presented findings and developed new techniques and methodologies that are of relevance for other researchers working on a range of taxa and questions, especially those investigating seabirds and other colonial breeders.

Our multiplex set of microsatellite markers will be useful for other researchers working on sooty terns or similar species, such as brown noddies and black noddies. Combining this multiplex set with 16 microsatellite markers recently developed for sooty terns in the Indian Ocean by Danckwerts *et al.* (2019) would allow for robust global population genetic analysis of this species.

Our findings on temporal population genetic structure revealed parallels with breeding migratory fish (Hendry & Day 2005). As far as we can determine investigations of which have not been undertaken in other taxa, but could tell us key information about a species' ecology. For example temporal genetic structuring with breeding seasons suggest high competition for breeding sites or other recourses such as food (Ribolli *et al.* 2017). This can occur over relatively short time scales. Our study found differences in genetic structure between birds breeding 34 days apart. In salmonids genetic differences were found between those laying eggs as little as two weeks apart (Ribolli *et al.* 2017). Such differences are not surprising given that incubation in sooty terns lasts 30 days, and thus asynchrony in breeding timing over this time-scale may prevent birds coming into contact with one another when they first arrive on the island during pair formation. We found spatial synchrony in breeding timing of zero to four days between hatch dates within sampling transects (i.e. nests < 100m apart) (Chapter 3) suggesting coordinated breeding timing in spatially clustered nests.

Our research has highlighted the importance of investigating fine-scale levels of population parameters. Detailed studies of single species and populations are needed if we are to better understand the significance of responses to variation in extrinsic and intrinsic factors for population persistence. Combining studies of population ecology with those of behaviour of individual organisms is also pertinent to our understanding of how and why such populations vary temporally. Individual behaviour is often dependent on the behaviour of others, and this in turn has implications for the population as a whole (Sutherland 1996). For example, seabird colonies sometimes experience mass desertion of breeding attempts when only specific individuals or groups are adversely affected by extrinsic factors such as predation or parasite load (Duffy 1983; Scopel & Diamond 2017).

A key outcome of our research is identifying the significance of chick social structure (Fig. 7.1) in influencing their survival to fledging. Survival-based estimates of breeding success are regularly undertaken using parameters such as habitat structure, age and breeding density that are thought to impact daily survival rates (see review by Maness and Anderson 2013). However, few studies include measures describing the social environment (Nuñez *et al.* 2014) and, perhaps more surprisingly, few studies across taxa have considered the importance of social structures of offspring (but see Royle *et al.* (2012); Stanton and Mann (2012); Ruch *et al.* (2014). The ontogeny of social structure is a key aspect of animal biology that has received little attention in non-human animals, but may lead to significant insights in our understanding of population ecology and evolutionary strategies. However, there are also parallels with human friendship formation. For example, forming friendships had positive consequences for cognitive development in human children (Hartup 1996).

We have developed several field techniques useful for other studies of sooty terns and seabird species for identifying adults, nests, and chicks, and methods for studying precocial offspring. Our analysis suggests that in precocial species that form crèches (see Chapter 6), movement behaviour is an important aspect of a species' ecology and most likely evolved for predator evasion where both parents are required to forage and leave offspring unattended (Le Bohec *et al.* 2005; Wilson 2009). Therefore, methods that are commonly used to study such species, such as fencing, may prevent ‘normal’ locomotory behaviour and alter predation risk thus biasing survival estimates.

Figure 7.1 Are you in my network? Sooty tern chicks, approximately 12 days old, that have formed a social group on Ascension Island. Friends were defined as those within two body lengths of each other. (Photo: L.J.H. Garrett).

7.5 Further work

Continuation of the long-term ringing-retrap and census data-sets on Ascension Island is paramount for the future assessment of population trends and the stability of the sooty tern population in the face of environmental change due to climate warming. Data on relative breeding success at the two breeding sites would give us a clearer understanding of the likely future population trends. Persistent ringing-retrap efforts, especially ringing of near-fledging age chicks, are also needed should investigations of the movement of individuals between sites and recruitment of birds into the breeding population be undertaken.

Application of network analysis using data from the adult ringing-retrap database would also be desirable. This continues to be reliant on the capture and geolocation of the marked individuals. The stability of social connections between breeding adults over multiple breeding seasons could be assessed through the use of lagged association rates but this would require the definition of a robust measure of connectedness between individuals.

Further work on the social environment of chicks is required to account for potential variation between breeding seasons. Unfortunately, it was not possible to collect data from more than one breeding season during this PhD given the closure of the runway on Ascension Island that occurred days before field work was due to commence in 2017. Further work into predator abundance and predation rates on eggs and chicks of sooty terns is also needed. Should predator control measures be implemented (as recommended by this research and Hughes (2014), accurate pre- and post-control abundance and distribution estimates of predatory species are essential in order to assess the outcomes of such conservation measures (Parkes & Murphy 2003). Such conservation efforts must be accompanied by population-level estimates of breeding success of sooty terns pre- and post-control.

