Understanding moult patterns in Albatrosses and Petrels breeding on Marion and Gough Islands

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DECLARATION

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Abstract

Moult is an energetically demanding process for birds, and the replacement of flight feathers impacts flight performance. As a result, few birds overlap moult with other key activities such as breeding or migrating. Feather growth rates show little change in relation to body size, so large birds with long flight feathers take a long time to grow individual feathers, making their moult even more challenging. Unless these birds can afford to become flightless for several weeks while they replace all their flight feathers simultaneously, many large birds lack sufficient time to breed and replace all their wing feathers each year. As a result, they have evolved complex moult strategies that replace a subset of feathers each year. Albatrosses and giant petrels are prime examples of birds facing this challenge. This study focusses on Wandering Albatrosses (*Diomedea exulans*) and Northern Giant Petrels (*Macronectes halli*) breeding at Marion Island and Southern Giant Petrels (*M. giganteus*) at Gough Island. I explore primary and secondary moult patterns in Wandering Albatrosses and secondary and greater secondary coverts in giant petrels in relation to breeding activity.

I used digital photography to record the wear patterns in the wings of Wandering Albatrosses and giant petrels. Using photographs of upperwings of marked individuals over time allowed the opportunity to track changes in the wear pattern among specific feathers, although scoring feather wear from images works better for darker feathers. The rate of wear among secondaries and their coverts differed across the wing, with the inner feathers wearing faster than the central feathers. Photographing the extended wings of albatrosses and petrels incubating eggs had no impact on hatching success. Using this method I was able to test the often held assumption that wing feather moult is largely symmetrical. In Wandering Albatrosses, moult symmetry was greatest in outer flight feathers, especially primaries. However, the pattern of increasing asymmetry towards the body was not consistent; inner primaries showed less symmetry than outer secondaries and inner secondaries were moulted with greater symmetry than central secondaries. Giant petrels preferentially replaced the inner and outer secondaries and the inner and outer greater secondary coverts, and feather symmetry was greatest in these feathers. All three species indicated some asymmetry in all feathers that had an incomplete annual

moult. Depending on the question being asked, I recommend scoring both wings when investigating moult patterns.

Wandering Albatrosses typically take a sabbatical year following a successful breeding attempt, and thus failed breeders usually have less time to moult between successive breeding attempts. Following a successful breeding attempt, Wandering Albatrosses from Marion Island replaced a similar number of primary feathers on average (males 7.9 and females 7.3) as birds from the Crozet Islands (males 8.8 and females 8.1) and South Georgia (males 8.6 and females 7.1). Wandering Albatrosses that do not skip a year following a failed breeding attempt, not only replaced fewer feathers on average, but showed a difference in number of feathers replaced between sexes at Marion Island (males 7.4, females 6.1), as previously reported at the Crozet Islands (males 8.3, females 6.5) and South Georgia (males 7.2, females 5.2). These results suggest that females are under greatest pressure when a breeding attempt fails. Because females from South Georgia replace fewer feathers, especially following a failed breeding attempt, they might be under more stress than females from populations breeding at islands in the Indian Ocean (Marion and Crozet). This parallels the contrasting population trends in these regions, with numbers increasing over the last few decades in the Indian Ocean (Marion and Crozet Islands) but decreasing steadily at South Georgia. General Linear Models (GLMs) showed that sex and time available to moult both influenced the number and mass of flight feathers replaced. Sex explained more variation in terms of number of feathers replaced (67%) than time available to moult (33%), but time available to moult explained 68% of the mass of flight feathers replaced. However, there is large variation among birds in the number of primaries and secodaries replaced, independent of time available for moult. Together, sex and time available to moult accounted for only 9.2% (number) and 11.9% (mass) of the variance in feathers replaced.

Giant petrels are one of the largest birds that undergo a complete primary moult each year without losing the ability to fly. They do this by overlapping their moult with breeding and by moulting several primaries at once. Being annual breeders, individuals that fail a breeding attempt have more time to moult than successful breeders, and therefore replaced more flight feathers. Northern Giant Petrels having a successful breeding attempt replaced on average the same percentage of secondary and greater secondary coverts in both sexes; Following a successful breeding attempt Southern Giant Petrels (both sexes) replaced more feathers (secondaries and greater secondary coverts) than Northern Giant Petrels. I found that in a failed breeding attempt giant petrels have more time to moult and therefore replaced more secondary feathers than successful breeders. GLMs showed that breeding outcome was the only variable that influenced the mass of feathers replaced in Northern Giant Petrels, accounting for 14% of the variance in feathers replaced, while sex was the only variable in Southern Giant Petrels, accounting for 6% of variance. When both species were modelled together with sex and breeding attempt as explanatory variales, only breeding attempt was significant, accounting for 11% of the variance in the mass of secondaries and coverts replaced.

In summary, the assumption that breeding activity, and thus the time between breeding attempts, influences the extent of moult in large birds with incomplete wing moults was supported for Wandering Albatrosses and Northern Giant Petrels. However, time available for moult explained only a small proportion of individual variation in moult extent in these species. Southern Giant Petrels replaced a similar mass of flight feathers, irrespective of breeding outcome. My results suggest that factors other than time between breeding attempts are important in determining the extent of wing moult.

My study highlights the important tradeoffs large birds are required to make when balancing moult and reproduction. Annual monitoring of moult patterns in known individuals provides a valuable tool to better understand moult patterns in these large, long-lived birds.

Chapter 1: General introduction and study design

Moult is an essential process in the life cycle of birds, whereby feathers get replaced periodically (Payne 1972). If birds do not moult regularly, it impacts flight performance due to loss of tail and wing area (Bridge 2006), reduces the insulative properties of feathers, affects the ability to attract mates and may increase predation risk (Slagsvold & Dale 1996). There is also climate change and migration shifts to consider when adressing moult patterns in birds. Climate change affects food availability (Pardo et al. 2017) and food availability influences migration dates (Gordo 2007). If migration times change it could affect feather quality due to less food available (Gordo 2007). Increased temperatures have resulted in birds breeding earlier than usual (Brown et al. 1999), but data for seabirds are less compelling (Keogan et al. 2018). Changes in breeding season and (where relevant) migration times may lead to shifts in both the timing and the duration of moult, with consequences that might be difficult to predict.

