Comparative breeding biology of the Northern Rockhopper Penguin *Eudyptes moseleyi* on Gough and Nightingale Islands

Rukaya Johaadien

Supervisor: Dr Peter G. Ryan

Co-supervisor: Dr Antje Steinfurth

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Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

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ABSTRACT

The Northern Rockhopper Penguin *Eudyptes moseleyi* is listed as Endangered due to an estimated 57% decrease in breeding numbers over the past 37 years. Approximately 85% of the global population breeds at the Tristan da Cunha archipelago (Tristan, Inaccessible and Nightingale Islands) and nearby Gough Island in the central South Atlantic Ocean. The population on Gough Island declined by 50-60% between 1982 and 2005, but in the Tristan da Cunha archipelago the population trend over the last few decades is believed to be stable despite long-term human exploitation (particularly egg collection on Nightingale Island in recent years). This study compares aspects of the breeding biology on Gough Island (where population numbers are decreasing) and Nightingale Island (where numbers are thought to be stable) based on data gathered from five colonies in the 2012/13 and 2013/4 breeding seasons. On Nightingale Island, breeding success was 6.5% lower and 40-day old chick mass 47% less (implying poor juvenile recruitment) compared to on Gough Island. Poor foraging conditions for birds on Nightingale Island is the most probable explanation for these results, and future studies should focus on the foraging locations used by birds on both islands. Additionally, egg collection practices on Nightingale Island may have had a negative impact on the population, and I recommend that the temporary ban on egg-collection at Nightingale Island is made permanent. It is also possible that the population on Gough Island is no longer in decline, or is declining for reasons unrelated to breeding success; to verify this and confirm the findings of this study, future population trends and chick fledging mass on both islands should be monitored over the long-term.

INTRODUCTION

Penguins (Spheniscidae), are a group of 18 species of marine, flightless birds living almost exclusively in the Southern Hemisphere. Although they spend most of their lives at sea, they are dependent on land for crucial parts of their life cycle: breeding, rearing chicks and moulting (Williams 1995). They are susceptible to human-induced disturbances, both direct (e.g. harvesting for food or bait) and indirect (e.g. alterations in trophic patterns due to climate change), on land and in the marine environment (Walther et al. 2002; Pörtner & Knust 2007; Boersma 2008). Ocean connectivity dictates that an effective on-shore and offshore penguin conservation programme would need to operate on a global decadal scale, necessitating long-term international cooperation and investment (Allison et al. 1998). Penguin conservation is therefore a difficult task, and it is unsurprising that 15 of the 18 species are listed as Threatened or Near Threatened by the IUCN (International Union for the Conservation of Nature). All seven species of crested penguins (*Eudyptes)* are listed as Threatened (an umbrella grouping that includes the categories Critically Endangered, Endangered and Vulnerable), with the Northern Rockhopper Penguin *Eudyptes moseleyi* categorised as Endangered, due to a 57% estimated reduction in global breeding pair numbers over the past 37 years (Birdlife International 2010). The current global population is estimated at 265 000 pairs, approximately 85% of which breed in the South Atlantic Ocean at the Tristan da Cunha archipelago (Tristan, Inaccessible and Nightingale Islands, with Middle and Stoltenhoff Islets) and nearby Gough Island, with the remaining 15% breeding in the Indian Ocean on Amsterdam and St Paul Islands (Cuthbert et al. 2009).

Global population change in ecology is defined as recruitment minus mortality (Brown & Brown 2000). While mortality is a crucial demographic parameter for the survival of long-lived species such

as the Northern Rockhopper Penguin, from a management perspective it is difficult to improve adult survival using island-based strategies pivotal in conservation efforts. Breeding success and juvenile recruitment are therefore of critical importance in maintaining population numbers and healthy population dynamics (in terms of demographics), particularly for slow-reproducing species such as penguins. However, breeding success and juvenile recruitment can vary substantially between different locations and colonies, and the factors driving this variation are poorly understood in ornithology (Brown & Brown 2001). Additionally, chick survival yields a relatively small change at the population level of long-lived species and is often not sufficient to halt the long-term decline.

By the time they are detected, location-specific components causing significant adverse changes in the population will usually have been in operation for many years. As a result, timely conservation measures are rarely implemented and often do not immediately improve population trends due to the typically low recruitment rates (Brown & Brown 2001). The impact of adverse population change is often exacerbated by shrinking and fragmentation effects on colonies and have important implications in formulating effective conservation plans (Croxall & Rothery 1991): colonies below a certain threshold size might enter a fatal decline because the edge-to-area ratio of a colony increases mortality risks, as predation generally occurs on colony edges (Jackson et al. 2005). Therefore, a timely, in-depth, and location-specific knowledge of demographic functioning (particularly the breeding success rates of a species) is crucial for effective conservation planning (Lande 1988; Croxall & Rothery 1991) and for use in conservation tools such as population viability analysis (White 2000).

Introduced species have played a role in the historical decline of the Northern Rockhopper Penguin: on Tristan (and briefly on Inaccessible Island), penguins were subject to predation by introduced wild pigs (*Sus scrofa),* which became extinct in the 1870s (Moseley 1892), and semi-feral dogs (*Canis familiaris*), which are recorded as having killed penguins in the 1960s (Falk-Rønne 1967). However,

historical population declines have occurred mainly as a result of human exploitation. On St Paul Island penguins were often used as bait for fishing (Guinard et al. 1998), and the decline on Tristan is widely attributed to human exploitation on a vast scale (egg collection, fishing bait, extraction of oil and head-plumes and feather collection from moulting birds) – in one year more than 25 200 penguin eggs were collected (Rogers & Rogers 1928; Richardson 1984). These practices stopped on the main island in the 1950s, with egg collection still permitted on Nightingale and Middle Islands (Elliott 1957). In the 1960s and 1970s egg collection trips typically lasted for several days, with over 25 000 eggs collected on each trip (Richardson 1984; Lovegrove 2012), although in recent years it is believed that fewer eggs are collected (Trevor Glass, personal communication). In theory egg collection should be sustainable, as only A-eggs (which are not usually viable) may be harvested, but this has never been enforced, and both A-eggs and B-eggs are harvested equally, based on data collected in 1999 (PG Ryan, unpublished data).

Following the cessation of direct exploitation, common factors adversely affecting penguin and seabird breeding success (and hence population trends) include poor chick provisioning (which affects chick mortality and juvenile recruitment, (Costa 1991; Olsson 1997; McClung et al. 2004; Oro et al. 2004; Crawford et al. 2006), disrupted behavioural patterns from increased human disturbance (Giese 1996) and oil spills (Giese et al. 2000; Wolfaardt et al. 2008). The causes of the recent decline of Northern Rockhopper Penguins are unknown, but have been linked to variations in sea surface temperature and El Nino Southern Oscillation (ENSO) events (Guinard et al. 1998), and to increased predation and competition by the Subantarctic Fur Seal *Arctocephalus tropicalis,* which have have increased following the decline of commercial sealing (Bester 1977; Ryan & Kerr 2011). It is also possible that guano collection (common practice on Nightingale Island) may adversely disturb the colony environment and micro-habitat, as has been seen in other species (Hays 1984).

General year-to-year variability should be considered when evaluating population declines. Changes in climate can affect foraging (Dehnhard et al. 2013a), and heavy rains can cause landslips which may routinely destroy penguin colonies, particularly on islands where colonies are located at the bottom of cliffs, such as Gough Island (Swales 1965). Predation of chicks by other seabirds (particularly the Subantarctic Skua (*Catharacta antarctica*) (Wilson et al. 2010)) is also a factor, and varies between years, locations and between different demographic portions of the populations (Ryan et al. 2008; Ryan & Kerr 2011; Cuthbert 2013).

Population trends and breeding studies

Three studies have examined the breeding success of Northern Rockhopper Penguins (Williams & Stone 1981; Guinard et al. 1998; Wilson et al. 2010). The most extensive study was undertaken over a period of three years on Amsterdam Island, where the proportion of nests producing a fledgling varied from 28% in 1993 to 52% in 1995 (Guinard et al. 1998). This increase in breeding success appears to be at odds with the population trends on Amsterdam and St Paul Islands documented between 1971 and 1993, and may simply be the result of inter-annual variation in breeding success in this species (Guinard et al. 1998). On Amsterdam Island the population decreased by 43% over this period and on St Paul Island the population increased by 56% (Figure 1). This increase was hypothesised as being a delayed recovery effect, as the population was heavily exploited in the 1930s by fishers on St Paul Island, while Amsterdam Island was apparently left untouched (Guinard et al. 1998). The study recorded around 33 900 breeding Northern Rockhopper Penguin pairs on these two islands in 1993. In 2003, a second study monitoring chicks (up until 28 days of age) on Amsterdam Island, and Southern Rockhopper Penguins in two other locations, showed that chick growth rates on Amsterdam Island were low, suggesting prey availability in the area might have been poor (Tremblay & Cherel 2003).
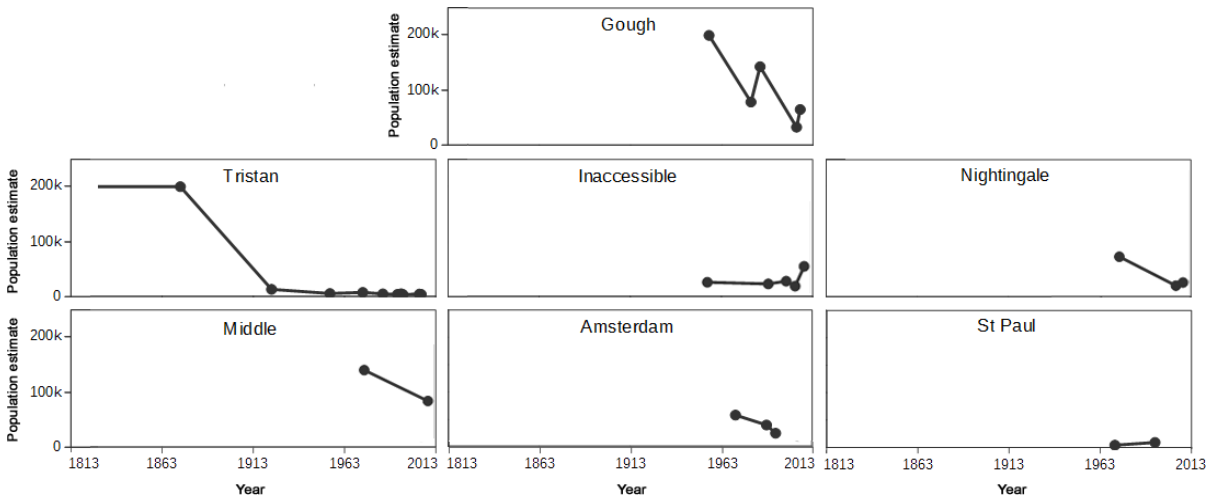
Figure 1: Northern Rockhopper Penguin *Eudyptes moseleyi* population trends throughout its range in the South Atlantic and Indian Oceans. Circles represent population censuses. Data extracted from published literature.

Data from the 2005-06 breeding season on Gough Island show that breeding success was on average 21% (based on two small colonies containing 50 and 52 nests) (Wilson et al. 2010). Hatching success was significantly higher in a nearby larger colony (67%) than in the smaller colonies (39% and 44%). In the same study, parental aggressiveness and the numbers of nesting birds in a 1.5 m radius were found to be positively correlated with breeding success (Wilson et al. 2010). Cuthbert et al (2009) estimated a decline of 50-60% in the Gough Island population over 23 years (3-4% per year), based on average census numbers from 1979 – 1984 and 2004 – 2006 (Figure 1). The most recent published data from Gough Island (Cuthbert et al. 2009) indicate that there are about 65 000 breeding pairs on the island, based on a 2006 census using scan counts of most of the coastline.