An ocean-wide analysis into the genetic structure of Atlantic sooty tern populations would promote our understanding of the phylogeography of the species. This would allow modelling of the recruitment, dispersal and immigration of birds between populations. It would also provide insights into the stability and potential resistance of the wider Atlantic metapopulation to future climate scenarios and resulting shifts in prey abundance. This is also poignant given the recent urgent call for the reassessment of conservation status of this species (Hughes *et al.* 2017b). In addition to genetic information on the dispersal of individuals between populations, tracking fledglings prior to breeding could give us much needed insight into their marine habitat use prior to breeding (Jaeger *et al.* 2017). Very little is known about juvenile sooty tern movements and this could be crucial for conservation management of the species in the form of designating MPAs, for example. Tracking of adults during their non-breeding migration has revealed considerable variation in the spatial use of the marine environment (S.J. Reynolds pers. comm.). Individuals travel approximately 2,900 km from Ascension Island (S.J. Reynolds unpubl. data). These data could be used to define at sea habitat use to extract environmental parameters thought to influence seabird breeding ecology such as sea surface temperature (Votier *et al.* 2011).

7.6 Conclusions

Taken together, our findings suggest behaviour at individual and group levels can have significant effects on population ecology, namely the movement of breeders, breeding timing and breeding outcomes. At the island scale it would appear that the population of sooty terns on Ascension Island has stabilised since the crash that occurred in the 1960s. Little variation in population size, high levels of genetic diversity coupled with low levels of genetic relatedness and thus low inbreeding depression suggest a 'healthy' population that is able to persist. However, there needs to be continued recognition of the shifting baseline phenomenon and an avoidance of complacency given that the population has reduced in size by over 80% since the 1950s. Despite what was considered a major threat to population growth – predation of adults and chicks by feral cats – being removed in 2003, the population has failed to increase. Although the population has remained relatively stable, we have identified a dramatic shift in population size between the remaining two breeding areas (i.e. Mars Bay and Waterside), with one showing growth while the other has declined. Despite evidence for high levels of memory and a high preference for returning to familiar breeding grounds, sooty terns on Ascension Island have exhibited breeding site dispersal, with breeding adults recruiting to Mars Bay in preference to Waterside what population size continues to decline. Persistent breeding failures can override an experienced breeder's tendency towards breeding site fidelity, and our assessment of contemporary chick survival to fledging revealed no successful breeders at the Waterside site. Although further data are needed to examine differences in breeding success between breeding sites, our analysis of long-term chick mark-recapture data showed that recruitment probability was higher at the growing breeding population, and indeed is likely a contributor to such growth. Prospecting to ascertain the relative quality of potential breeding areas is more frequent in naïve breeders compared to experienced birds. Thus, it seems possible that heterogeneity in site quality exists between the two breeding sites on Ascension.

Social and physical environments (e.g. habitat cover) were key predictors of chick survival. There was high variation in chick survivorship and breeding success was low compared to previous estimates from both this and other populations (see Chapter 5), with no chicks reaching fledging age at the breeding site (i.e. Waterside) where the population was declining. Given that the number and strength of social connections between individuals influence chick survival, factors that affect the ability to socialise (e.g. breeding density, population size, distribution of colony clusters) may have major consequences for fitness outcomes (Fig. 7.2).

Predicted changes in climate warming may further exasperate the scarcity and decline in nutritional value of available prey (Reynolds *et al.* 2019). Flexibility in behavioural responses to changes in environmental conditions has been noted in other populations of sooty terns (e.g. see Colchero 2008). However, although single season breeding failures may have little effect on population persistence, recurrent breeding failures are likely to cause population declines (Cury *et al.* 2011) or complete dispersal of the colony (Scopel & Diamond 2017) to new breeding areas. Therefore, it is recommended that further assessment of the drivers of population size be undertaken. The conservation goals for population increase must be realistic (Pauly 1995), and it is unlikely that the population recovery will return to former levels. However, population forecasting (for an example see Genovart *et al.* 2016), using outputs from our multi-event modelling, such as recruitment age and juvenile survival, would allow for more accurate modelling of? risks from future environmental threats such as climate change. In terms of conservation management, there has been some discussion as to the relative feasibility and benefits of predator control measures for the sooty tern breeding areas on Ascension Island (AIGCFD pers. comm). These data provide a baseline from which to evaluate different scenarios for the potential increase in breeding success that may result from predator control measures. This will inform cost-benefit analyses for the implementation of such measures.

This research has taken a multidisciplinary approach to understand the population ecology of a highly social seabird and in doing so has revealed complex interactions between extrinsic and intrinsic factors. We have shown that the scale upon which one assesses such factors is important for our interpretation of population stability and what signals cause for conservation concern. Such signals as the identified intra-population trends should not be ignored if we are to avoid future catastrophic population declines as those that occurred in the mid-20th century.

Figure 7.2 Sooty tern with a two-day old chick on Ascension Island 2016. (Photo: L.J.H. Garrett).

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Appendix 1

E-SURGE model specifications for adult mark-recapture data

The top model (P model 5 in Table 2.4) was parameterised in E-SURGE as follows.

Data were loaded into E-SURGE specifying the number of states was 5: “11”, “12”, “21”, “22” and “dead“, where 1 = site 1 (Mars Bay) and 2 = site 2 (Waterside). The number of events was 3: “seen at site 1”, “seen at site 2” and “not seen”). There was one age class and an external covariate for effort.