Moult occurs when a new feather grows, pushing the old feather out of its follicle. The growth of new feathers is an energetically demanding process and therefore in most species moult is temporally separated from other costly activities such as breeding or migrating (Payne 1972). In order to better understand life history traits and energy costs, we need a thorough knowledge of moult patterns within a species (Bugoni et al. 2014). The rate at which feathers grow is rather consistent irrespective of body size (Rohwer et al. 2009, Rohwer & Rohwer 2013), so large birds with long flight feathers (the largest feathers on most birds) take longer to grow individual feathers than small birds (Rohwer et al. 2009). Feather growth rates range from about 2 to 8 mm per day (Rohwer & Rohwer 2013), whereas primaries range in length from 30 to 700 mm (Rohwer et al. 2009). Rohwer & Rohwer (2013) found that feather groups (primaries, secondaries, rectrices and secondary coverts) and feather lengths are factors that affect growth rate. Even though longer feathers grow somewhat faster than short feathers (Rohwer & Rohwer 2013), it takes at least five times longer to replace the longest primary than the shortest.

One solution for large birds is to moult all flight feathers simultaneously (Rohwer et al. 2011). However, many birds cannot afford to become flightless for several weeks. Another solution is to overlap moult and breeding. Breeding Falconiformes start flight feather moult during incubation, suspend it during chick rearing, then resume moult after breeding (Stresemann & Stresemann 1966). Giant petrels (*Macronectes* spp.) and Black-browed Albatrosses (*Thalassarche melanophris*) are examples of large seabirds that overlap breeding and moult. Giant petrels are able to replace all their primaries by overlapping breeding and moult and by moulting multiple primaries at once (Hunter 1984a). Catry et al. (2013) reported that Black-browed Albatrosses from the Falklands start primary moult while still rearing chicks, unlike birds of the same species from South Georgia. However, overlaping moult and breeding is not generally an option for seabirds where both partners share incubation and providing for the chick (Hunter 1984a, Catry et al. 2013).

The time needed to raise a chick increases with body size, so large birds such as albatrosses have a very long reproductive cycle (Tickell 2000). This leaves them very little time for other activities such as moult (Rohwer et al. 2011). Because most albatrosses do not moult while breeding (Harris 1973, Furness 1988, Prince et al. 1993) they would not have enough time to moult completely between completion of breeding in one year and commence of breeding in the subsequent year, accordingly birds breed every other year following a successful breeding attempt (Jouventin and Dobson 2002). For example, most albatrosses replace the outer three primaries (P8-10) distally (away from the body) and the inner seven primaries (P7-1) proximally (towards the body) (Pyle 2008). Retaining old feathers may impair flight and other key functions performed by feathers or birds may be forced to skip breeding in order to replace their old feathers (Rohwer et al. 2011).

In this study, I compare moult patterns in Wandering Albatrosses (*Diomedea exulans*) and giant petrels. In Wandering Albatrosses I explore moult patterns in primaries and secondaries, whereas in giant petrels I explore the extent of moult in the secondaries and greater secondary coverts. I use photographs of the upperwings of breeding individuals to minimize disturbance to breeding birds while also increasing the accuracy of the scoring method compared to scoring moult from live birds (Hunter 1984a, Furness 1988). Other studies have used photographs of birds in flight to assess moult (Keijl 2011, Bugoni et al. 2014, Vieira et al. 2017), and ringers use photographs of the spread wings of birds in the hand to score moult (Ginn & Melville 1983, Snyder et al. 1987), but this technique does not appear to have been widely adopted for seabirds at their breeding sites (see Chapter 2).

Study species

Wandering Albatrosses

Adult Wandering Albatrosses return to their colonies in December and mostly lay eggs in January; chicks hatch in March and fledge in November. This leaves very little time for adults to recover after breeding, and as a result very few pairs attempt to breed in successive years after raising a chick (Tickell 1968). Previous studies have found that the extent of primary moult in adult Wandering Albatrosses is related to the time between breeding attempts (Weimerskirch 1991, Prince et al. 1997). Almost all Wandering Albatrosses skip a year after a successful breeding attempt (few actually do breed again after a successful attempt), and thus have more time to moult than birds that fail a breeding attempt early on during the season, allowing them to lay again the following year. Adults that fail in their breeding attempt and try to breed again the following year (i.e. have 5-11 months between breeding attempts) replace fewer primaries (average 6.0) than successful breeders (7-8 primaries; Prince et al. 1997). Weimerskirch (1991) suggested that sexual dimorphism, where females are approximately 80% of the mass of males, plays an important role in the number of feathers replaced. After breeding for the first time, both sexes moult fewer primaries than experienced birds (Weimerskirch 1991). Male first time breeders from Crozet Islands and South Georgia replaced the same number of feathers (6.7), but females from Crozet Islands (6.2) replaced more than females from South Georgia (4.5) (Weimerskirch 1991; Prince et al. 1997). Weimerskirch (1991) found that males replaced more primaries than females and suggested that moult is an important constraint that may compete with breeding, especially in females. It is more costly for female Wandering Albatrosses to raise offspring than it is for males and this may be a reason why females replace fewer primary feathers than males (Weimerskirch et al. 1997).

Great albatrosses, such as the Wandering Albatross, have up to 40 secondaries (Ginn & Melville 1983) and secondary moult has not been explored in any detail in breeding albatrosses. However, Prince et al. (1997) reported three generations of secondary feathers in pre-breeding Wandering Albatrosses and most third year secondary feathers were distributed in the central part of the wing. Non breeding males always replaced more secondaries than females and this leads to females having more third generation secondaries (Prince et al. 1997).