A breeding study in 1980-81 on the main island of Tristan, in the Tristan da Cunha archipelago estimated an average hatching success of 56% (higher than recorded at either Amsterdam or Gough Islands) and put the percentage of nests producing a fledged chick at approximately 54% (Williams & Stone 1981). This high breeding success is at odds with the population trend (Figure 1): in 2009 Tristan

had 6 700 Northern Rockhopper Penguin breeding pairs (Robson et al. 2011), far fewer than recorded in 1824 when Tristan was described as having "thousands and hundreds of thousands" of penguins (Verrill 1895). Following heavy declines, the Northern Rockhopper Penguin officially became a protected species in 1984 (Cuthbert et al. 2009). Since then, regular counts suggest that the population on Tristan is broadly stable. It may have even increased slightly in the last two decades; between 3 200 – 4 500 pairs were estimated for seven years between 1992 and 2005 (Cuthbert et al. 2009), and 6 700 pairs in 2006 (Robson et al. 2011).

Trends in penguin numbers on Inaccessible Island are poorly known, and no breeding studies have occurred there. Inaccessible Island was thought to have a stable population of 22 300 pairs, based on estimates made in 1955 (Elliott 1957), 1989 (Ryan et al. 1990), 1999 and 2004 (Ryan 2006). In 2009 a more thorough survey estimated around 55 000 pairs (Figure 1), an increase most likely due to methodological errors in the previous surveys (Robson et al. 2011).

The breeding success of Northern Rockhopper Penguins on Nightingale Island has not been documented (despite being the only site still subject to human exploitation) and few studies have assessed population trends on the island (Figure 1). In 1973, 25 000 pairs were estimated to breed on Nightingale Island (Richardson 1984), 19 500 pairs in 2007, (Cuthbert et al. 2009) and 25 000 pairs again in 2009 (Robson et al. 2011). The population had therefore been considered stable until March 2011, when the MS *Oliva* (carrying 65 000 tonnes of soya beans and 1 500 tonnes of bunker oil) ran aground off the north-western coast of Nightingale Island. Thousands of penguins at the end of the moulting process were oiled on Middle, Nightingale and Inaccessible Islands (RSPB 2012). The long-term effects of the oil spill are unknown, although initial assessments indicate that the population has not been severely affected (RSPB 2012). Legislation permitting residents of Tristan (Tristanians) to

harvest eggs from Nightingale has been temporarily discontinued while the post-oil spill situation is evaluated further (Cuthbert et al. 2009; RSPB 2012).

Nightingale Island has two small (0.1 km^2) off-shore islets, Middle and Stoltenhoff Islands, of which the latter is less accessible due to sheer 80 m high sea cliffs and does not support any penguins (Richardson 1984; Ryan et al. 2010). Low-lying Middle Island (50 m above sea level) is separated from Nightingale Island in the south by a 300 m-wide channel (Baker et al. 1964), and in 1973 was estimated to hold 100 000 breeding pairs of Northern Rockhopper Penguins (Richardson 1984). A second survey in 2009 estimated 83 000 pairs (Robson et al. 2011), suggesting (when taking into account the imprecise nature of the estimates) that population on Middle Island has remained roughly stable over the last two to three decades (Figure 1).

Rationale

The global population declines provide a bleak outlook for the future of the Northern Rockhopper Penguin, and yet it has proven difficult to formulate an effective conservation plan for this species (Birdlife International 2010; Dehnhard et al. 2013b). Understanding the factors driving population trends is crucial for effective conservation, and yet few studies have focussed on breeding success and chick growth for the Northern Rockhopper Penguin. The study monitoring breeding success on Amsterdam and St Paul Islands in the Indian Ocean was conducted over 20 years ago, and the breeding studies that cover the species range in the South Atlantic are not extensive, encompassing only one year on Tristan (conducted over 30 years ago), and one year on Gough Island. There is a need for more extensive surveys providing a more detailed understanding of the breeding biology of this Endangered species in its core range in the South Atlantic.

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The breeding biology of Northern Rockhopper Penguins on Gough Island and the Tristan da Cunha archipelago is of particularly interest because together these localities provide breeding habitat for 85% of the global population and have markedly different population trends. In this study, I compare the breeding success and chick growth of Northern Rockhopper Penguins at two study sites (Gough and Nightingale Islands) over two consecutive breeding seasons (2012/13 and 2013/14).

I monitored chick growth in tandem with breeding success to aid in determining stresses on the population (Barrett & Rikardsen 1992). Like other seabirds, the Northern Rockhopper Penguin favours survival over current reproductive attempts, thus focussing on their own maintenance over the provisioning of their offspring (Pianka 1970; Stearns 1976; Booth & McQuaid 2013). Chick growth is therefore a highly variable characteristic influenced by the unpredictable food availability and by complex time and energy constraints on the parents during the breeding season (Dunn 1975; Hudson 1983), and thus is a sensitive indicator of adverse conditions affecting population trends.

My aim was to detect any differences between the breeding biology of Northern Rockhopper Penguins in a declining population (Gough Island) and a seemingly stable population (Nightingale Island). I expected to find lower breeding success and less robust chick growth on Gough Island compared to Nightingale Island, reflecting the long-term declines in the population on Gough Island.

I supplemented this comparison of breeding biology between islands with an exploration of the influence of inter-colony variation on breeding success and chick growth. I used this information with a map of colonies on Nightingale Island in the 1970s to examine historical changes on the island. The effect of increased fragmentation and size reduction in colonies on breeding success has been explored for other seabird species (Jackson et al. 2005; Sherley et al. 2014), but has only been quantified for Northern Rockhopper Penguins on Gough Island during the incubation and hatching period (Wilson et

al. 2010). Few studies of penguin species have examined inter-colony variation in breeding success, and yet it may be a crucial tool for developing our understanding of population dynamics, the mechanisms of population regulation (Frederiksen et al. 2005), and the possible demographic implications of large-scale events such as climate change (Dehnhard et al. 2013b).

METHODS

Study species

Little is known of the breeding biology of the Northern Rockhopper Penguin, as it was considered a sub-species of the Rockhopper penguin (*Eudyptes chrysocome*) until 2006. Most studies of rockhopper penguins took place at more southerly breeding locations, pertaining to what is now known as the Southern Rockhopper Penguin (*Eudyptes chrysocome*). The decision to split the species was based on morphological, vocal and genetic differences which suggest that the populations divided 680 000 years ago with little or no subsequent gene flow exchange (Jouventin et al. 2006). The remote nature of the Northern Rockhopper Penguin's breeding sites was a disincentive for the undertaking of breeding and demographic studies on Rockhopper Penguins in Tristan, Gough and Amsterdam/St Paul Islands, and, until the 2006 species split, there was no imperative need to remedy this (Birdlife International 2010).

Northern Rockhopper Penguins nest in colonies of variable size and nest-density (Richardson 1984; Wilson et al. 2010). Their nests are built out of grass, sticks, feathers and stones in the most suitable available natural habitat, ranging from rocky shores to dense tussock grass. Like other crested penguins, Northern and Southern Rockhopper Penguins lay two eggs. The first egg (A-egg) is laid four days before and is on average about 25% smaller in volume than the B-egg (Demongin et al. 2010a). Rockhopper Penguins producing larger than average B-eggs tend to also produce larger A-eggs, although the volume of A-eggs is twice as variable as that of B-eggs (Demongin et al. 2010a). In more than 99% of cases, the A-egg fails to produce a fledged chick (Cuthbert 2013), even in captivity when food resources are abundant (Stein & Williams 2013). This order of laying (a small egg followed by a

large, more favoured egg) is unique among birds. The obligate brood reduction also is unusual, as is the extreme size difference between the eggs. The reasons for these remarkable traits are still debated (Stein & Williams 2013).

Eggs are incubated for 32–34 days, with the first week of incubation undertaken by the male and female together. Following this, the male leaves to forage and the female stays on the nest and fasts for 3 weeks (Poisbleau et al. 2008). The male returns to the nest about a week before hatching to relieve the female, and she returns as the chicks hatch in order to feed them. The B-eggs usually hatch first, as they are prioritised by being placed more directly against the brood pouch (Burger & Williams 1979). When two eggs hatch, the A-chick invariably dies of starvation within the first week (Cuthbert 2013). Chicks stay in the nest for 20–26 days, known as the "guard" phase, when they are protected by the males while being fed regularly by the females. Following the guard phase, the chick enters the "crèche" phase during which it forms a group with other chicks for thermoregulation and protection from predators (Cuthbert 2013), while waiting to be fed by both males and females (Williams 1995). Northern Rockhopper Penguins appear to vary their diet through the different stages of chick growth: during guard they primarily consume zooplankton, transitioning to fish when chicks crèche (Booth & McQuaid 2013). Chicks eventually moult into a juvenile plumage and fledge 9–10 weeks after hatching, and then go to sea to forage for themselves, only returning to land to moult into their adult the following year (Cuthbert 2013).

Study sites

Gough Island and the Tristan da Cunha archipelago (Tristan, Inaccessible and Nightingale Islands) are part of a chain of South Atlantic volcanic sea-mounts on the east slope of the mid-Atlantic ridge (Ryan 2007). They are separated by about 400 km of sea that is over 3 000 m deep (Figure 2).

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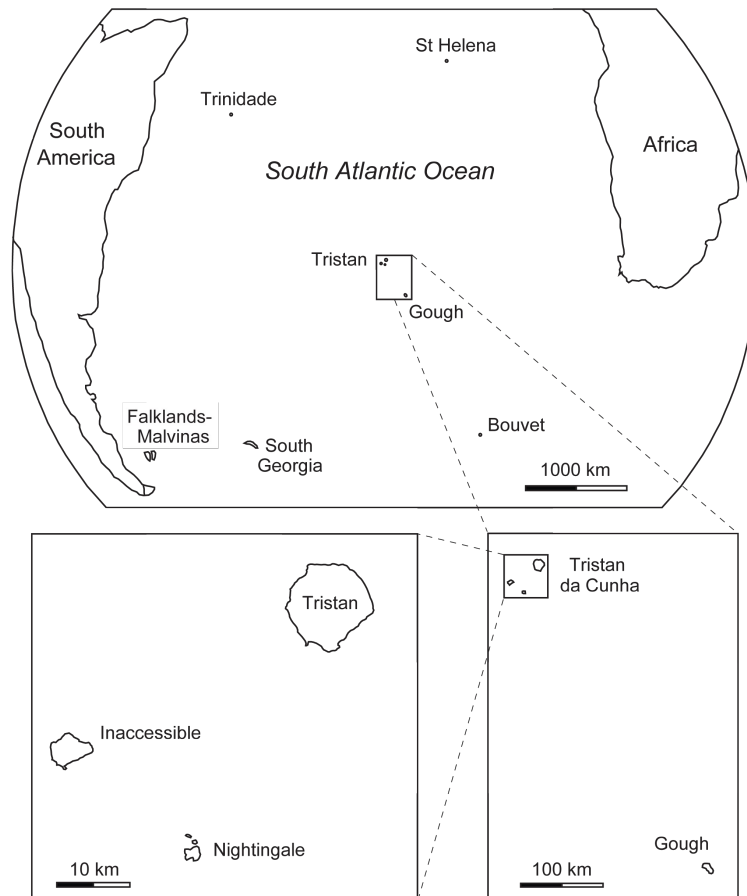
Figure 2: The Tristan da Cunha group (Tristan, Inaccessible, Nightingale, Stoltenhoff and Middle Islands) and Gough Island.

Gough Island

Gough Island (37°18'S, 40°19'W) has an area of 65 km^2 and is uninhabited apart from a weather and scientific research base in the south, manned by six to nine non-permanent staff. The mean annual rainfall at sea-level is 3145 mm and mean monthly temperatures are at their lowest in August (8.9 °C) and highest in February (14.5 °C) (Jones et al. 2003).

Northern Rockhopper Penguins on Gough Island begin breeding at the onset of the austral summer in early October, with chicks fledging in late January/early February (Wilson et al. 2010). They nest on

rocky slopes between the coastal cliffs in pebble and vegetation-lined depressions around much of the island's coast (Figure 3, left). Colonies are typically smaller than in the Tristan da Cunha archipelago (Wilson et al. 2010), and are fragmented within expansive areas of what appears to be previously occupied habitat (Cuthbert et al. 2009), implying colony shrinkages due to a large-scale population decrease.