In the GEPAT interface ‘*’ entries denote the complement of the sum of positive row entries, and ‘-’ entries denote zeroes (impossible transitions). Π = Initial state, Φ = Transition dependent on survival, and P = Event matrices (capture probabilities). Notation was as follows:

$$\Pi = [\pi \quad \pi \quad \pi \quad *]$$

$$\Phi = \begin{bmatrix} \Phi & \Phi & - & - & * \\ - & - & \Phi & \Phi & * \\ \Phi & \Phi & - & - & * \\ - & - & \Phi & \Phi & * \\ - & - & - & - & * \end{bmatrix}$$

$$P = \begin{bmatrix} * & p & - \\ * & - & p \\ * & p & - \\ * & - & p \\ * & - & - \end{bmatrix}$$

In the GEMACO interface ‘i’ denotes constancy, ‘t’ means time effect, ‘x’ denotes a covariate effect, and ‘from’ means that parameters are not equal in each matrix row. For the chosen model, I used ‘i’ for initial parameters and ‘from.to’ for transition probabilities, and for events, we made them conditional on search effort (external covariate). Thus, I used: ‘firste+nexte.[i+ [to(2_3).t(2_20)]*x]’. In the IVFV interface, I constrained the initial capture probability to 1 for encounter, as this was the time of marking.

Appendix 2

E-SURGE model specifications for chick recruitment

The model which describes chick recruitment by age (model 4 in Table 2.5) was parameterised in E-SURGE as follows. The number of states was 5: “Non-breeder at site 1”, “Breeder at site 1”, “Non-breeder at site 2”, “Breeder at site 2” and “dead“, where 1 = site 1 (Mars Bay) and 2 = site 2 (Waterside). The number of events was 3: “seen at site 1”, “seen at site 2” and “not seen”), there were 20 age classes and an external covariate for effort.

In the GEPAT interface ‘*’ entries denote the complement of the sum of positive row entries, and ‘-’ entries denote zeroes. Π = Initial state, Φ = Survival, β = Breeder recruitment, and P = Event matrices (capture probabilities).

Notation was as follows: $\Pi = [\pi \quad \pi \quad \pi \quad *]$

$$\Phi = \begin{bmatrix} \Phi & - & - & - & * \\ - & \Phi & - & - & * \\ - & - & \Phi & - & * \\ - & - & - & \Phi & * \\ - & - & - & - & * \end{bmatrix}$$

$$\Phi = \begin{bmatrix} * & \Phi & - & \Phi & * \\ - & * & - & - & * \\ - & \Phi & - & \Phi & * \\ - & - & - & * & * \\ - & - & - & - & * \end{bmatrix}$$

$$P = \begin{bmatrix} * & p & - \\ * & p & - \\ * & - & p \\ * & - & p \\ * & - & - \end{bmatrix}$$

In the GEMACO interface ‘i’ denotes constancy, ‘a’ means age, ‘t’ means time effect, ‘x’ denotes a covariate effect, and ‘from’ means that parameters are not equal in each matrix row. For the age varying model, I used ‘i’ for initial parameters, ‘from’ for survival probabilities, ‘a(3_12, 13:16).to(2 4)+others’ for the breeder recruitment probabilities (where 3_12 = all ages from three to 12 and 13:16 groups ages between 13 and 16). The ‘others’ is the notation for all other ages. For events I used: ‘firste+nexte.[i+[to(2_3).t(2_20)]*x]’. In the IVFV interface, I constrained the last parameter in the breeder transition probability to zero, as this was the ‘others’. I also constrained the initial capture probability to 1 for encounter, as this was the time of marking.

Appendix 3

Details of the 50 microsatellite markers tested in sooty terns. Markers Ofu1 to Ofu26 (inclusive) were included in the final multiplex set (see Table 3.1).

Locus	Clone name and ENA accession number		Primer sequence (5'- 3')	Repeat motif	Fluoro-Label (F)	T_m	*n*	A	Observed (Expected) allele size (bp)	Outcome
Ofu1	Trn17616	F	TGTTTAAGCAGTAAAGACAAAGCCTAC	$CA_{(17)}$	6-FAM	60.78	22	12	202-227	Poly. See Table 3.1
	LT903723	R	GGTGCGTTTAGAGTGCTTCTTTAG			60.56			(211)	
Ofu2	Trn23851	F	GGCTGTAGCGAGCAGTTAGG	$AC_{(15)}$	HEX	60.18	22	8	189-359	Poly. See Table 3.1
	LT903724	R	GAAGCTTGGGTGCAGGTG			60.40			(209)	
Ofu3	Trn25452	F	GGCTGTAGCGAGCAGTTAGG	$CA_{(16)}$	6-FAM	60.74	23	10	144-166	Poly. See Table 3.1
	LT903725	R	GAAGCTTGGGTGCAGGTG			60.74			(170)	
Ofu4	Trn4256	F	CCTGTTGCCAAGAAATAAATCTTAC	$AC_{(18)}$	HEX	59.51	22	13	141-175	Poly. See Table 3.1
	LT903726	R	TGAAGAAGCGTGGCTGTG			59.68			(150)	
Ofu5	Trn171	F	TCCCTACTTGACTTTGGAAACATC	$TG_{(21)}$	6-FAM	60.72	20	12	86-131	Poly. See Table 3.1
	LT903727	R	TGTACAACACTGTTCCATCATGC			60.86			(103)	
Ofu6	Trn352	F	GCGTTCGGCATCAAGTTAG	$CA_{(16)}$	HEX	59.43	22	9	265-281	Poly. See Table 3.1
	LT903728	R	ATCCCTGCAAAGCACACAG			59.85			(282)	
Ofu7	Trn436	F	TTGCTACAAACCTTGGTTATTGAC	$TG_{(19)}$	HEX	59.49	22	10	154-184	Poly. See Table