Giant Petrels

Giant petrels are among the largest birds that replace all their primary feathers every year without losing the ability to fly (Hunter 1984a). They have similar sized wings as the smaller albatrosses, which puts them under similar stresses due to the limited time available to moult. Albatrosses do not replace all their primary feathers every year, however, some breed every year (Furness 1988).Giant petrels are able to breed and replace all their primaries each year by overlapping breeding and moult and moulting multiple primaries at once (Hunter 1984a). They start their primary moult during chick rearing and moult becomes more rapid towards late chick rearing (approximately 13 weeks after hatching) with 3-5 primaries moulting simultaneously. Breeding adults are able to increase the rate of primary moult towards the end of chick rearing by investing less in their offspring (Hunter 1984a). Northern Giant Petrels breed ~6 weeks before Southern Giant Petrels Males of both species start their primary moult before females and this may be due to females attending to reproductive activities such as egg formation (Hunter (1984a). Male Northern Giant Petrels start primary moult halfway through incubation, whereas females only start at least three weeks into chick rearing (Hunter 1984a). Hunter (1984a) found that male Southern Giant Petrels breeding on Bird Island, South Georgia start primary moult at egg-laying, whilst females do so close to egg-hatching. Like most petrels, the primaries are moulted from the innermost to the outermost, although several feathers are grown at once. Giant petrels have between 26-29 secondaries and most birds do not start replacing secondaries until they are at least halfway through their primary moult (Hunter 1984a). Hunter (1984a) reported that individuals did not moult all their secondaries each year, resulting in at least two generations of secondaries in most birds. Despite this overlap between breeding and moult, birds that failed moulted earlier and at a faster rate than successful birds (Hunter 1984a). When failure occurred birds started moulting immediately, this was true for individuals that were not already in moult but there were also some that started moulting earlier than the usual date (Hunter 1984a). Failed birds moulted more primary feathers (no data for secondaries) and reached higher moult scores faster than successful birds and this was determined throughout incubation to brooding season (Hunter 1984). Hunter (1984a) reported that when loss of an egg or chick occurred, it affected the timing of moult in breeding adults. He further reported that the rate at which old feathers are dropped is dependent on sex, species and breeding stage. There has been no study of greater covert moult in giant petrels.

Study design and hypotheses

The aim of this study is to improve our understanding of moult patterns in flight feathers of Wandering Albatrosses and giant petrels breeding at Marion and Gough Islands. Both giant petrels breed on Marion Island; however long-term monitoring for Southern Giant Petrels stopped in 1994-1995 due to concerns about disturbance and therefore data from Southern Giant Petrels from Gough Island were used (Cooper et al 2001). Previous studies of moult in adult albatrosses and giant petrels have focused mostly on primary flight feathers (Weimerskirch 1991, Hunter 1984a), whereas this study explores moult in the secondaries and greater secondary coverts. This study further aims to test if there are similar patterns between flight feathers among species and also if these patterns are different among sexes.

This introductory chapter explains the process of moult and the challenges faced by large birds that cannot undergo a flightless moult. I summarise the current knowledge of moult patterns in the flight feathers of albatrosses and giant petrels, and set the scene for the rest of the thesis.

The second chapter demonstrates the use of photography as a method to study moult in breeding Wandering Albatrosses and giant petrels. It investigates the usefulness and limitations of the method and tests whether flight feathers can be aged reliably based on appearance alone by photographing the same birds every year for three years. I also show that photographing incubating birds had no impact on their breeding success.

The third chapter investigates the symmetry of flight feather replacement in the wings of Wandering Albatrosses and giant petrels. The use of photography made it fairly easy to assess moult in both wings. Most studies assume that wing feather moult is largely symmetrical and therefore base inferences on moult patterns from just one wing (Harris 1973, Hunter 1984a, Furness 1988, Rohwer et al. 2011, Bugoni et al. 2014, Vieira et al. 2017). Brooke (1981) concluded that primary moult is usually symmetrical among four albatross species, whereas secondaries showed little or no symmetry. However, his sample sizes were small and he was not able to quantify the degree of symmetry with any confidence. Arroyo et al. (2004) also found that breeding European Storm Petrels (*Hydrobates pelagicus*) have higher symmetry of replacement among their primaries than secondaries. I hypothesise that moult should be most symmetrical in the outer wing, because outer feathers (primaries) are more important for flight, and test whether this is indeed the case. In giant petrels, where partial moult is confined to the secondaries, I expect that outer secondaries are more likely to be moulted than the inner secondaries and that moult symmetry to be greatest in outer secondaries than inner secondaries. I also expect similar patterns in the greater secondary coverts. I discuss the results in relation to current knowledge on moult symmetry and make future recommendations for exploring moult patterns.

The fourth chapter explores the extent of moult, expressed as both the number and mass of flight feathers replaced, in adult Wandering Albatrosses and giant petrels in relation to their breeding activity. I hypothesise that the extent of moult should relate to the time available for moulting between successive breeding attempts. In the case of Wandering Albatrosses, birds that rear a chick or fail late in the breeding season and take a year off between breeding attempts should be able to replace more feathers than birds that fail early in the breeding season, and return to breed again the following season. Previous studies have explored primary moult in Wandering Albatrosses breeding at Possession Island, Crozet Islands, and Bird Island, South Georgia (Weimerskirch 1991, Prince et al. 1997), but I extend the study to include secondary feathers and test if the extent of moult is similar between primaries and secondaries, or there is any evidence of a tradeoff between the two feather tracts. By comparison, giant petrels are annual breeders, and so failed breeders should be able to replace more flight feathers per year than successful breeders. Because they replace all primaries each year, for giant petrels I explore the replacement of the secondaries and greater secondary coverts, and again test if the extent of moult in these tracts is correlated or compensatory. For all three species, I also test whether these patterns differ with sex.

The final chapter summarises the main findings and provides recommendations for future research.