Nightingale Island

The main islands in the Tristan da Cunha group (Tristan, Inaccessible and Nightingale Islands) are closer to a human settlement than other Northern Rockhopper Penguin breeding locations, as there is a British settlement of some 270 people on the main island of Tristan, which has been inhabited since 1810 (Wace & Holdgate 1976). Northern Rockhopper Penguins in the Tristan da Cunha island group begin breeding in early September, approximately a month earlier than on Gough, with chicks fledging

in early January. Temperatures during the breeding season vary between 10 ºC and 25 ºC, and the mean annual rainfall is 1 680 mm (The World Bank 2014).

Nightingale Island is separated from Inaccessible Island by 20 km, and from Tristan by about 30 km (Figure 2). At 3.2 km^2 it is the smallest island in the Tristan da Cunha archipelago. The highest point, High Ridge, is approximately 400 m above sea level. The majority of the island is covered by dense, 2 m high grass tussocks (*Spartina arundinacea*) which form the habitat for the Northern Rockhopper Penguin colonies (Ryan 2007), shown in Figure 3. A small area in the north-east of the island contains one large colony and three satellite colonies, and there is one small colony on the south coast. In the past two years the largest colony (Sergeant Major) was estimated to contain about 15 500 breeding pairs; the four small colonies ranging from 250 to 1 000 breeding pairs (2013 census).

Tristanians holiday on (and take tourists to) Nightingale Island during the summer, and annually visit the island to harvest penguin guano (about 20 m^3 each year, carried in 0.2 m^3 sacks) from Sergeant Major at the end of the breeding season (Tristan da Cunha Government 2013). Since the 1970s, Tristanians have erected approximately 50 huts on the island close to the penguin colonies, and cut two paths through the grass tussocks (which today separate the Sergeant Major from the satellite colonies). The location and spread of the penguin colonies on the island before these developments is unknown.

Field work

Gough Island

In 2012 and 2013, three colonies on the south-east coast of Gough Island (Figure 4, left) were used to record breeding success for this study: Admirals (40.343°S, 9.878°W), Seal Beach (40.212°S, 9.530°W) and Tumbledown (40.214°S, 9.506°W), which contain about 1 000, 1 600 and 650 breeding pairs respectively. Full-colony ground counts (Figure 5) were undertaken after laying (12 – 18 October 2012 and 17 – 19 October 2013), just after hatching (18 – 21 November 2012 and 22 – 23 November 2013), and just before fledging (10 – 11 January 2013 and 17 January 2014) using techniques described in the Gough Island Bird Monitoring Manual (Cuthbert & Sommer 2004).
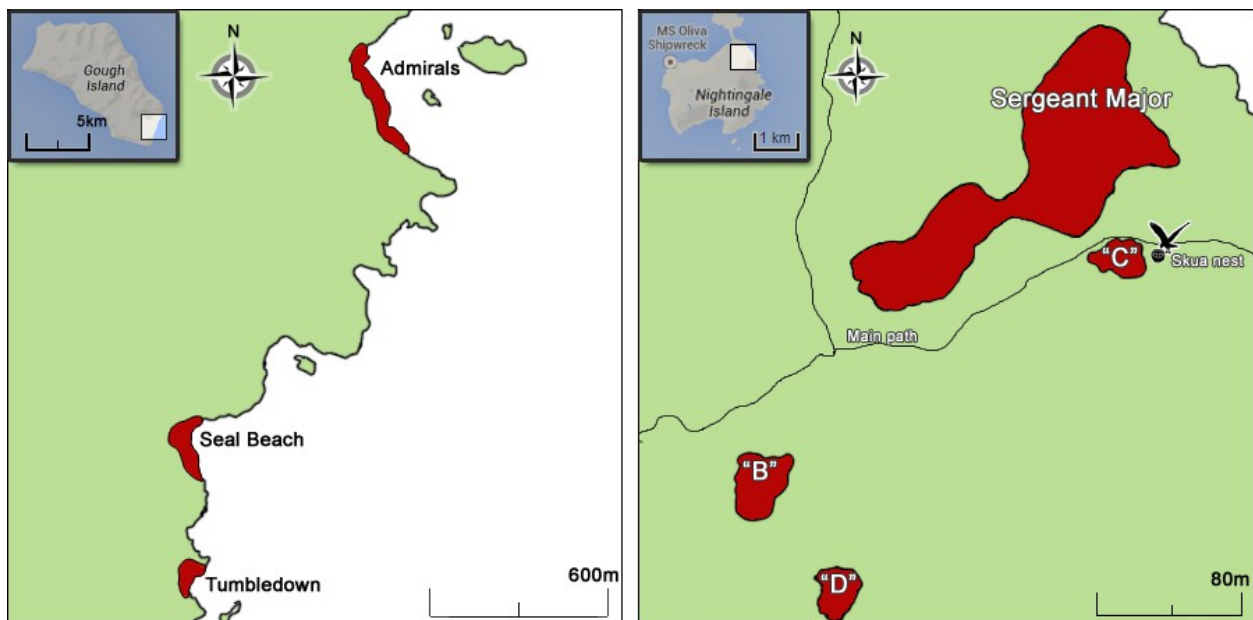
Figure 4: Northern Rockhopper Penguin colonies on Gough (left) and Nightingale (right) Islands used in this study.
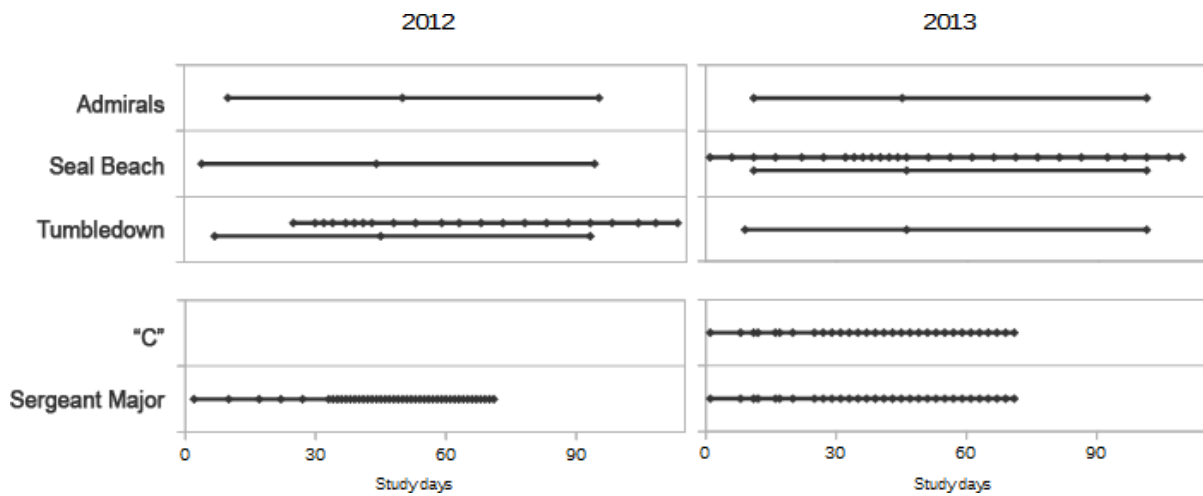
The eggs in 49 random nests at Tumbledown were measured at the beginning of the 2012 breeding season (10 October 2012). Unfortunately due to time constraints, these nests were not marked and monitored through the season as they were in the 2013/14 breeding season on Gough and on Nightingale Island. Instead, 85 nests at Tumbledown were marked approximately two thirds of the way through incubation (2 November 2012). The nests were checked and any chicks measured and weighed every two to six days (Figure 5) until the chicks had either fledged or were moulting into juvenile plumage prior to fledging (29 January 2013).

Measurement methods were kept consistent between years and between islands, as follows: egg length and breadth was measured to the nearest 0.1 mm with calipers; chick head length was measured from the tip of the culmen to the back of the head to the nearest 0.1 mm using calipers, and chick flipper length was was measured from the axilla to the flipper tip to the nearest 1 mm using a ruler. Additionally, in order to control for the digestive state of the chick (Hudson 1983; Williams 1990), chicks were weighed using a digital scale (accurate to the nearest 5 g) at roughly the same time of day.

To identify chicks after they left the nest, they were individually marked with an adhesive Tesa tape flipper band (5 mm-wide strip Tesa-Tape Nr. 4651, Beiersdorf AG, Germany) marked with a Tipex number. Following Calvo & Furness (1992), B-chicks (first-hatched chicks) were marked with blue animal marker to distinguish them from A-chicks. If a parent was observed to be feeding a chick, measurements were taken at a later time in order to not disturb the feeding process.

In the 2013/14 breeding season, 100 nests were marked at Seal Beach and monitored from 9 October 2013, during the laying period. Eggs were measured on the first date they were observed in the nest. During incubation, nests were checked every five days; and once the first chick had hatched (6 November 2013), nests were checked every second day (Figure 5) until the majority of chicks had hatched. Chicks were measured and weighed once hatched, and then re-measured every five days until 25 January 2014. On two occasions in 2012 and one in 2013, inclement weather precluded checking nests and measuring chicks on the allotted day, in which case the study was resumed at the next possible date.

Nightingale Island

In 2012, 102 nests were marked along the eastern periphery of Sergeant Major (37.254°S, 12.2832°W, Figure 4). Seventy nests were marked at the start of the laying period (16 September 2012), and the remaining 32 were marked eight days later. Nests were chosen around the periphery of the colony in order to minimize disturbance. Eggs were measured on the first date they were observed in the nest (usually when the nests were initially marked, as the egg(s) had already been laid). During incubation, nests were checked every five days, and once the first chick had hatched (17 October 2012) nests were checked daily. Chicks were measured and weighed once hatched, and then re-measured every five days until 24 November 2012, at the same time of day (9h00 – 11h00). At this stage, chicks were about 40

days from fledging (Figure 5), but unfortunately it was not possible to monitor chicks until the end of the breeding season as the researchers had to leave the island for logistical reasons.

In 2013, 102 nests were again marked in Sergeant Major, in roughly the same area as the year before. An additional 54 nests were marked in "C" (37.252°S, 12.2833°W, Figure 4), which were used to compare how breeding success might differ between the large Sergeant Major colony and the smaller Nightingale Island colonies. The nests in both colonies were marked at the start of the laying period (15 September 2013). Eggs were measured on the first day they were observed in the nest, and once the first chick hatched (10 October 2012), nests were checked every two days. Chicks were measured and weighed once hatched and then re-measured every six days until until 24 November 2013, which was again about 40 days from fledging (Figure 5). Sergeant Major was checked in the mornings from 9h00 – 12h30, and "C" from 14h00 to 16h00. On 24 of November, measurements were taken of five and ten random chicks in the "B" and "D" colonies respectively. These measurements were taken as control data; to detect any possible bias in the main growth data caused by the disturbance and stress of human proximity and regularly being handled for measurements (e.g. Vertigan et al. 2012). Hatching date was inferred from the dryness of the eggshell and chick. Chicks were recorded as hatching on the day of checking if their eggshells were still noticeably damp (with a membrane which peels easily from the shell) or if they had egg membrane clinging to their down.

In 2013, I recorded the range of reactions of adult penguins to the temporary removal of eggs and chicks (for measurement) following Wilson et al. (2010): (1) parents abandon nest; (2) parents remain on the nest but were passive towards the observer; (3) tentative biting of observer; (4) aggressive biting of observer; and (5) highly aggressive defence, where breeders bit and wing-clapped the observer.

Data analysis

Data analysis was undertaken in R v3.0.1 (R Core Team 2013). I used the *survival* (Therneau 2014) and *survMisc* (Dardis 2013) packages for chick survival analyses. In order to determine that the sample sizes were sufficiently large to detect a 16% difference between breeding success averages on Gough and Nightingale Islands (based on data collected in 2012), I performed a power analysis prior to collecting data in 2013. This mitigated the risk of concluding there is no significant difference between islands when in fact such a difference exists (a type II error ß). Standard errors were calculated for all mean estimates.