Locus	Clone name and ENA accession number		Primer sequence (5'- 3')	Repeat motif	Fluoro-Label (F)	T_m	*n*	A	Observed (Expected) allele size (bp)	Outcome
										3.1
	LT903729	R	GCAACCTTAGCATTACCTAGCTG			59.51			(165)	
Ofu8	Trn640	F	GGGTTACTGCTGGTCAGAGC	GA$_{(15)}$	6-FAM	59.87	23	14	272-328	Poly. See Table 3.1
	LT903730	R	GCTCTAGGCCAATTTCATCATC			60.07			(289)	
Ofu9	Trn643	F	CTAAGCTGAAATTCCTGAACTGG	TG$_{(20)}$	6-FAM	59.44	23	14	174-206	Poly. See Table 3.1
	LT903731	R	CAACTACAGACATCCCACAAGC			59.66			(185)	
Ofu10	Trn16824	F	GGAAGGAGCATTCAGTCTGC	CTT$_{(26)}$	6-FAM	59.96	20	17	132-210	Poly. See Table 3.1
	LT903732	R	GATGCTCAGATGCTTGCTAGG			60.13			(167)	
Ofu11	Trn13992	F	AAAGTCTGTCACACATCCAACG	TATC$_{(15)}$	6-FAM	60.07	22	8	155-203	Poly. See Table 3.1
	LT903733	R	CACGGTGCCAGTTAATAATGC			60.39			(203)	
Ofu12	Trn129	F	TTAAGCAGAAAGCCAGAGTGG	CT$_{(14)}$	6-FAM	59.64	22	9	300-330	Poly. See Table 3.1
	LT903734	R	CTTAGTGTGCTTGGTAAAGACTGAAC			59.83			(314)	
Ofu13	Trn839	F	GAGGCCACCCTTACACCTC	TCCA$_{(14)}$	HEX	59.52	22	8	142-171	Poly. See Table 3.1
	LT903735	R	AAATGAGCTTGGCTTTACGC			59.50			(169)	
Ofu14	Trn897	F	GATCTTTCCCAGTAGCACCTATG	CA$_{(14)}$	HEX	59.17	19	7	350-365	Poly. See Table 3.1
	LT903736	R	CCACCTGGCTGGATAACAG			59.10			(349)	
Ofu15	Trn191	F	AAAGAGTCTCCACCTGAAGCAG	CA$_{(14)}$	6-FAM	60.05	22	10	333-354	Poly. See Table 3.1

Locus	Clone name and ENA accession number		Primer sequence (5'- 3')	Repeat motif	Fluoro-Label (F)	T_m	*n*	A	Observed (Expected) allele size (bp)	Outcome
	LT903737	R	AGCAATATCCCTGGCAGTACC			60.35			(340)	
Ofu16	Trn484	F	TTTCCTCCTGAGACTTGCGTA	CA$_{(13)}$	6-FAM	60.00	22	7	314-327	Poly. See Table 3.1
	LT903738	R	AAACCAAACTGGCATCAAATAAGT			60.16			(324)	
Ofu17	Trn715	F	CACCTTATCAAGGGCAATGG	AC$_{(12)}$	HEX	60.32	23	10	185-207	Poly. See Table 3.1
	LT903739	R	TTGGATGGATAAAGCAAGCTG			60.22			(194)	
Ofu18	Trn269	F	ATCCCTGTCACTCCCATGAC	TC$_{(12)}$	HEX	59.77	22	5	298-306	Poly. See Table 3.1
	LT903740	R	TGCACATGGAAAGTTGCTTC			59.85			(303)	
Ofu19	Trn15	F	TTAGCCCTTTACCCAAATGC	AC$_{(12)}$	6-FAM	59.08	23	8	94-116	Poly. See Table 3.1
	LT903741	R	ATTACGTCAGCCTCCTCCAG			59.31			(115)	
Ofu20	Trn551	F	CCCAGTGACTCGCTTGCT	TTGG$_{(11)}$	HEX	60.14	22	9	216-262	Poly. See Table 3.1
	LT903742	R	CTGCAACAGCCTTTCAGTCA			60.18			(221)	
Ofu21	Trn121	F	GGCTTAGAAATACTGCCTTTGC	GT$_{(11)}$	6-FAM	59.44	22	20	269-321	Poly. See Table 3.1
	LT903743	R	CTGCTGGTCTGTAAACCATTTATC			59.12			(278)	
Ofu22	Trn652	F	TTTGCAACAGAAACCTTATCCTG	AC$_{(11)}$	6-FAM	60.15	23	6	152-164	Poly. See Table 3.1
	LT903744	R	TATATTGCCTCTGGCCGTTG			60.98			(162)	
Ofu23	Trn407	F	CCTGCATATCCCAATATCATCC	CCAT$_{(10)}$	HEX	60.38	20	10	142-183	Poly. See Table 3.1
	LT903745	R	GGGAGGTTCAGGTTGTAATGC			60.74			(171)	
Ofu24	Trn442	F	ATGCATGGAAGCTGCTAACC	ATCT$_{(9)}$	6-FAM	60.24	22	8	148-177	Poly. See Table