Chapter 2

Using digital photography as a tool to study moult patterns

Abstract

Traditional methods used to obtain moult data from birds include examination of museum specimens and scoring birds in the hand. Some studies have used photographs of birds in flight, although this method has some limitations. In this chapter I explore the use of digital photography as a method to study moult in breeding albatrosses and giant petrels. I used photographs of upperwings of known breeding individuals to infer the age of primaries, secondaries and greater secondary coverts (i.e. whether they had been replaced in the previous year or not). Wandering Albatrosses and Northern Giant Petrels were photographed for three consecutive breeding seasons, and Southern Giant Petrels were photographed for four breeding seasons. Repeat photography of the same individual in successive years presents the opportunity to track the rate of wear and replacement patterns of feathers over time. Photographs were colour contrasted to exaggerate wear differences and thus assign an age class to each feather. The scoring technique works better for darker feathers. It is important to ensure the wing is fully spread, so that all feathers are visible, and to prevent the hands holding the wing from obscuring any feathers of interest. The process of photographing Wandering Albatrosses took longer than for giant petrels, but the method had no impact on hatching success of birds photographed compared to those not photographed. The method showed that the inner secondaries and associated coverts wear much faster than the central secondaries, and this needs to be considered when aging feathers of unknown birds. I found that photography is a useful and reliable method to study moult and recommend that it be explored in other species which are tolerant to being captured at the nest.

Introduction

Moult is an essential process for birds (Payne 1972) and most studies have focused on flight feathers especially primaries (Furness 1988, Weimerskirch 1991, Tickell 2000, Chapter 1). Traditional methods used to obtain moult data from wild birds include from dead birds (e.g. museum specimens (Craig 1983) or caught on fishing gear (Ramos et al. 2009) and from live birds in the hand, which is often used by ringers (Ginn & Melville 1983, Snyder et al. 1987). Recently, the development of digital photography has opened the door for scoring moult from free-ranging birds in flight (Howell 2010). This allows for taking multiple high definition images, but it creates challenges regarding the independence of samples (given the potential for multiple images of the same individual), like most sampling techniques, and it typically precludes tracking moult in known individuals. Digital photography also can be used to rapidly capture moult data from birds in the hand (e.g. during ringing) to reduce handling times and thus stress to birds, which can be especially problematic for breeding birds. Photography also creates a permanent moult archive whereby photos are stored and made available for future research. Using photography to obtain moult data from seabirds at colonies allows for easy capture of a large sample size. As far as I know, this is the first study that uses photography to study moult patterns in breeding seabirds at their colonies.

Most seabirds moult at sea and therefore moult data are not readily available to researchers. For this reason most data on active moult typically comes from dead birds that were collected for skins (Craig 1983, a non seabird example), caught accidentally by fishing vessels (Ramos et al. 2009) or found dead on beaches (Cooper et al. 1991). Bugoni et al. (2014) used cast netting to catch birds at sea in order to obtain moult data. Birds at colonies can also provide data on the extent of moult and in some cases active moult, such as giant petrels which moult while breeding (Hunter 1984a). To date, most moult scoring on breeding seabirds has focused on the primaries (e.g. Furness 1988, Weimerskirch 1991), in part because of the much greater time required to score moult in secondaries and other feather tracts.

In this study, I explore the potential of digital photography as a method to study moult patterns in breeding Wandering Albatrosses and giant petrels. I investigate the advantages and disadvantages of using this method and test whether flight feathers can be aged using appearance alone. Some studies infer that feathers are retained for multiple years based on differences in wear patterns (Howell 2010, Pyle 2016). I test this assumption by photographing the same individuals every year for 3-4 years. By comparing the hatching success of birds photographed compared to birds in the same study colonies not photographed, I assess the impact of the method. If the method used to photograph birds has an impact, I expect hatching success to be less in birds that were photographed than birds not photographed. I show that digital photography provides an effective method to study moult in Wandering Albatrosses and giant petrels, not only in the primaries but also in other wing feather tracts.

Materials and Methods

In this study, photographs were taken of the spread wings of incubating adult Wandering Albatrosses (Figure 2.1) and Northern Giant Petrels breeding at Marion Island (46º 54'S, 37º 51'E), the larger (290 km^2) of the two Prince Edward Islands, situated in the southwest Indian Ocean, and Southern Giant Petrels breeding at Gough Island (40º 21'S, 9º 53'W) in the central South Atlantic Ocean. All birds were individually banded in long-term study colonies and some birds were photographed in three consecutive seasons, 2014-2017 (see Chapter 1). Photographs were taken with a Canon digital SLR (5D or 700D) camera fitted with a Canon 17-40 mm, 18-55 mm or 24-105 mm lens. Moult was scored from photographs of the upperwings of breeding individuals. Most photographs were taken during late incubation to reduce the risk of individuals abandoning eggs, which prevented sampling some birds that failed early during the incubation process. Photographs were taken from 11 September to 1 October (Northern Giant Petrels), 15 September to 8 October (Southern Giant Petrels) and 3 February to 22 April (Wandering Albatrosses). We did not take photos during chick rearing period as chances of getting both adults at the nest were lower during this period. All birds that were included in this study (both photographed and non-photographed) were part of long-term study colonies where regular nest monitoring was made throughout the breeding season to determine the outcome of each breeding attempt.

Giant petrels were photographed *in situ*. Because only the secondaries and associated coverts were investigated for these birds, it was possible to gently extend each wing in turn by holding the outer primaries. With practice, a single person could spread the wing and take a series of images (2-4 per wing). By comparison, the entire wing of Wandering Albatrosses (primaries and secondaries) had to be photographed. Coupled with the larger size of the albatrosses, this required each bird to be restrained by one person, while a second person fully spread each wing in turn and a third person took the images (Figure 2.1). Because this was a much more invasive process, the egg was removed and kept safe to prevent it from being broken or being taken by a predator. Needless to say, the process for photographing Wandering Albatrosses was longer than for giant petrels.

The wing was spread sufficiently to expose all feathers of interest. In the case of the albatrosses, the wing was not held by the flight feathers as this made it difficult to score all feathers accurately. When photographing birds it is important to prevent obscuring of objects (hand) on the wing which makes scoring difficult (Figure 2.2). Only a subset of birds in each colony was photographed at Marion Island to allow assessment of the impact on the birds. This was done by comparing hatching success of pairs where one or both partners were photographed to that of control pairs where neither partner was photographed. Hatching success was calculated by using the number of birds that hatched divided by the number of birds photographed or not photographed. Birds that appeared particularly nervous when approached were not photographed. Nervousness was assessed by carefully observing the behaviour of the bird whether it was unsettled or wanting to get off the nest.