General assumptions and terms used in the survival analyses

Northern Rockhopper Penguins are highly synchronous breeders that take approximately 110 days to incubate eggs and raise chicks (Williams 1980). In this study, only the data collected on Gough Island in 2013 at Seal Beach colony covered the entire 110 day span; other data observations (i.e., the egg and resultant chick) were right-censored (i.e., it is unknown whether a chick fledged or not). I used survival analysis techniques to perform a regression to account for right-censored observations in the Nightingale Island datasets, and to determine whether there was a difference in the pattern of failures between datasets. Survival analysis has similar aims as the Mayfield method and its extensions in calculating nest survival (Nur et al. 2004), but does not assume that the likelihood of dying on any day in the observation period is a constant. Survival analysis is also used to aid in the identification of specific causes of egg and chick mortality (Davis & McCaffrey 1986; Renner & Davis 2008).

Failure: If an egg did not hatch, failure was defined during as occurring on the day which a nest was abandoned by both parents permanently. For example, if a nest was abandoned by the female on day 21 but was found occupied by a male on day 24, who remained until day 34, then day 34 would be the

date of failure. This is because occasionally some eggs hatched despite being abandoned during one of the earlier checks. For chicks, failure was defined as death, or the first day on which an individual was not found subsequently. This is because skuas often swallow chicks whole leaving no trace of the body (on five occasions chick flipper bands were found in skua pellets).

Survival objects: A building block of survival analysis in R is the *Survival object*, which is used in all model building. This is created using the *Surv* function, and is made up of a series of event times and event statuses for each observation. Event time is the age (in this study this was recorded in days) at which an individual either failed or was censored, and event status is a binomial variable indicating whether an event occurred or not (Dardis 2013). Right censored observations were eggs which successfully hatched when generating egg survival functions, and chicks on Gough Island and chicks still alive at the end of the study period on Nightingale Island when generating chick survival functions.

Survival functions: A survival function $S(t)$ is the probability that an individual does not experience an event (which in this study may be death or hatching) for longer than t (Hetzel 2008). In R, the standard non-parametric Kaplan-Meier estimator (Kaplan & Meier 1958) is used to estimate the survival function for lifetime data by passing a *Survival object* into the *survfit* function. This also estimates variance in the survival function based on the Greenwood formula (Greenwood 1926).

Comparing survival functions: It is possible to test for differences in survival functions by passing a formula into the *survdiff* function, which uses the *G-rho* family of log-rank tests. The formula passed into the *survdiff* function consists of a survival object as the response variable, and a single discrete predictor variable (Hougaard 2000). It cannot incorporate continuous or multiple independent predictor

variables or be used to perform a regression, and it does not provide a mean difference between survival curves (Lee & Wang 2003).

The hazard function: The hazard function h(t) of survival time T gives the probability of failure on a day, assuming the individual has survived to the beginning of that day.

Comparing hazard functions: In R, the semi-parametric Cox proportional-hazards regression model (which uses a Wald test) is used to detect differences in hazard functions for lifetime data by passing a formula into the *coxph* function. The formula consists of a *Survival object* as the response variable and either a single or a multiple predictor variables, which may be discrete or continuous. Because of this flexibility, the Cox proportional-hazard regression model is the most popular model in survival analysis (Kaplan & Meier 1958). A major assumption made in this model is that the hazard ratio is not time dependent, e.g., if the hazard on day 18 for individuals within a certain categorical predictor group (such as Nightingale Island in this study) is twice that for individuals within another category (such as Gough Island), then at any other time it will still be twice whatever the risk of failure to individuals in the other group is. This assumption is tested by plotting $\log(-\log(S(t)))$ against time separately for the different hazard functions and visually assessing whether the lines are parallel, and by using the *cox.zph* function to assess the Schoenfeld residuals (Greenwood 1926).

Breeding success

As Northern Rockhopper Penguins rarely if ever raise more than one chick (Cuthbert 2013), I calculated overall breeding success as being equal to hatching success multiplied by chick survival, i.e., the proportion of nests that produced fledged chicks. Hatching success was estimated as the proportion of nests to hatch at least one chick. I performed a Cox proportional-hazard regression to determine incomplete chick survival rates for the latter 40 days of the breeding season on Nightingale

Island, based on the Tumbledown 2012 and Seal Beach 2013 marked nest datasets so the data were comparable with the data gathered on Gough Island. Using these extrapolated values, I compared average breeding success on Gough and Nightingale Islands using a quasibinomial GLM (generalized linear model) with a logit link to account for over-dispersion in the data, with breeding success as the dependent variable and year and island as predictors.

Examining the causes of breeding failure

Hatching success and chick survival

Examining differences in breeding success at a finer scale (e.g., chick survival and hatching success) than overall breeding success can provide researchers with information about possible causal factors driving breeding failure (Davis & McCaffrey 1986; Nur et al. 2004; Groscolas et al. 2008; Vertigan et al. 2012). With this aim, I compared hatching success and Cox proportional-hazard (Cox PH) chick survival estimates (i.e., chick survival over the entire breeding season) between datasets separately using quasi-binomial family GLMs with a logit link to account for over-dispersion in the data (which was tested for with a chi-square test based on the residual deviance and degrees of freedom).

Additionally, I investigated colony size (number of nests in a colony) as one of the possible drivers of breeding success directly, as the size of colonies has been shown to impact breeding success in many seabird species (Brown & Brown 2001) and Sergeant Major on Nightingale Island currently has seven times more breeding pairs than the largest colony on Gough Island (Cuthbert et al. 2009). I used quasi-binomial GLMs to determine separately whether colony size had an effect on hatching success on Gough Island (while controlling for year) and Nightingale Island (in 2013 only as this was the only year two different-sized colonies were sampled), in order to control for the variety of colony sizes on the two islands as well as any potential island effect.

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Incubation failure patterns

To determine whether incubation failure occurred in the same pattern over time, I used survival analysis techniques to generate a Kaplan-Meier estimate of the survival function for Tumbledown and Sergeant Major in 2012, and Seal Beach, Sergeant Major and "C" in 2013 (i.e., all datasets containing regular nest checks). On Gough Island, the nests marked at Tumbledown were only followed from 10 days before hatching, and therefore the model used data generated by a Kaplan-Meier estimate (based on the other weighted datasets) to infer incubation failure for the first 24 days of the study period for this dataset. I assessed visually the pattern of nest failures during incubation for all five datasets, and investigated a pattern in the survival functions by comparing the Kaplan-Meier estimate of the survival function for Nightingale in 2013 and the other datasets combined. Definitions of the survival and hazard functions, a description of how they are compared and how goodness of fit is tested are given above (Data analysis)

Guard phase length

The length of the guard phase has been used in other studies on penguin species to detect differences in food availability (Chiaradia & Nisbet 2006; Saraux et al. 2011). I compared guard phase lengths (using year and island as predictors) between datasets where nests were marked and regularly monitored (five datasets; Sergeant Major and "C" on Nightingale Island and Tumbledown in 2012 and Seal Beach in 2013 on Gough Island). I only used chicks that successfully crèched. I defined guard phase length (the response variable) for each chick as being the number of days between hatching date and crèching date, the latter determined as being midway between when a chick was first recorded crèching and the previous check.

To investigate possible repercussions of a shorter guard phase, I used the data taken from the marked nests on Gough and Nightingale Islands (five datasets), and anatomised chick survival into guard

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survival and crèche survival functions, which were then compared using survival analysis while controlling for year and island effects. I also compared the failure pattern (i.e., survival function using survival analysis) during the guard and crèche phases in Sergeant Major in 2012 and 2013.

Egg size and parental response to threats as indicators of parental fitness

Egg size has been shown in other ornithological studies to be an indicator of maternal experience and health (Bolton 1991; Croxall et al. 1992; Christians 2002). I estimated the volume (in cm^3) of A and B-eggs as length (cm) x breadth^2 (cm) x 0.512 (Stonehouse 1966). To compare between colonies and years, I used a Gaussian GLM with egg volume as the dependent variable. I also tested whether B-egg volume was correlated with B-egg hatching success or B-egg chick survival by modelling the incubation and chick hazard functions with the volume of B-eggs as a continuous predictor variable while controlling for island and year. I used B-eggs because there was less deviation between the size of B-eggs than A-eggs, which has also been found in other studies (Demongin et al. 2010a). For this I only used four datasets, as eggs were not measured for chicks within the study colony on Gough Island in 2012.

Breeding success has been significantly linked to parental responses to threats in Northern Rockhopper Penguins on Gough Island (Wilson et al. 2010). To explore this as a possible factor in this study, I averaged the response to threats scores (rounded to one decimal place) for breeding birds at each nest on Nightingale in 2013. Using this, I compared chick hazard functions with response to threats as a continuous predictor variable. I also compared breeder response to threats between "C" and Sergeant Major on Nightingale Island using a Gaussian GLM.

Chick growth

Chick growth was analysed in R using the *nlme* package (Pinheiro et al. 2011) and the

FlexParamCurve package (Oswald et al. 2012). I assessed visually the growth curves for flipper

length, head length and weight against chick age for all chicks that survived until the end of the study

period. It was possible to use weight as a proxy for chick body condition because I knew the exact age

of individuals (Beintema 1994; Green 2001; Robinson et al. 2005; Labocha et al. 2014). I used the

FlexParamCurve package to evaluate the fit of different parametric curves described in Oswald et al

(2012) to the growth data of chicks on Gough Island that survived until the end of the study period

(fledging).

I used a linear mixed effects model to determine whether there was a difference in the growth patterns

of chicks which survived until the end of the study periods on Gough and Nightingale Islands while

controlling for year. I also checked for differences between growth curves in Sergeant Major in 2012

and 2013, and "C" and Sergeant Major in 2013. I checked the goodness of fit by plotting the model

residuals in a histogram, showing that they approached normality. I used these results to support trends

found in chick survival in these datasets.

The extent of penguin colonies on Nightingale Island in the 1970s

Northern Rockhopper Penguins on Nightingale Island have been subject to human disturbance and

exploitation since the 1950s (Cuthbert et al. 2009). In December 2013 I interviewed three Tristan

residents who visited Nightingale Island regularly in the 1970s (Herbert Glass, Ches Lavarello and

Douglas Swain) to record their recollection of the location and extent of penguin colonies.

Interviewees were selected based upon the recommendation of the Tristan Conservation Department. I

began the interview by giving each of them some background information about this study, expressing

an interest in learning how penguin colonies change over time. Each was asked to draw the areas

where they recall there being penguin colonies in the 1970s on a blank sketch map of the north-eastern area of Nightingale Island. I overlayed all three maps to create a consensus map, areas present in only one or two maps were discarded.
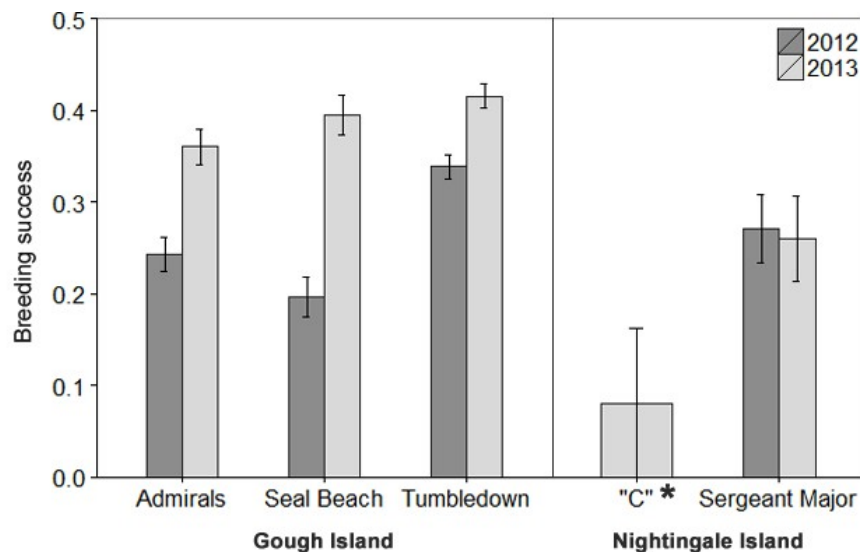
RESULTS

Breeding success

Unless otherwise stated, all errors reported are standard errors. While controlling for year, breeding success was about 6.5% higher on Gough Island (0.33 ± 0.018, $z = -2.065$, $p = 0.039$) than on Nightingale Island (hatching success multiplied by Cox PH chick survival, 0.265 ± 0.031) (Figure 6).