Locus	Clone name and ENA accession number		Primer sequence (5’- 3’)	Repeat motif	Fluoro-Label (F)	T_m	*n*	A	Observed (Expected) allele size (bp)	Outcome
										3.1
	LT903746	R	ATCTGAGGTGGTCATCATTCTTAAC			59.80			(169)	
Ofu25	Trn126	F	TAGACCAGGCTGCTCAAAGC	TTTGT$_{(8)}$	HEX	60.68	22	10	221-226	Poly. See Table 3.1
	LT903747	R	TCCACCTCACCGTACTGGAT			60.39			(239)	
Ofu26	Trn825	F	CCTGGGAATAAACAGGAAAGC	AAAC$_{(8)}$	6-FAM	59.95	22	4	189-198	Poly. See Table 3.1
	LT903748	R	ATCAGCCAAGGTTTGACCAC			59.97			(190)	
Ofu27	Trn11858	F	AGTCACCTCAGAAACTGATTTGG	TTCC$_{(17)}$	HEX	59.67	13M	20	225-447 (238)	Poly.
	LT903749	R	CGATGAGGCAGTTAGCACAG			59.62	10F	8	229-325 (238)	Z – Linked
Ofu28	Trn15171	F	CAGCAGACTACTGAACACCACAG	GT$_{(18)}$	6-FAM	60.08	21	18	119-215	Poly. but rejected due to deviation from HWE ($p < 0.0001$) and high null allele frequency (0.16)
	LT903750	R	TTGGAGTTGGGAGAGTTTGG			60.02			(140)	
Ofu29	Trn18160	F	ACCACCAGTTATTTGCTCCTTC	CT$_{(15)}$	6-FAM	59.53	22	6	199-218	Mono.
	LT903751	R	TCTCTAGGGCGCCTATACTGAC			59.90			(204)	
Ofu30	Trn20523	F	CCATGTCCTCCAGAGATGCT	TG $_{(29)}$	6-FAM	60.22	23	2	171-203	Unreliable
	LT903752	R	GGCACTCGCATACATTCACA			60.70			(235)	
Ofu31	Trn3313	F	GCAGGGAGAAATCCTGGAG	CA$_{(15)}$	HEX	59.43	21	21	119-187	Unreliable

Locus	**Clone name and ENA accession number**		**Primer sequence (5'- 3')**	**Repeat motif**	**Fluoro-Label (F)**	T_m	n	**A**	**Observed (Expected) allele size (bp)**	**Outcome**
	LT903753	R	GTATTTCGGCGATGCAATG			59.85			(146)	
Ofu32	Trn7015	F	TAATGTCCGCCGAGCTTC	GT$_{(26)}$	HEX	59.91	23	-	-	No amp.
	LT903754	R	AACGGCGACTGTCAGAGTG			60.04			(182)	
Ofu33	Trn7163	F	[HEX]TTCCCTTCTGCCAGGTTTC	GT$_{(16)}$	HEX	60.18	21	2	234-387	Mono.
	LT903755	R	GTGTTTCATTGCCGTATGTCC			60.25			(200)	
Ofu34	Trn7656	F	TATGATGCATGCACACTAATGC	CA$_{(22)}$	6-FAM	59.62	23	-	-	No amp.
	LT903756	R	TACCTCCCACTCCAAAGACG			60.10			(149)	
Ofu35	Trn8311	F	GAAAGTCAACCTTCCCTCCAG	AC$_{(16)}$	6-FAM	60.10	22	6	135-145	Unreliable
	LT903757	R	CCTGTGCTTTGAAGGGACTC			59.84			(150)	
Ofu36	Trn281	F	AATACAGCCCTGCTCGTTTG	GT$_{(17)}$	HEX	60.27	23	-	-	No amp.
	LT903758	R	GATCATGCCCACCGACTC			60.01			(123)	
Ofu37	Trn381	F	CCATCATGGTATCTGCCTTTC	GAA$_{(23)}$	6-FAM	59.40	13M	14	160-255 (190)	Poly.
	LT903759	R	AGCATTGGTAATCACAAAATCG			59.01	10F	8	160-271 (190)	Z-Linked
Ofu38	Trn8242	F	TGCAATGCCAGTAGATGGAC	AC$_{(34)}$	HEX	59.68	22	9	118-162	Unreliable
	LT903760	R	TGCGTTCCGTTAAGCAGAG			60.14			(169)	
Ofu39	Trn12673	F	TTGGATTCGCACACCATTC	ATCTC$_{(20)}$	6-FAM	60.47	23	-	-	No amp.
	LT903761	R	GTGGCACTGACCAGAGGAAG			60.86			(293)	
Ofu40	Trn13248	F	CTTGATAGGCAGGGATGGAG	AAAG$_{(38)}$	HEX	59.65	23	-	-	No amp.
	LT903762	R	CATGATTTATCTTGGCCTCTAGC			59.28			(293)	
Ofu41	Trn379	F	TGACACAAGGTCAGCAGGAG	GT$_{(14)}$	6-FAM	60.02	19	14	136-168	Unreliable
	LT903763	R	AGCAGACAAGCCCCAGTTC			60.40			(146)	
Ofu42	Trn193	F	TGAGTTTAATGCTATCTGCCTGTTAC	TG$_{(13)}$	HEX	60.10	22	11	222-252	Poly. but
	LT903764	R	TCCAGCCTCAGCCACTATTC			60.36			(225)	rejected due to deviation