Feather age of flight feathers (primaries and secondaries) was scored from images of the spread upperwings using similar methods to Ginn & Melville (1983) and Furness (1988). Birds that were photographed in this study were not in active moult. As a result, I only scored wear contrast between feathers of different generations. I attempted to score up to three feather generations (new, old and very old). Photographs were colour contrasted and saturation increased to the maximum using Fast Stone Image Viewer 5.3 to exaggerate wear contrast differences and thus assign an age class (Figure 2.3). This made it easier to visualise the wear contrasts among feathers. Both wings were photographed for most birds sampled, and I used the wing with the best image (Van Bemmelen et al. 2018) to estimate the number, mass and probability of feather replacement.

Figure 2.1: Fieldworkers restrain an incubating Wandering Albatross at Marion Island and spread one wing in preparation for taking moult photographs of the upperwing.

Figure 2.2: A Northern Giant Petrel at Marion Island showing wing feathers not perfectly aligned.

Figure 2.3: The upperwing of a Northern Giant Petrel (R-G48) at Marion Island showing an unmodified (top) and modified image (bottom), where the saturation was increased to exaggerate wear contrast differences.

Results

A total of 243 breeding Wandering Albatrosses, 108 Northern and 191 Southern Giant Petrels were photographed during the 2014/15, 2015/16, 2016/17 breeding seasons. Southern Giant Petrels were photographed for an additional year, 2017/2018. The scoring technique worked better for darker feathers. Old feathers (brown and abraded) were easily differentiated from new feathers (black and sharp-edged) (Figure 2.4). By comparing images of the same bird in two to three successive years, it was clear that feathers initially scored as "very old" (assumed to be *ca* 2 years old) were replaced in the same year as an "old" feather (1 year old). Very old feathers were mostly found in the inner secondaries (and secondary coverts). By photographing 14 Wandering Albatrosses, 15 Northern and 15 Southern Giant Petrels for two to three successive years, I found that 89% showed a pattern of accelerated wear in the inner secondaries (Figure 2.5). This indicated that the inner feathers, which are more exposed when the bird is at rest, wear faster than the central secondaries and coverts feathers. Therefore I simply scored old feathers (brown and abraded) as 0 and new feathers (black and sharp-edged) as 1. There was no evidence that photographing birds for moult scoring influenced their breeding performance. The handling time for the giant petrels (less than 1 minute) was much faster compared to the Wandering Albatrosses Hatching success was if anything slightly higher for birds photographed compared to birds not photographed (Table 2.1).

Figure 2.4: The upperwing of a Wandering Albatross at Marion Island showing different levels of wear across the wing (indicated by arrows).

Figure 2.5: The upperwing of a Northern Giant Petrel R-V86 taken in two successive breeding seasons at Marion Island showing faster apparent wear among the inner and the outer greater secondary coverts (circles show fresh feathers in 2014 exhibiting different wear levels 1 year later).

Table 2.1: Hatching success (%) of Wandering Albatrosses and Northern Giant Petrels at Marion Island study colonies, comparing pairs where one or both members of the pair was photographed with pairs where neither partner was photographed in different breeding seasons to assess the impact of handling; values in parentheses are sample size (N).

Species	Breeding season	Both partners photographed	One partner photographed	No birds photographed
Wandering Albatross	2014/15	100 (8)	99 (114)	49 (53)
	2015/16	100 (6)	87 (61)	68 (116)
	2016/17	84 (25)	85 (110)	65 (68)
	2014-17	(39)	(285)	(237)
Northern Giant Petrel	2014/15	100 (7)	88 (43)	34 (47)
	2015/16	78 (9)	85 (27)	70 (66)
	2016/17	64 (25)	39 (49)	60 (62)
	2014-17	(41)	(119)	(175)

Discussion

This chapter highlights the potential of using field photography to study avian moult (Keijl 2011, Vieira et al. 2017). Photography has two distinct applications, it can be used in free ranging birds where photographs are taken opportunistically of birds in flight at sea (Keijl 2011, Bugoni et al. 2014, Vieira et al. 2017), or on land (Snyder et al. 1987, Zuberogoitia et al. 2013, 2016). The second application involves taking photographs of birds in the hand, either dead or alive (Hasselquist et al. 1988, Solheim 2012). For live birds, using photography to score moult is less invasive when scoring birds in the hand (both primaries and secondaries), because it greatly reduces handling time by capturing primaries and secondaries simultaneously. This also allows for larger numbers of individuals to be sampled (Vieira et al. 2017).

None of the species in the study period was in active moult. Hunter (1984a) found that Southern Giant Petrels at South Georgia started moulting while incubating, but there was no evidence of this among the Southern Giant Petrels at Gough Island. The only birds seen in moult during the study were non-breeders loafing in the colony. Gough Island is the northernmost breeding location of Southern Giant Petrels, and this latitudinal difference may account for the delayed onset of moult compared to birds breeding farther south (Hunter 1984a), which might be under greater time constraints to complete primary moult before winter.

Among breeding seabirds, the convenience of the photographic method facilitates the study of moult in the same individuals over time. This allows us to track the change in wear of a given feather over time. Because none of my birds were in active moult, I was only able to assess the difference in feather wear. I demonstrated that the inner secondaries and their coverts wear more quickly than the central feathers. This pattern presumably occurs because these feathers are more exposed on the folded wing and are thus subject to more wear (Zuberogoitia et al. 2013). This result has important implications for studies which infer greater than two generations of feathers based on wear contrasts on different parts of the wing.

Photography generates a permanent record of individual wings, and allows more than one person to score moult, thus increasing objectivity and repeatability of moult scores, improving the accuracy of the moult scores. The ability to enhance colour contrasts artificially also facilitates scoring moult patterns, especially when working with darker feathers. But perhaps most importantly, photography allows us to investigate more of the wing, including the secondaries and coverts compared to scoring from live birds, which typically is confined to the primaries. As a result, photography offers a more reliable and accurate method to study moult (Vieira et al. 2017). The only limitation of this method was that the wing had to be held properly so that key feathers are not obscured and feathers can be aligned for comparisons across successive seasons.