Figure 6: Northern Rockhopper Penguin breeding success (proportion of nests producing a fledged chick) at colonies on Gough and Nightingale Islands in 2012 and 2013. Error bars show standard errors.

Year only impacted breeding success on Gough Island ($t = 3.85$, $p = 0.031$), where birds breeding in 2013 were 1.83 ± 0.16 times more likely to produce fledged chicks than in 2012. However, this comparison is complicated by the fact that different breeding colonies on Gough Island were used in 2012 and 2013, and the data collected in 2012 are potentially compromised by the lack of early

incubation observations. Colony size affected breeding success on Nightingale Island, where birds breeding in Sergeant Major were 4.04 ± 0.55 times more likely to produce fledged chicks than in "C" in the same year (z = 2.563, p < 0.001).

Hatching success and incubation failure patterns

Eggs were significantly (z = 17.368, p < 0.001) more likely to hatch on Nightingale Island (0.716 ± 0.08) than on Gough Island in 2013 (0.572 ± 0.041), but not 2012 (z = 0.393, p = 0.732). Overall, hatching success (Figure 7) was significantly higher (t = 7.973, p < 0.001) in 2013, when it was on average 1.735 ± 0.051 times higher than in 2012.

As with breeding success, colony size only impacted significantly (z = 8.017, p < 0.001) on hatching success on Nightingale Island (Gough Island: z = 0.138, p = 0.89), where eggs were 1.288 ± 0.087 times more likely to hatch in Sergeant Major compared to "C". There was no significant difference (z =
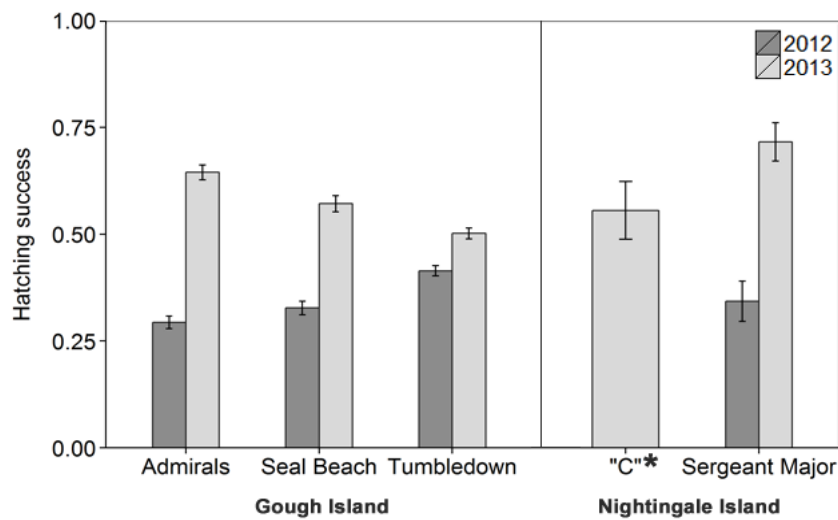
* No data collected in 2012

0.41, p = 0.742) detected when comparing the control data with the marked nest data on Nightingale Island.

The pattern of incubation failure between years on Nightingale Island was very different: incubation failure occurred at an approximately constant rate during 2012 (which is similar to the pattern of incubation failure at Gough Island in 2013), and in 2013 incubation failure was very low until hatching (Figure 8, top). Effectively, the datasets can be separated into two significantly different patterns ($\chi^2 = 8.1$, df = 1, p = 0.004): a "constant failure throughout incubation" pattern, and "low failure up until hatching, followed by high failure" pattern (Figure 8, bottom).
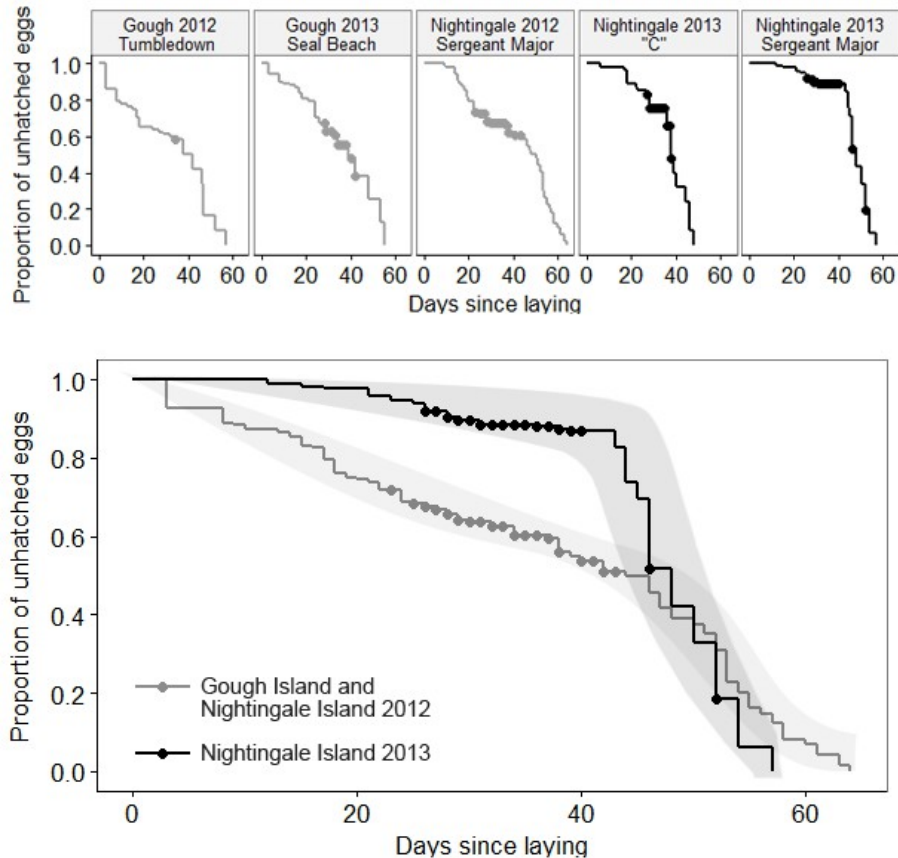
Chick survival

 The Cox PH model (Figure 9) estimated chick survival on Nightingale Island to be 0.144 ± 0.384 in "C", 0.788 ± 0.028 in Sergeant Major in 2012 and 0.363 ± 0.048 in Sergeant Major in 2013. The model was conservative, estimating only slight decreases in chick survival past the 40 day mark. The model estimated chick survival to be higher than recorded at day 40 for "C" chicks, due to a high standard error in the data caused by the small sample size (there were only four chicks still alive after day 40).

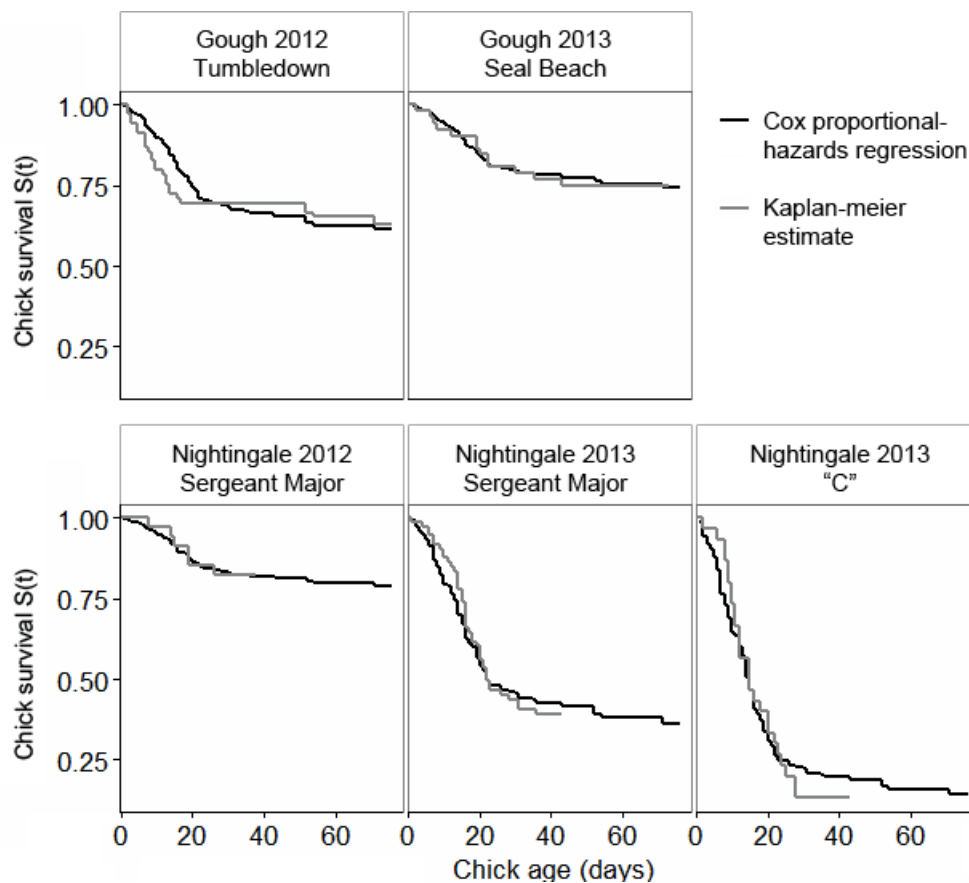

Figure 9: Kaplan-Meier estimates and Cox proportional-hazard regressions for Northern Rockhoppe Penguin chick survival at colonies on Gough and Nightingale Islands in 2012 and 2013.

Based on the Cox PH regression values, chick survival (Figure 10) was significantly ($t = -8.63$, $p = 0.014$) lower on Nightingale Island (0.3628 ± 0.038) than on Gough Island (0.729 ± 0.08) in 2013, but

not in 2012 (z = -0.789, p = 0.43). Chick survival did not differ significantly (t = -0.355, p = 0.741) by year on Gough Island, but was significantly (z = -73.62, p < 0.001) higher on Nightingale Island in Sergeant Major 2012 (0.788 ± 0.003) than in 2013 (0.363 ± 0.004). Colony size also did not impact significantly (t = 1.985, p = 0.141) on chick survival on Gough Island, but did on Nightingale Island (z = 2.78, p = 0.005), where chicks were over two and a half times more likely to survive in Sergeant Major (0.363 ± 0.048) than in "C" (0.144 ± 0.048).
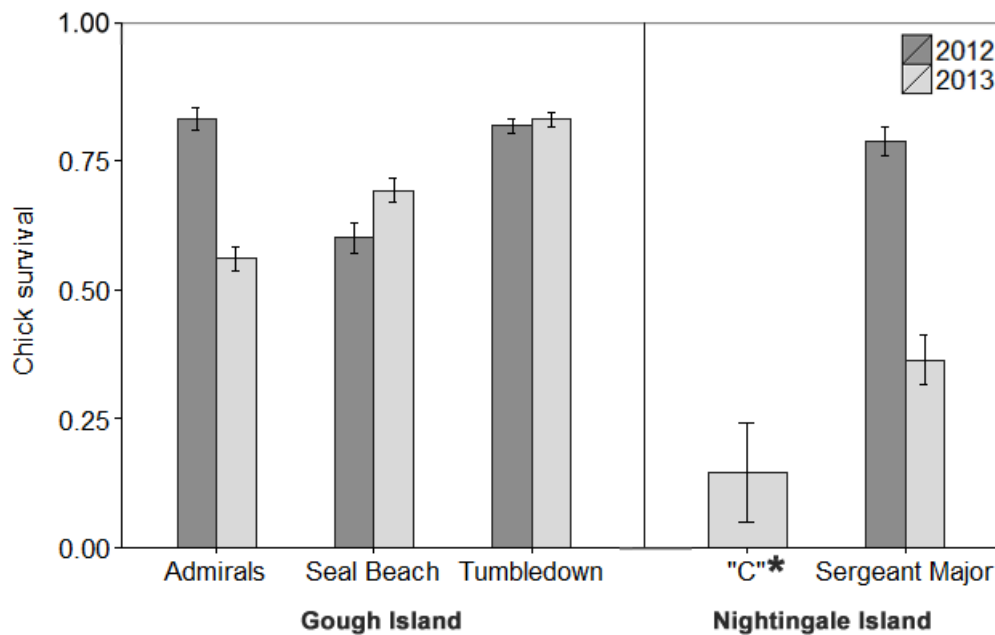
* No data collected in 2012

Figure 10: Northern Rockhopper Penguin chick survival (proportion of hatched chicks which fledge) at colonies on Gough and Nightingale Islands in 2012 and 2013. Error bars show standard errors.