Locus	Clone name and ENA accession number		Primer sequence (5’- 3’)	Repeat motif	Fluoro-Label (F)	T_m	*n*	A	Observed (Expected) allele size (bp)	Outcome
										from HWE ($p < 0.0001$) and high null allele frequency (0.23)
Ofu43	Trn40	F	ACTGGACAGCTTGTCCTTGC	TG$_{(13)}$	6-FAM	60.45	10M	5	156-168 (212)	Poly.
	LT903765	R	CGTGGGCAGAGACGATATTC			60.62	10F	4	160-168 (212)	Z-Linked
Ofu44	Trn655	F	GATCAGGCAGTTGGACTAAATGA	CTATC$_{(13)}$	HEX	60.50	22	10	300-364	Unreliable
	LT903766	R	CTGAGCCTGGAGGTCTTCAA			60.52			(315)	
Ofu45	Trn106	F	ACAAGTGAGCAGGCAGCAG	TG$_{(13)}$	6-FAM	60.35	23	-	-	No amp.
	LT903767	R	TTTATGGGAGCTGCTGAACC			60.21			(270)	
Ofu46	Trn814	F	GTCGGGAAGAGCTGTCTCAG	GT$_{(11)}$	6-FAM	60.14	23	8	292-312	Unreliable
	LT903768	R	AACCGGCAGTCAATTTGC			59.65			(304)	
Ofu47	Trn685	F	TGTACATTCAGTGTCCAGTTGCT	CTAC$_{(11)}$	HEX	59.72	19	10	276-312	Unreliable
	LT903769	R	GATCACACTAAACTTAAGCAGAAATGA			59.35			(303)	
Ofu48	Trn516	F	ACCAGAAGTGCGGAAAGATG	GGAT$_{(8)}$	HEX	60.25	18	2	445-461	Mono.
	LT903770	R	GGTCCTTCAGGGAGCTACG			59.81			(233)	
Ofu49	Trn468	F	TTTCTTGCTGGCAGAGGTG	TGC$_{(8)}$	6-FAM	60.12	21	2	226-232	Mono.
	LT903771	R	GCGAACTCATGAACTTCAACC			59.73			(231)	
Ofu50	Trn841	F	TGTGGCCATGCAAGAGATAG	GTG$_{(8)}$	HEX	59.82	22	2	263-394	Mono.
	LT903772	R	GATCCACTGAACCACTATGTGC			59.48			(263)	

ENA is the European Nucleotide Archive: https://www.ncbi.nlm.nih.gov/bioproject/PRJEB21955, T_m is the Primer melting temperature calculated using PRIMER3 v 0.4.0 (Koressaar & Remm 2007; Untergasser *et al*. 2012), *n* is the number of individuals tested, A number of alleles observed Poly. = polymorphic, Loci were homozygous in all females (F) genotyped but heterozygous in some males (M), suggesting Z-linkage (individuals were sexed using three markers (Z002A and Z002D (Dawson 2007) and Z43B (Dawson *et al*. 2016), Mono. = monomorphic, No amp. is where the primer failed to amplify, Unreliable is due to any of the following: amplification of non-primer peaks, poor scoreability of alleles or poor consistency of controls. The PCR programme used was: 95°C for 15 min, followed by 44 cycles of 94°C for 30 s, 56°C for 90 s, 72°C for 90 s and a final step of 72°C for 30 min.

Appendix 4

Details of microsatellite markers used for sooty tern genotyping and genotyping error rates.

Locus	Clone name, ENA accession number/Reference	Multiplex/ Fluoro-Label (F)	*n*	A	Allele size range (bp)	H_O	H_E	Est null allele Freq.	ε_1 (n = 50)	ε_2 (n = 50)
Ofu01	Trn17616 LT903723	7/NED	217	20	197-243	0.86	0.88	0.012	0.006	0.011
Ofu02	Trn23851 LT903724	2/HEX	218	29	189-361	0.93	0.94	0.003	0.012	0.000
Ofu03	Trn25452 LT903725	5/6-FAM	219	16	138-176	0.80	0.84	0.030	0.007	0.019
Ofu04	Trn4256 LT903726	5/HEX	219	24	128-180	0.84	0.87	0.027	0.000	0.012
Ofu05	Trn171 LT903727	4/6-FAM	216	23	87-133	0.89	0.92	0.014	0.006	0.011
Ofu06*	Trn352 LT903728	7/HEX	218	13	246-282	0.73	0.86	0.09	-	-
Ofu07	Trn436 LT903729	4/NED	219	10	156-208	0.82	0.88	0.039	0.010	0.000
Ofu08	Trn640 LT903730	1/6-FAM	219	38	272-368	0.87	0.90	0.016	0.010	0.000
Ofu09	Trn643 LT903731	6/6-FAM	219	19	164-212	0.92	0.92	-0.001	0.017	0.000
Ofu10	Trn16824 LT903732	2/NED	218	29	130-230	0.93	0.94	0.003	0.016	0.005
Ofu11	Trn13992	1/6-FAM	219	16	156-208	0.56	0.62	0.061	0.032	0.000