The method used to photograph breeding seabirds did not have an impact on their breeding success. Repeat photography of marked individuals allows us to relate moult information to specific individual information (e.g. breeding success), which can be tracked in relation to moult patterns over several breeding seasons (see Chapter 4). I conclude that digital photography is a useful and reliable method to study moult and therefore I recommend it for exploring moult in other species and in other feather tracts (e.g. greater and median coverts).

Chapter 3:

Investigating feather replacement and symmetry in adult Wandering Albatrosses and giant petrels

Abstract

Scoring moult from live birds can be stressful and time-consuming, especially large-winged birds such as albatrosses and giant petrels, so most studies assume that moult is symmetrical and only score moult from one wing. Using digital photography to study moult allows the opportunity to assess moult symmetry with little extra impact on the birds. I explore Type 1 moult asymmetry (i.e. between year asymmetry) in relation to the probability of feather replacement in Wandering Albatrosses (primaries and secondaries) and giant petrels (secondaries and greater secondary coverts). Adult Wandering Albatrosses prioritised replacing the outer primaries (P10-P7), outer secondaries (S1-S3), and inner secondaries (S25-S27). Giant petrels (which replace all primaries each year) also prioritised replacing outer secondaries (S1-S3) and their inner secondaries (S20-S26), and showed a similar pattern in their greater secondary coverts. All three species exhibited some asymmetry in all feather tracts that underwent an incomplete annual moult. Moult symmetry was related to the probability of feather replacement, suggesting that symmetry is greatest among feathers that are most important for birds to replace each year. However, the probability of asymmetry is dependent in part on the probability of feather replacement, peaking when the probability of feather replacement is close to 50%. Comparison with a random null model shows that the degree of asymmetry in Wandering Albatrosses was always much less than expected by chance, indicating selection for symmetrical moult across the wing. By comparison, giant petrels tended to show asymmetry not significantly different from random in some secondaries and most secondary coverts. Future moult studies should include both wings, especially if using digital photography to collect moult data, to ascertain whether there are consistent differences among species and feather tracts in terms of the selection for symmetry.

Introduction

The moult of flight feathers poses a significant challenge to birds, which have evolved several strategies to minimise the impact of reduced wing area on their day-to-day activities (Rohwer et al. 2011). Most species replace their flight feathers sequentially, retaining the ability to fly, but aerodynamic efficiency is compromised by gaps in the wing created by growing new feathers (Hedenström and Sunada 1999). This impact is exacerbated if the gaps in the wing are not symmetrical (Thomas 1993) and thus we might expect selection to favor symmetrical wing moult (e.g. Brommer et al. 2003, Minias and Iciek 2013). However, most studies only score one wing for moult and assume that flight feather moult is more or less symmetrical (e.g. Harris 1973, Hunter 1984a, Furness 1988, Rohwer et al. 2011, Bugoni et al. 2014) in part because handling live birds to assess moult can be stressful and time consuming, especially in large birds, which have large numbers of flight feathers. As a result, there have been relatively few studies of moult symmetry, most of which have been on raptors. Houston (1975) found that in White-backed Vultures (*Gyps africanus*), 62% of the primaries were replaced symmetrically whereas the secondaries did not show symmetry. Zuberogoitia et al. (2016) found that adult Bearded Vultures (*Gypaetus barbatus*) have a high degree of asymmetry in secondary and tail feathers, and similar patterns have been noted in Common Buzzards (*Buteo buteo*) (Zuberogoitia et al. 2005). Pyle (2006, 2016) found asymmetry in the wing moult of herons and egrets (Ardeidae), especially in the secondaries, although he noted that accidental loss of feathers also may contribute to asymmetry. Among seabirds, Brooke (1981) reported that moult in four albatross species is usually symmetrical among the primaries but that there is little or no symmetry among the secondaries.

These studies suggest that asymmetry of flight feather moult is more frequent in the secondaries and tail, which might be perceived as feathers that are less critical for flight than the primaries (Zuberogoitia et al. 2005 and 2013). One way to demonstrate this might be to test whether the probability of asymmetry is related to the probability of feather replacement, assuming that the latter factor is an indicator of feather importance. However, the likelihood of asymmetry is dependent in part on the probability of feather replacement; there is no possibility of asymmetry if the probability of replacement is 0 or 1, and if replacement is random on either wing, the probability of asymmetry peaks when the probability of replacement is 0.5. To assess the significance of feather moult symmetry at a particular site, I compared the observed number of asymmetry records to a null model which assumed random replacement at that site (see methods for details). Clearly there is a need for more data to better understand patterns of moult asymmetry in large birds, and to critically test claims that replacement is 'random' in some feather tracts (Zuberogoitia et al. 2013).

Digital photography can be used as a method to score moult in birds with minimal disturbance (Chapter 2), and so provides a useful tool to explore moult asymmetry because there is little additional handling time required to photograph both wings compared to a single wing. Moult symmetry consists of between-season asymmetry (Weimerskirch 1991) and within-season asymmetry (Arroyo et al. 2004). Both are related to timing of moult, but between season asymmetry (Type 1) only applies to birds that do not replace all their flight feathers each year, and assesses whether feather pairs are replaced symmetrically or not between seasons (Weimerskirch 1991; Prince et al. 1997, this study). Such birds are usually not in active moult when scoring feather age (Weimerskirch 1991, Brommer et al. 2003). By comparison, within season asymmetry (Type 2) occurs during a single moult cycle when paired feathers are replaced at different times. To detect Type 2 asymmetry, birds have to be in active moult (Arroyo et al. 2004, Ramos et al. 2009). In this chapter, I explore the Type 1 symmetry of flight feather replacement among three large seabirds. Specifically, I test the hypothesis that symmetry is greater in feathers with a greater 'importance' in terms of flight function, and I explore the relationship between the probability of feather replacement and likelihood of asymmetry across the wing in all three species using a random null model based on the incidence of feather replacement.