Chick growth

On average, 35 day old chicks on Nightingale Island weighed less and had smaller flippers and heads compared to chicks of the same age on Gough Island (Table 1).

Table 1: Weight (g), flipper length (mm) and head size (mm) averages of 35 day old Northern Rockhopper Penguin chicks on colonies on Gough and Nightingale Islands in 2012 and 2013. Values ± standard deviation.

	Weight (g)	Flipper length (mm)	Head size (mm)
Gough 2012 (Tumbledown)	1522.27 ± 433.64	153.09 ± 8.19	90.36 ± 2.6
Gough 2013 (Seal Beach)	1451.67 ±142.27	150.33 ± 6.02	92.1 ± 5.73
Nightingale 2012 (Sergeant Major)	1060 ± 169.71	131.5 ± 9.19	86.4 ± 1.98
Nightingale 2013 ("C")	692.5 ± 53.03	119.5 ± 2.12	79.25 ± 3.18
Nightingale 2013 (Sergeant Major)	746.25 ± 55.73	119.75 ± 11.32	79.13 ± 3.63

Growth on Gough Island followed a smooth positive-negative Gompertz curve without much variation. This curve had an asymptotic mass above the average adult weight – approximately 2 kg for this species (Cuthbert 2013). Although flipper and head length on Nightingale Island also conformed to this pattern, chicks were underweight on Nightingale Island. Chick mass (Figure 11, right) on Nightingale Island was significantly (t = -7.672, p < 0.001) lower by about 47%, or 730 (sd = 395 g), for chicks aged between 35 and 40 days (covering the last set of growth measurements taken on Nightingale) compared to chicks of the same age on Gough Island while controlling for a year effect. On Nightingale Island in 2013, the 15 control data for chick growth fell within the confidence intervals for "C". The age of the control chicks were estimated by comparing flipper and head length measurements (Figure 11, left).

It was not possible to test whether chick growth was affected by year or colony size on Gough Island, because only two datasets were available from different colonies in different years. On Nightingale Island there was no significant difference between growth curves in Sergeant Major in 2012 and 2013 (t = -1.613, p = 0.109), or between the "C" and Sergeant Major colonies in 2013 (t = -1.669, p = 0.096). This may be due to the small sample size (measurements were obtained from fewer than ten chicks after day 30 due to low chick survival) at "C".
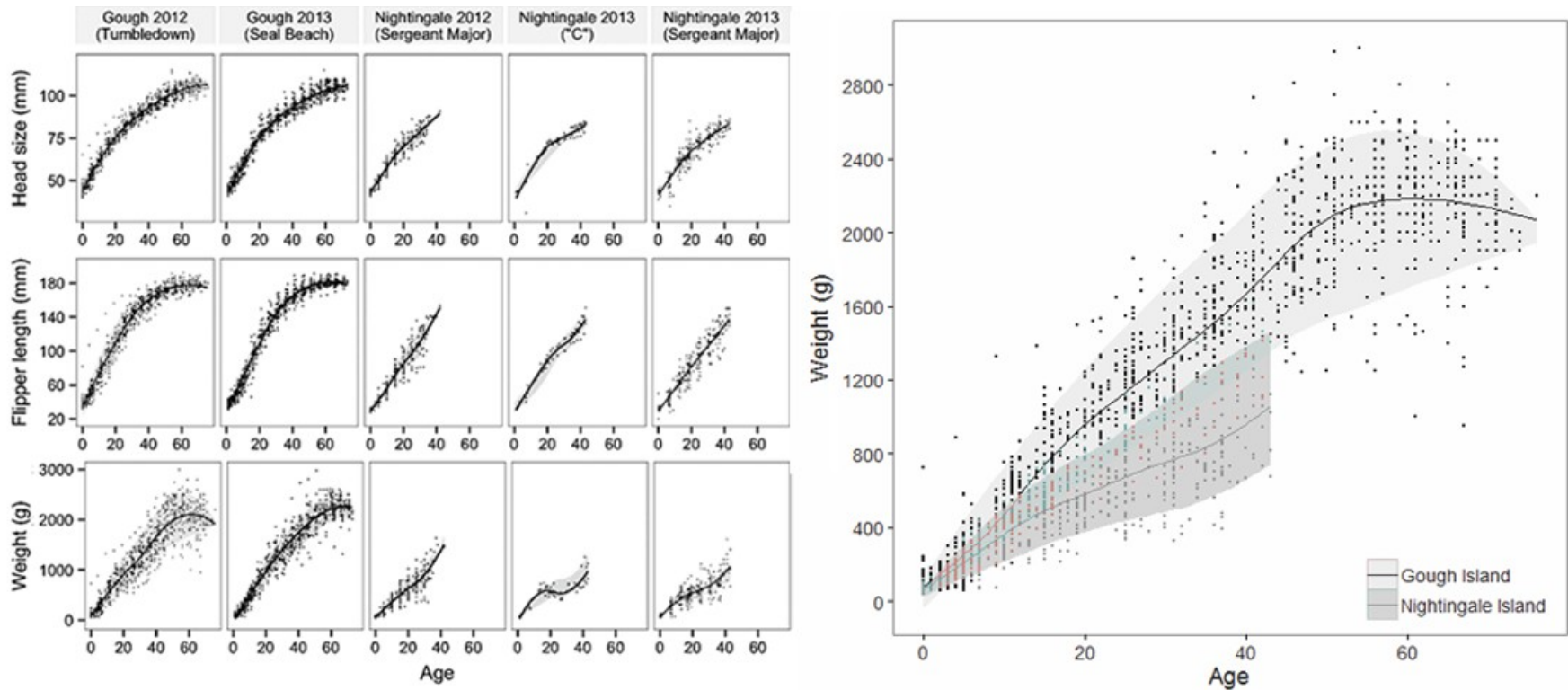
Figure 11: Left: Head, flipper and weight measurements taken from Northern Rockhopper Penguin chicks at colonies on Gough and Nightingale Islands in 2012 and 2013. Right: Averaged weight measurements for chicks on Gough and Nightingale Islands. The solid line and shaded areas are the LOESS (local regression) smoothed mean and confidence intervals respectively, and the dots are individual growth measurements.

Guard phase length

The guard phase (Figure 12) lasted 20.6 (sd = 3.7) days at both colonies on Gough and Nightingale Islands in 2012 and on Gough Island in 2013 (χ^2 = 0.8, df = 2, p = 0.678), but decreased to only 14 (sd = 2.4) days on Nightingale Island in 2013 (χ^2 = 152, df = 4, p = 0.005).
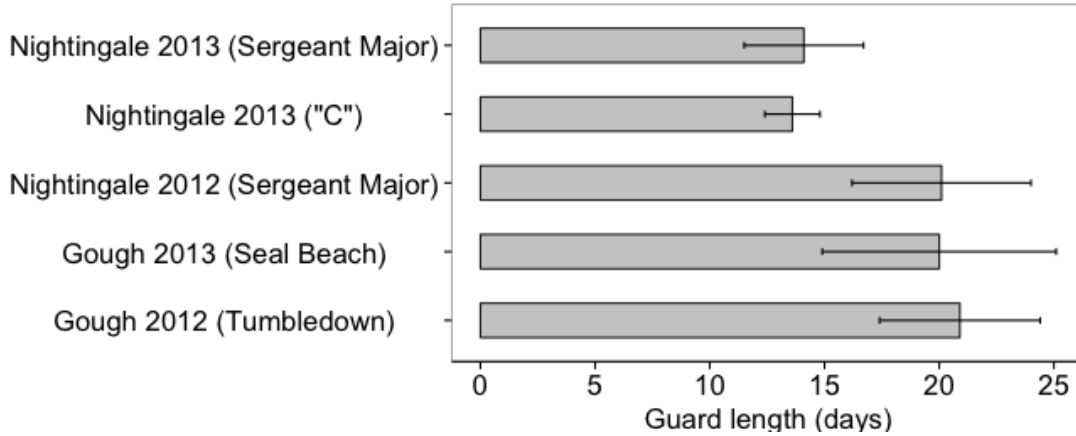
Daily survival on Gough and Nightingale Islands in 2012 (Figure 13) was slightly lower (by about 0.00895) during guard than crèche (t = -2.966, p = 0.041). On Nightingale in 2013 survival was far lower (by over half) during crèche than guard (t = -3.11, p = 0.031).
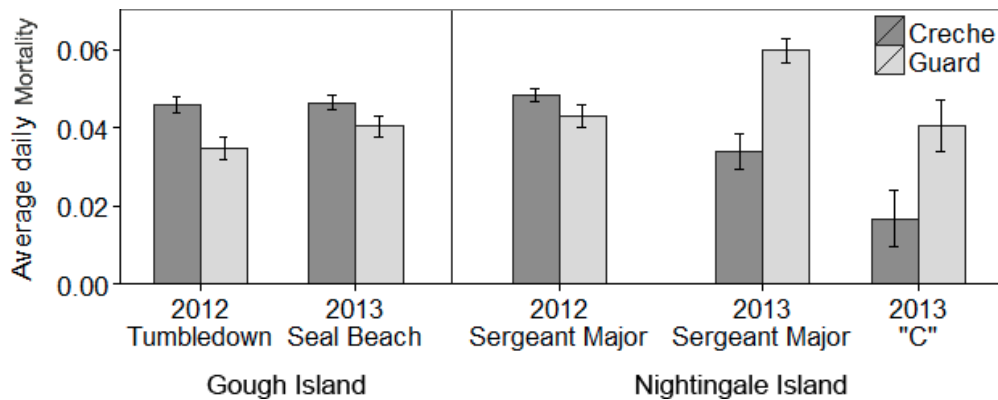
During guard, survival in Sergeant Major was not significantly different between years (χ^2 = 2.4, df = 2, p = 0.119). However, it differed during crèche (χ^2 = 14.1, df = 1, p < 0.001), when survival was lower (by nearly half) in 2013, the year with the shorter guard phase. The "C" colony had the greatest disparity between guard and crèche chick survival, probably due to increased predation.

Egg size and parental response to threats

A-eggs on Nightingale Island were significantly smaller (by 11.63 cm^3, t = -8.278, p < 0.001) while controlling for a year effect compared to Gough Island, where average A-egg volume was 82.67 (sd = 15.17 cm^3, Figure 14). A-egg size did not vary significantly between years on either island, and only varied between colonies on Nightingale Island, where A-eggs were slightly smaller in the "C" colony (4.84 cm^3 smaller than in Sergeant Major in 2013).