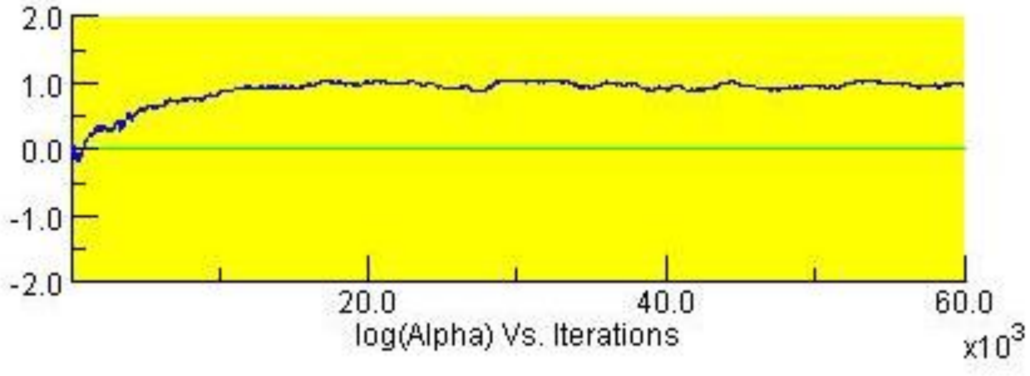
Locus	Clone name, ENA accession number/Reference	Multiplex/ Fluoro-Label (F)	*n*	A	Allele size range (bp)	H_O	H_E	Est null allele Freq.	ε_1 (n = 50)	ε_2 (n = 50)
	LT903733									
Ofu12	Trn129 LT903734	3/6-FAM	219	13	300-334	0.76	0.78	0.013	0.000	0.006
Ofu13	Ofu839 LT903735	6/HEX	219	10	133-171	0.78	0.81	0.019	0.006	0.000
Ofu14	Ofu897 LT903736	4/HEX	214	12	345-369	0.83	0.81	-0.01	0.007	0.006
Ofu15	Trn191 LT903737	2/6-FAM	218	14	328-356	0.78	0.79	0.007	0.015	0.000
Ofu16	Trn484 LT903738	6/6-FAM	219	9	313-331	0.66	0.67	0.007	0.006	0.000
Ofu17	Trn715 LT903739	5/NED	218	15	181-213	0.77	0.86	0.056	0.000	0.000
Ofu18	Trn269 LT903740	1/HEX	218	6	296-306	0.73	0.79	0.023	0.015	0.000
Ofu19	Trn15 LT903741	6/6-FAM	219	12	94-120	0.73	0.76	0.018	0.000	0.000
Ofu20	Trn551 LT903742	3/HEX	219	21	217-287	0.87	0.89	0.014	0.026	0.000
Ofu21	Trn121 LT903743	5/6-FAM	219	35	265-337	0.96	0.96	-0.002	0.017	0.012
Ofu22	Trn652 LT903744	6/NED	219	9	150-168	0.74	0.74	-0.004	0.011	0.000
Ofu23	Trn407 LT903745	1/HEX	218	15	142-204	0.80	0.80	-0.002	0.005	0.000
Ofu24	Trn442 LT903746	3/6-FAM	219	9	143-181	0.86	0.84	-0.013	0.000	0.000

Locus	Clone name, ENA accession number/Reference	Multiplex/ Fluoro-Label (F)	*n*	A	Allele size range (bp)	H_O	H_E	Est null allele Freq.	$\mathcal{E}_1$ (n = 50)	$\mathcal{E}_2$ (n = 50)
Ofu25	Trn126 LT903747	5/HEX	218	19	222-284	0.73	0.76	0.019	0.12	0.008
Ofu26	Trn825 LT903748	4/6-FAM	218	8	186-206	0.61	0.60	-0.003	0.005	0.000
Z002A	Dawson (2007)	2/6-FAM	107M	1	249 (Z)	0	-	-	-	-
			112F	2	249 (Z) and 252 (W)	1.00	-	-		
Z002D	Dawson (2007)	1/6-FAM	107M	1	127 (Z)	0	-	-	-	-
			112F	2	122 (W) and 127 (Z)	1.00	-	-		
Z43B	Dawson et al. (2016)	7/6-FAM	107M	1	270 (Z)	0	-	-	-	-
			112F	2	266 (W) and 270 (Z)	1.00	-	-		

ENA is the European Nucleotide Archive: https://www.ncbi.nlm.nih.gov/bioproject/PRJEB21955, *n* is the number of individuals tested, A is the number of alleles observed, H_O is the observed heterozygosity, H_E is the expected heterozygosity, Est null allele Freq. is the estimated null allele frequency, M is the number of males and F is the number of females identified using the sex-typing markers (Z002A, Z002B (Dawson 2007) and Z43B (Dawson *et al*. 2016). $\mathcal{E}_1$ is the allelic dropout rate, $\mathcal{E}_2$ is the false allele rate, note n = 50 for the estimation of genotyping error rate. * locus Ofu06 not included in full analysis.

Appendix 5

Convergence of the alpha chain during STRUCTURE analysis.

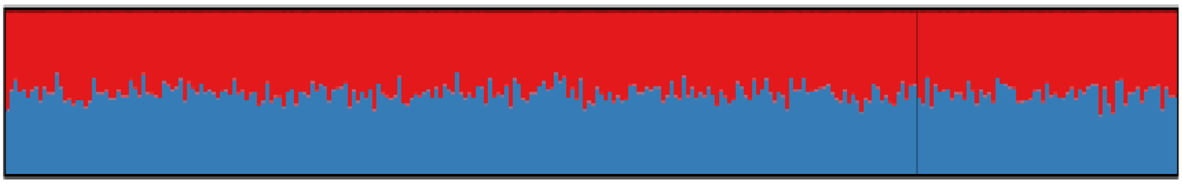


Appendix Figure 5.1 Variation in *alpha* during increasing iterations in a run using STRUCTURE. Example illustrates run 3 of *K* = 1 with a burn-in period of 100,000.