Materials and Methods

I scored the ages (new or old) of feathers from photographs of incubating seabirds (Chapter 2). The probability of replacement was estimated from all birds; however; symmetry was estimated for birds with both wings photographed. Sample sizes differed among feathers because not all feathers could be scored on both wings (if one was obscured) and this was especially challenging for the inner secondaries. It is presumably for this reason that Brommer et al. (2003) restricted their analysis to the outer 10 secondaries in their study of moult asymmetry in Ural Owls (*Strix uralensis*).

For each feather (primary, secondary or greater covert), the probability of replacement for a given species was estimated by photographing the left wing of each bird (i.e. the age of all feathers at a given location (e.g. S4) was summed as expressed as a proportion of the total number of S4 feathers sampled). Symmetry of moult was recorded by assigning “1” when corresponding feathers on left and right wings were the same age and “0” when they differed in age. The proportion of individuals with symmetrical moult was calculated for each feather location for three species: Wandering Albatross (primaries and secondaries) and both giant petrels (secondaries and greater secondary coverts). To test whether asymmetry at a particular feather position is random or not, I used Pearson’s Chi-squared goodness-of-fit tests (with Yates’ correction) to compare observed versus expected frequencies assuming replacement at a given feather location is random. The null model estimated the random probability of asymmetry as:

$$P(\text{random asymmetry}) = 2 \times P(\text{feather replacement}) \times [1-P(\text{feather replacement})]$$

Results

Both wings were photographed on 198 Wandering Albatrosses and 88 Northern Giant Petrels during the 2014/15, 2015/16 and 2016/17 breeding seasons at Marion Island, and on 76 Southern Giant Petrels during the 2016/17 breeding season at Gough Island.

Among Wandering Albatrosses, most individuals prioritised replacing the outer primaries (P10-P7), outer secondaries (S1-S3), and inner secondaries close to the body (S25-S27; Figure 3.1). Giant petrels replace all their primary feathers each year (Hunter 1984a), and so there was no chance of asymmetry among these feathers. Giant petrels prioritised replacing their outer secondaries (S1-S3, with all Southern Giant Petrels sampled replacing S1 and S2), and their inner secondaries (S20-S26) than their central feathers, and showed similar patterns to this in the greater secondary coverts. Thus all three species prioritised replacement in similar areas in the secondaries (Figure 3.1). Giant petrels also were most likely to replace their outer (GC1-GC3) and inner greater secondary coverts (GC20-GC26), following a similar pattern to that found in the secondaries (Figure 3.2).

In Wandering Albatrosses the relationship between feather symmetry and probability of feather replacement indicated that primaries, especially outer primaries (P10-P7) had a stronger relationship than secondaries while the outer secondaries were strongest within the secondaries (Figure 3.3). Similar patterns were observed in secondaries and greater secondary coverts of giant petrels (Appendices 3.1 and 3.2). Wandering Albatrosses showed consistent selection for symmetrical replacement of flight feathers across the wing (primaries and secondaries; Figure 3.4 and Appendix 3.3). In giant petrels the replacement of the secondaries and greater secondary coverts was more random, with the proportion of asymmetry significantly different from random (Figures 3.4 and 3.5, Appendices 3.4 and 3.5).

Among Wandering Albatrosses, symmetry was greater in the outer than inner primaries. However, the pattern of increasing asymmetry towards the body was not consistent; the inner primaries showed less symmetry than outer secondaries (Figure 3.4). Symmetry was similar in the outer (S1-S3) and the inner (S30-S32) secondaries, with lower values for the central secondaries (Figure 3.4). Greater coverts in giant petrels showed similar pattern as the secondaries, but many fewer feather locations were significantly different from random in both species (Figure 3.5). Moult symmetry in primaries (88.5%) was greater than secondaries (69.5%) in Wandering Albatrosses and moult symmetry in secondaries of Northern Giant Petrels (74.7%) was slightly greater than Southern Giant Petrels (71.6%). However, symmetry of the greater coverts was significantly lower than that among the secondaries in both species of giant petrels (Northern 60.0% and Southern 66.9%).