Figure 14: Mean A-egg size for Northern Rockhopper Penguins at colonies on Gough (Tumbledown and Seal Beach) and Nightingale (Sergeant Major and "C") Islands in 2012 and 2013. Error bars show standard deviation.

B-eggs on Nightingale Island were significantly smaller (by 11.89 cm^3, t = -7.457, p < 0.001) while controlling for a year effect compared to Gough Island, where average B-egg volume was 107.68 (sd = 1.55 cm^3, Figure 15).
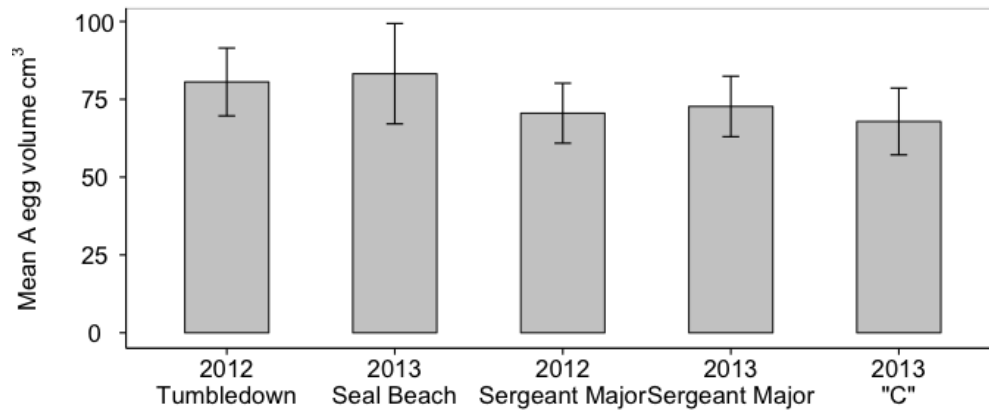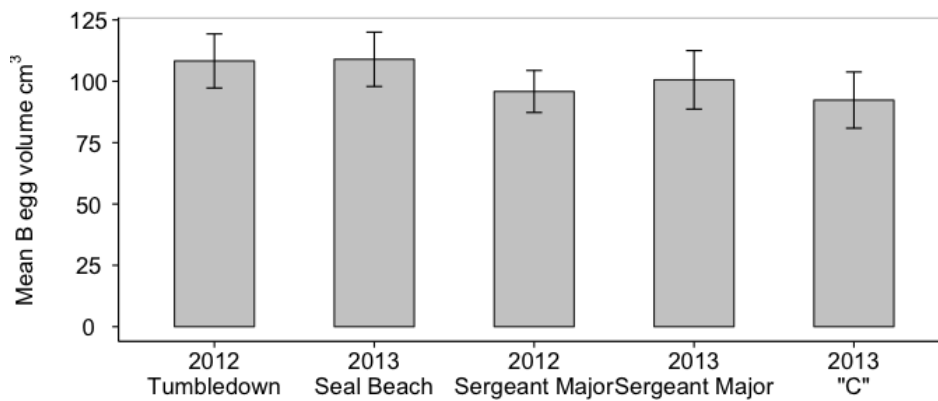

Figure 15: Mean B-egg size for Northern Rockhopper Penguins at colonies on Gough (Tumbledown and Seal Beach) and Nightingale (Sergeant Major and "C") Islands in 2012 and 2013. Error bars show standard deviation.

B-egg size only varied significantly between years and between colonies on Nightingale Island, where

B-eggs were slightly smaller in 2012 (4.74 cm^3 smaller than in 2013), and in the "C" colony (9.31 cm^3

smaller than in Sergeant Major in 2013). A-egg and B-egg data are summarised in Table 2.

Table 2: Northern Rockhopper Penguin A-egg and B-egg length and breadth averages (cm) on colonies on Gough and Nightingale Islands in 2012 and 2013. Values ± standard deviation.

	A-egg length (cm)	A egg breadth (cm)	B-egg length (cm)	B egg breadth (cm)
Gough 2012 (Tumbledown)	63.63 ± 3.16	49.61 ± 2.22	70.1 ± 3.13	54.84 ± 2.25
Gough 2013 (Seal Beach)	64.45 ± 4.16	49.95 ± 3.21	70.12 ± 2.26	55.01 ± 2.2
Nightingale 2012 (Sergeant Major)	60.76 ± 2.06	47.5 ± 2.67	67.76 ± 2.3	52.5 ± 1.9
Nightingale 2013 ("C")	60.61 ± 2.74	47.86 ± 2.18	66.93 ± 3.01	51.78 ± 2.48
Nightingale 2013 (Sergeant Major)	61.69 ± 3.28	46.6 ± 3.1	68.63 ± 2.68	53.41 ± 2.82

B-egg volume was not significantly linked to chick survival ($\chi^2 = 0.79$, df = 2, p = 0.68), but was

significantly positively correlated ($\chi^2 = 7.26$, df = 1, p = 0.007) with hatching success while controlling

for island and year: for every additional 1 cm^3 of egg volume, hatching probability increased by

0.0145% (e.g., a 30 cm^3 increase in egg volume improved hatching success by 13%). Chicks with

aggressive parents were not significantly more likely to survive when controlling for colony size ($\chi^2 =$

6.62, df = 2, p = 0.64918). Aggressiveness was more closely linked to colony size: breeding pairs in

Sergeant Major were significantly more aggressive than in "C" (t = -2.382, p = 0.0187).

Changes in penguin colonies on Nightingale Island

The map of colonies on Nightingale Island in the 1970s (Figure 16) shows reductions in colony size, particularly in the small satellite colonies. These also appear to have moved by approximately 90 m to the west, and it is possible that "B" and "D" were once part of the larger 1970 colony approximately 90 m to the east.
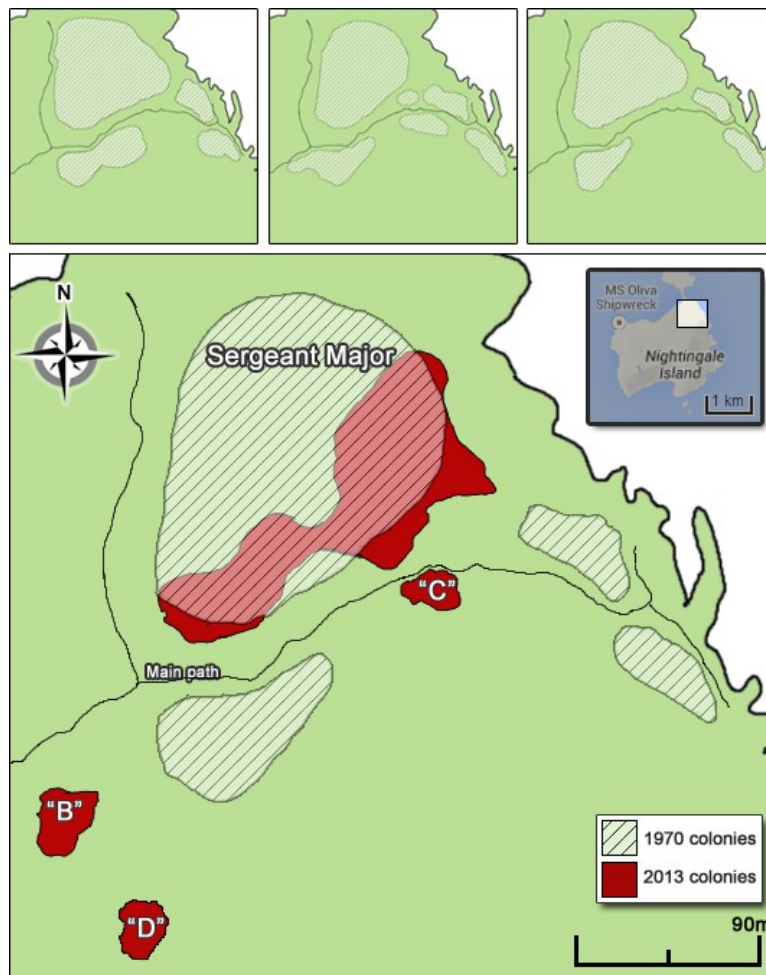
Figure 16: The approximate distribution of Northern Rockhopper Penguin colonies on Nightingale Island in 1970 compared to 2013. The colonies in 1970 are based upon three maps (top) sketched by three Tristanians who visited the island regularly at the time.

The map should be interpreted with care as human memory is subject to error and the 2 m-high tussock-grass on Nightingale Island makes a visual assessment of the size of an area difficult. Nonetheless, the colony locations are likely to be accurate, as islanders used the path and the position of High Ridge to work out where they used to collect eggs and enter the colonies. I have deliberately not quantitatively assessed all colony shrinkages from the map I have generated, and have used the map to work out only *where* colonies were in the 1970s and to work out the general size difference in Sergeant Major, which has reduced by about half, from roughly 22 400 m^2 in the 1970s to 10 800 m^2 in 2013.

DISCUSSION

My results were unexpected; breeding success was higher by about 6.5% on Gough Island (with a declining population) than on Nightingale Island (with a stable population). However, the incubation period on Gough Island in 2012 was not fully observed, which could impact slightly on the measured breeding success for the year on that island. Additionally, as breeding success on Nightingale Island was also not observed for the full breeding seasons, total breeding success on Nightingale Island was calculated based on cautious estimates from the Cox PH regression. The only other multi-year estimate of breeding success in this species revealed considerable variation (up to 23%) between years (Guinard et al. 1998). A 6.5% difference in a species with such high inter-annual variability could therefore be considered to be biologically insignificant, and two years of data is probably not sufficient to reveal whether the 6.5% difference holds true in the longer term.

Chick mass was 47% lower on Nightingale Island than on Gough Island, which indicates that breeding conditions were poorer during the past two years at the Tristan da Cunha archipelago. Chick growth is a more sensitive indicator of adverse conditions for seabirds than failure rates (Cairns 1988; Saraux et al. 2011; McDuie et al. 2013), particularly in the Northern Rockhopper Penguin, where parents prioritise their own survival over chick provisioning (Booth & McQuaid 2013). However, although low fledging mass is often associated with low juvenile survival (Kildaw & Irons 2005), Dehnhard et al. (2014) could show no clear effect of fledging body mass on juvenile return rate for Southern Rockhopper Penguins.. It is therefore unclear whether the lower chick mass on Nightingale Island may be having an impact on recruitment and long-term population trends in the area.

Colony size appeared to impact breeding success and chick growth on Nightingale Island only, possibly because the size ratio between the smallest and largest colony on Nightingale Island (31:1) is far greater than on Gough Island (where it is 15:8). The lower breeding success in "C" may be due to phenotypic differences among birds, as birds of particular ages or abilities may sort into different sized colonies (Carney & Sydeman 1999; Viblanc et al. 2012). This is supported by the variance seen in the egg sizes on Nightingale Island: there are significantly smaller A-eggs and B-eggs in "C", suggesting that, based on other seabirds (Croxall et al. 1992; Brown & Brown 1999), breeding pairs might be more experienced or in better condition in the larger Sergeant Major colony. B-egg size was positively correlated with hatching success but not chick survival, which also suggests that B-egg volume may be an indicator of parental health. Birds in Sergeant Major also had a more intense response to threats, but when controlling for a colony effect I found that chicks with aggressive parents were not more likely to survive. This implies that the level of aggression among birds in Sergeant Major is the product of the higher levels of stress in a large colony (resulting from large numbers of birds nesting together Brown et al. 1990), rather than it being particularly associated with parental fitness, as suggested by Wilson et al. (2010) on Gough Island.