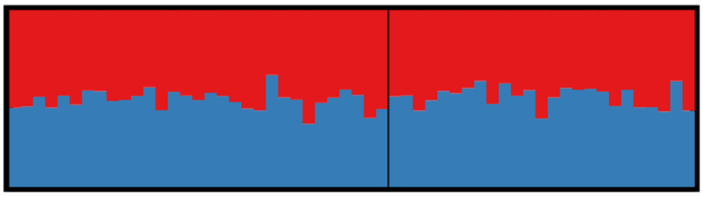
Appendix 6

The polymorphic information content (PIC) was used to select loci with the lowest PIC values as a further measure to assess genetic diversity given that the microsatellite loci used were highly variable which may have prevented identification of population structure.

a)



b)



Appendix Figure 6.1 STRUCTURE plots showing a lack of genetic differentiation between sampling sites using **a)** the 10 markers with the lowest PIC values and 219 unrelated individuals, and **b)** with the least related individuals (Mars Bay = 31 and Waterside = 25 individuals).

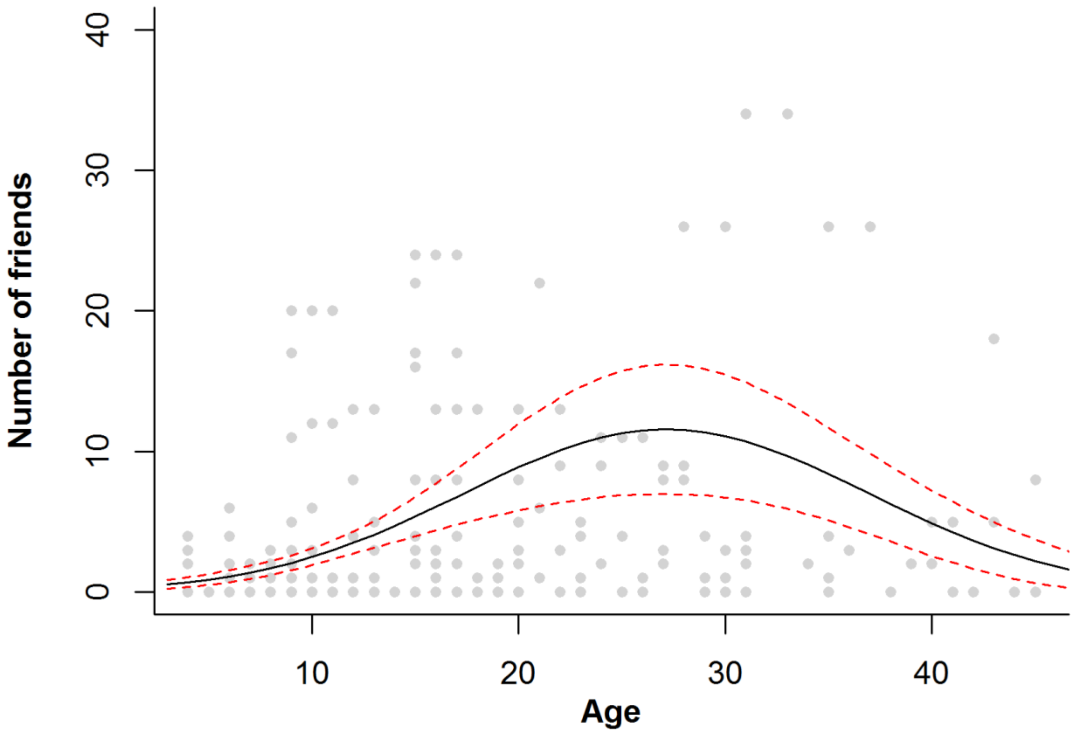
Appendix 7

Outputs of the relationship between the number of chick friends and chick age.

The number of chick friends varied with chick age (Appendix Table 7.1). There was high variation in the number of friends at all age ranges (Appendix Fig. 7.1). However, there was a significant quadratic effect of age in the model (Appendix Table 7.1). As chicks aged they formed larger groups (Appendix Fig. 7.1). At approximately 28 days of age numbers peaked and then declined as chicks approached fledging.

Appendix Table 7.1 Results of a negative binomial zero-inflated mixed model (glmmTMB package, R Version 3.4.2) examining the number of chick associates by sooty tern chick age. The model included a quadratic function of age and chick ID as a random effect.

Predictor	**Coeff.**	**SE**	**Z**	***P***
Intercept	-1.61	0.44	-3.65	< 0.001
Age	0.28	0.04	6.51	< 0.001
Age^2	-0.005	0.0009	-5.36	< 0.001
Zero-inflation model	-2.23	0.85	-2.64	0.008



Appendix Figure 7.1 The number of focal sooty tern chick friends by age on Ascension Island in 2015-2016. Grey dots represent the raw data. The solid black line is the prediction curve from a zero-inflated mixed model regressing the number of friends against chick age with a quadratic function of age. Dashed red lines are the 95% confidence intervals. The random effect is not included in the model for visualization purposes. n = 297 observations.