Hatching success was about 15% higher on Nightingale Island than on Gough Island in 2013. On Nightingale Island in 2013, failure was low from the start of incubation until hatching 34 days later, but there was a higher rate of failure earlier in incubation in 2012 (Figure 8). This is probably due to early nest abandonment in 2012, as females on Nightingale Island were in poor condition that year, weighing on average 1.6 kg in comparison to 2.25 kg on Gough Island (A. Steinfurth, unpublished data). On Gough Island there was a similar pattern of failure during incubation in both years, following the same pattern seen on Nightingale Island in 2012 (effectively a constant rate of failure throughout incubation). This is unlikely also to be due to early nest abandonment (as it was on Nightingale Island),

as females on Gough Island were in good condition and presumably capable of completing the incubation fast, which suggests that hatching success is routinely lower on Gough Island compared to Nightingale Island. This conclusion seems reasonable when considering the disparate colony environments: the exposed nests on the rocky slopes of Gough Island are more vulnerable to disturbance (Brown et al. 1990; Wilson et al. 2010), severe rainfall events (Demongin et al. 2010b) and predation by skuas (Swales 1965; St. Clair & St. Clair 1996) than the nests sheltered by dense tussock grass on Nightingale Island (Figure 3). Hatching success on Nightingale Island in 2013 (about 72%) was higher than has ever been recorded on Gough Island, where Wilson et al (2010) observed the highest hatching success rate to be about 67% in a sub-colony at Seal Beach in 2005/6.

Chick survival, on the other hand, seems to be similar on both islands and consistent with levels observed on Gough Island by Wilson et al (2010), apart from in 2013, when Nightingale Island experienced a 25% shorter guard phase. Although not many studies have examined the plasticity of guard phase length in crested penguins, a dramatic reduction in guard phase length such as this is unusual for in some species; Chiaradia & Nisbet (2006) recorded that Little Penguins (*Eudyptula minor*) reduced the length of their guard phase only when food availability was particularly poor. Chicks crèching on Nightingale Island face an additional predator to those on Gough Island: the Tristan Thrush is a well known opportunistic predator of seabird eggs, chicks and even adults of smaller petrels (Ryan & Ronconi 2010). By crèching earlier, chicks were exposed to skua and thrush predation at a younger age, resulting in over triple the number of failures during early crèche; there was no difference between guard phase survival in Sergeant Major between 2012 and 2013.

If, as discussed above,hatching success should routinely be higher on Nightingale Island, and chick survival should routinely be similar (at least while food availability is similar) between islands, it follows that breeding success should be habitually higher on Nightingale Island than Gough Island.

However, my results indicate that compared to on Gough Island, hatching success was lower on Nightingale Island in 2012, and chick survival was lower on Nightingale Island in 2013. As a result of this, Nightingale Island experienced lower overall breeding success in both years. Several potential explanations for this lower breeding success are examined below.

Foraging conditions

On Nightingale Island in 2012, nest abandonment was high because females were underweight at the start of the season, almost certainly due to poor foraging conditions that year. In 2013, the short guard phase implies that foraging was poor for males between the start of the season and the last week of incubation and guard. By comparison, females on Gough Island were of average weight (A. Steinfurth, personal communication) and the guard phase was of standard duration in both years, indicating that prey availability was higher in foraging areas used by birds on Gough Island compared to those used by birds on Nightingale Island (Charrassin et al. 1998; Ballard et al. 2010; Dehnhard et al. 2011; Saraux et al. 2011). Chick mass and growth patterns corroborate this conclusion: chick growth on Nightingale Island was poor in comparison to both Gough Island (47% less) and a similar study undertaken on Amsterdam Island, where it was 30% less for 20 to 25 day-old chicks in 2003 when prey availability was considered to be poor (Tremblay & Cherel 2003). In Little Penguins, chick body mass is a good indicator of the length of parent foraging trip durations (Inchausti et al. 2003; Cherel & Hobson 2007). Based upon this evidence it is reasonable to conclude that foraging conditions were better for penguins on Gough Island than on Nightingale Island in 2012 and 2013, and that birds on Nightingale Island have to forage for longer and/or further than birds on Gough Island (A. Steinfurth et al, unpublished data).

Disparate foraging conditions may be caused by geographical location: Gough Island is the only Northern Rockhopper Penguin habitat south of the Subtropical Front, which is likely to affect food

supply (Moreno et al. 1997). It is unlikely that fishing pressure is an issue for Northern Rockhopper Penguins around Gough and Nightingale islands, as the only commercial fishery in the vicinity targets Tristan Rock Lobster *Jasus tristani*, which does not form part of the diet of the Northern Rockhopper Penguin (Cuthbert 2013). In the past the population may have been harvested as bycatch by driftnet fisheries operating in the area, but this practice has been banned around Tristan da Cunha since the 1990s (Ryan & Cooper 1991). Environmental conditions affecting prey may be a factor: wind direction and timing has also been linked (through bottom-up trophic chains) to breeding success for Rhinoceros Auklets *Cerorhinca monocerata* (Borstad et al. 2011) and windspeed is correlated with foraging success in the breeding season for Southern Rockhopper Penguins (Dehnhard et al. 2013a). It is also possible that the 2011 oil spill may have affected foraging in the area around Nightingale Island.

Fur seals and the population trend on Gough Island

There are two possible explanations for the comparatively higher breeding success and more stable chick growth on Gough Island despite its steep decline in population numbers. Firstly, if these declines are primarily due to an increase in the fur -seal population (Bester 1977; Bester et al. 2006) (and therefore fur-seal predation of adult and juvenile Northern Rockhopper Penguins), it may enhance breeding success by reducing competition for food during the breeding season. Secondly, although undoubtedly there have been substantial population declines in the past on Gough Island, data from unpublished censuses of colonies on the more easily-accessible south of the island from 2011 to 2013 show that population numbers in this region have been stable in the past three years (P. G. Ryan, personal communication). Therefore, it is possible that the Northern Rockhopper Penguin population on Gough Island is no longer in decline and this is reflected in the aspects of the breeding biology of the species examined in this study.

Oiling and disturbance on Nightingale Island

Both oiling and human disturbance are potential candidates for low breeding success on Nightingale. It is not possible to disentangle the two factors without having access to both an oiled population that was not harvested and a population that was harvested but not oiled. However, I believe that the 2011 *MS Oliva* oil spill on Nightingale Island is unlikely to explain the low breeding success there. Penguins rehabilitated after oiling have been shown to have reduced breeding success (Giese et al. 2000; Wolfaardt et al. 2008), but fewer than a thousand oiled penguins on Nightingale Island were rehabilitated (Birdlife International 2010). This is a very small percentage of the total population on Nightingale, Middle and Inaccessible Islands, so it is very unlikely they formed a substantial proportion of the sampled nests in 2012/13.

As well as poor foraging conditions, human disturbance may have negatively affected breeding success on Nightingale Island. The islanders' recollections of Northern Rockhopper Penguin colonies on Nightingale Island in the 1970s indicate that there have certainly been long-term historical changes: Sergeant Major has halved in size and the satellite colonies have either moved or have been re-established following extinction. This is probably due to frequent human disturbance, particularly harvesting of penguins for fishing bait in the 1970s and 1980s and egg collection (Wace & Holdgate 1976). It is likely that these activities put a great deal of stress on the penguin population, as colonization events are generally rare in seabirds (Brown & Brown 2001; Cam et al. 2004; Kildaw & Irons 2005) and crested penguins in particular are considered to have high nest-site fidelity (Williams & Rodwell 1992; Clair & McLean 1999). Egg collection and guano harvesting trips over the years have probably promoted colony shrinkage and subdivision, increasing edge effects and exposure to predators. Additionally, I believe that these egg collections may have played a more direct role in the poor breeding success observed on the island in this study. Penguins often exhibit long-term

behavioural changes in response to human disturbance, which have been known to affect breeding success (Giese 1996; Holmes et al. 2006; Viblanc et al. 2012). Although egg-collection is supposed to be restricted to A-eggs, there is evidence that both eggs were harvested by Tristanians in 1999 (P. G. Ryan, personal communication), and it is probable that both A and B eggs were taken during more recent trips, resulting in an unsuccessful breeding attempt for the pair. This induced breeding failure might cause pairs to divorce and seek new mates and nesting sites, following the "win-stay, lose-switch" pattern commonly observed in seabirds (Mínguez et al. 2001; Oro & Ruxton 2001; Kokko et al. 2004; Jovani et al. 2008). As a general rule, divorced pairs experience lower breeding success, which is thought to be caused by the loss of the benefits of nest-site and mate fidelity (e.g., increased reproductive synchrony) which heighten the reproductive success of monogamous birds (Rowley 1983; Ens et al. 1996).

Despite the reduction in size in Sergeant Major and the possible negative impact of egg collection both on breeding success and on the overall population stability, the population on Nightingale Island appears to be broadly stable according to recent census numbers from 2010 to 2013 (Glass et al., unpublished data). However, I believe the population has declined over the long-term. The census methods used to determine the population numbers in 1973 are likely to be erroneous, being based on both a far lower nesting density (0.5 nests per m^2, based on a single sample) than subsequently recorded for this species (average 1.4 ± 0.37 nests per m^2 on Nightingale Island). With this corrected, Nightingale Island would have 70 000 breeding pairs in 1973 (not 25 000), implying population declines of 76% on Nightingale Island in the past 40 years, a figure consistent with the estimated declines of 67% on Middle Island using a similar correction in the methodology used in the 1973 census there. These reductions would support the theory that historical disturbance has had a long-term negative impact on the population in the locality.

The disparity in egg-sizes between the two islands in general may also be indicative of the detrimental long-term effect of harvesting and egg collection practices on Nightingale Island: B-eggs on Gough Island (108 cm^3 when discounting a slight year effect) were about 12% larger than on Nightingale Island (96 cm^3), and A-eggs showed a similar trend. The egg volume recorded on Gough Island is similar to records from the late 1970s and 1980s on the islands, where B-eggs on Gough Island were recorded at 113.9 ± 2.6 cm^3 (Williams 1980). On Tristan, average B-egg volume in 1980 was 115.69 cm^3 (no standard deviation given, Williams & Stone 1981), and 99.46 ± 7.78 cm^3 in 1999 (P. G. Ryan, personal communication), suggesting that egg size may be getting smaller in the archipelago. On Amsterdam and St Paul Islands B-egg volume was similar to that recorded on Gough Island in this study; on average 107.25 cm^3 (no standard deviation given, (Duroselle & Tollu 1977; Tollu 1978)).

Conclusions and recommendations

Although the data used in this study only encompasses two years, the poor breeding success and the magnitude of the low chick growth on Nightingale Island suggest that my findings may reflect material differences in breeding conditions between the islands. Poor foraging conditions in the past two years are the most likely cause of this; prey availability in the areas used to forage prior to breeding and in the locality of the breeding islands are crucial for breeding success and healthy chick growth. Further research should investigate environmental differences in areas where Northern Rockhopper Penguins on Gough and Nightingale Islands (and on Amsterdam and St Paul Islands) forage, and how their foraging behaviour differs.

The causes of the population decline on Gough Island, and indeed whether the population numbers are still decreasing should also be investigated. My results indicate that if a decline is still occurring on the island it is not due to poor breeding success or adverse foraging conditions (at least during the past two years), supporting the theory that decreasing population numbers may be due to predation by the fur

seal population on the island, which is growing following the cessation of the commercial sealing era (Bester et al. 2006). As has been observed by Ryan and Kerr (2011), little can be done to ameliorate this effect due to the ruggedness of the coastline and remote nature of Gough Island. However, predator-prey dynamics in meta-populations tend to be self-regulating systems naturally adapted to deal with fluctuations and oscillations (Holling 1973), and the possible predator-prey imbalance on Gough Island may therefore stabilise without human assistance. It is important to continue to monitor the Gough Island population trends, and, if possible, to quantify fur seal predation rates.

Finally, it is possible the temporarily-halted egg collection practices have impacted (and may still be impacting) the population on Nightingale Island. Breeding success and chick growth should be monitored on the island in future, to see whether improvements are occurring, and in particular it would be useful to confirm that fledging mass is below average on Nightingale Island by weighing chicks pre-fledging (a power analysis could be used to determine a sufficient sample number). Considering the species' Endangered status and the past effects of exploitation on penguins in the area, if egg-collection practices are reinstated on the island, it would be beneficial to conduct a study in tandem with the collections, to monitor how the affected breeding pairs react.

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