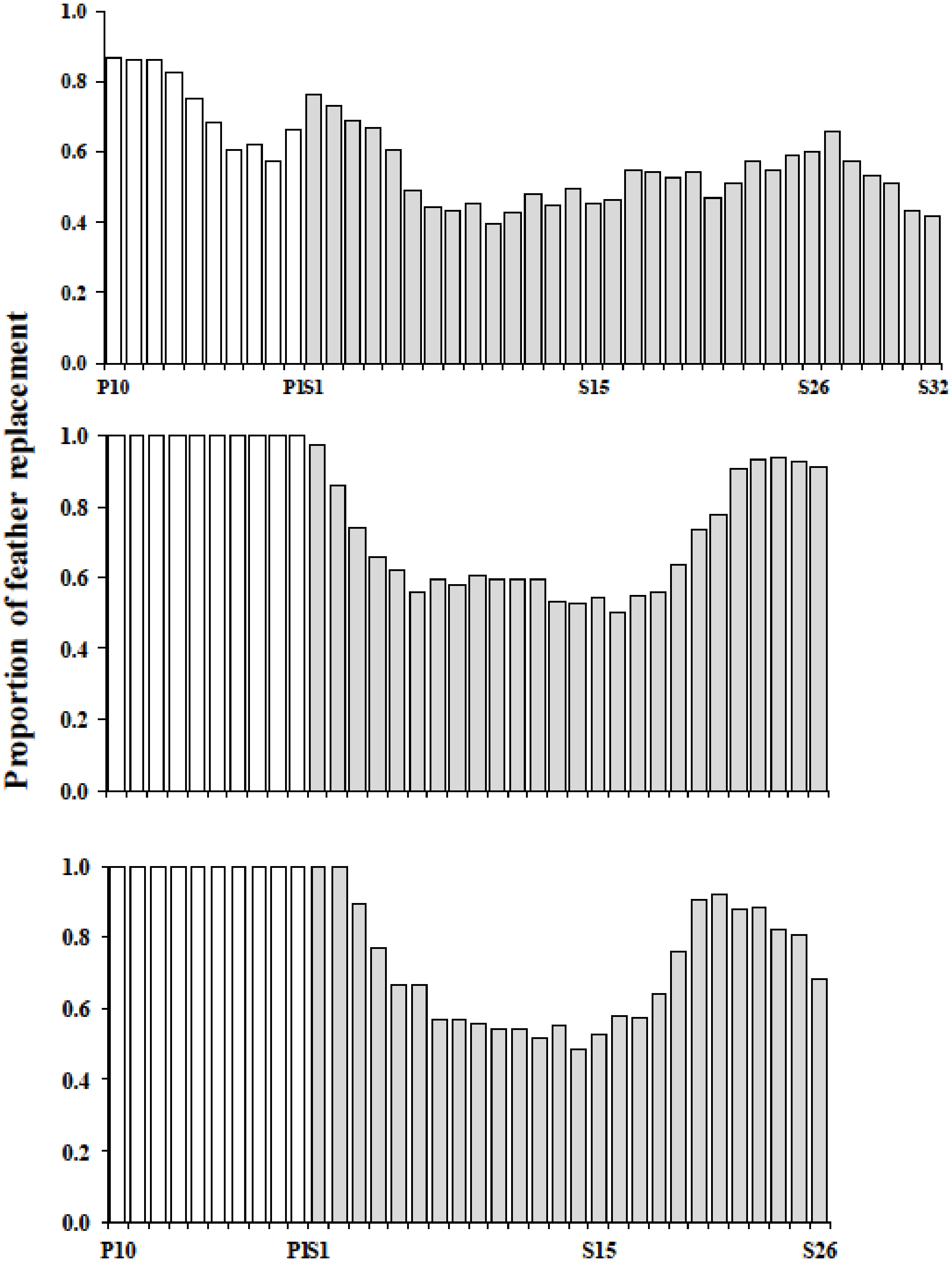


Figure 3.1: Proportion of flight feather replacement (one wing only) of Wandering Albatrosses (top, n=214) and Northern (middle, n=102) and Southern Giant Petrels (bottom, n=200) in primaries (P) and secondaries (S).

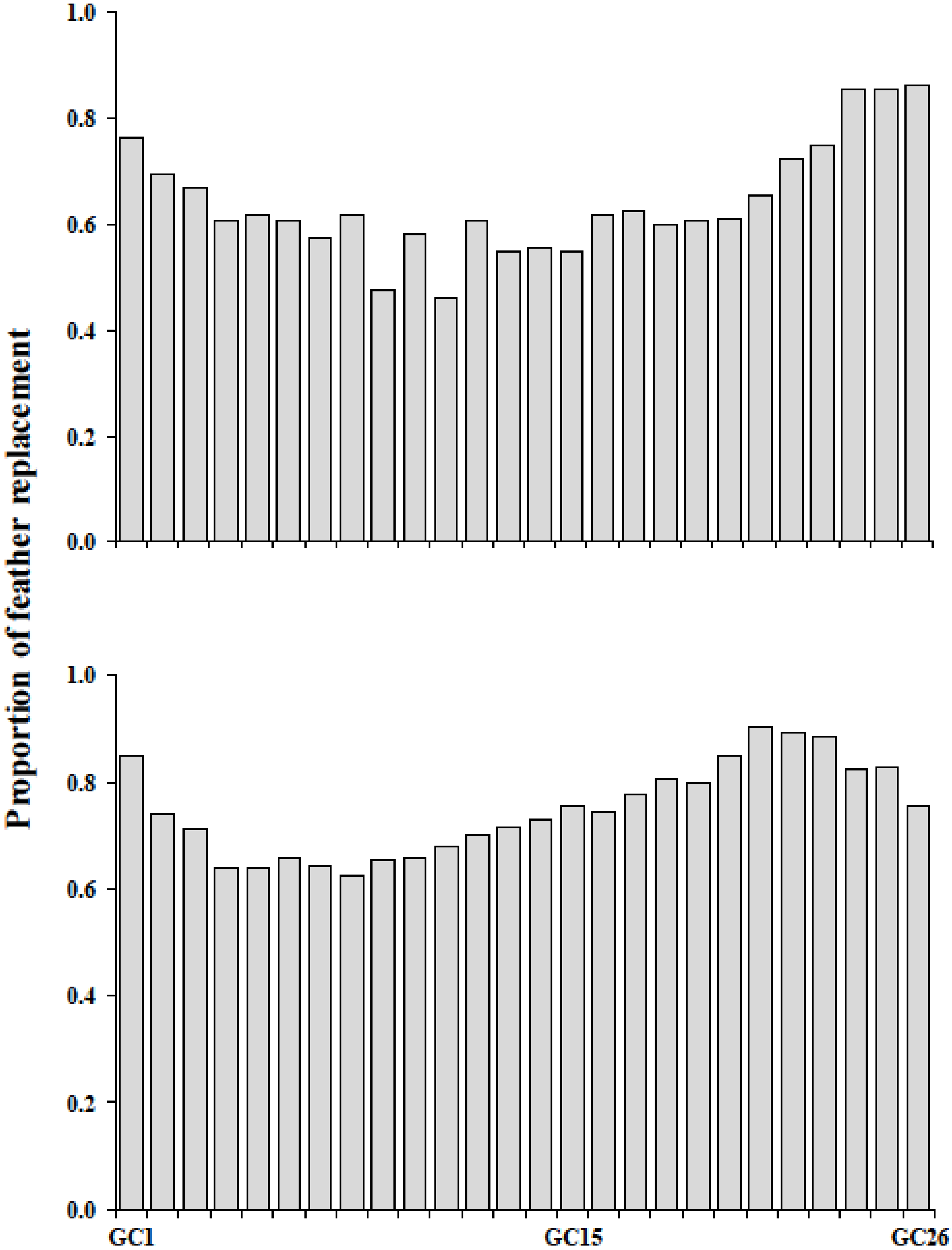


Figure 3.2: Proportion of greater secondary covert replacement among Northern (top: n=102) and Southern Giant Petrels (bottom; n=200).

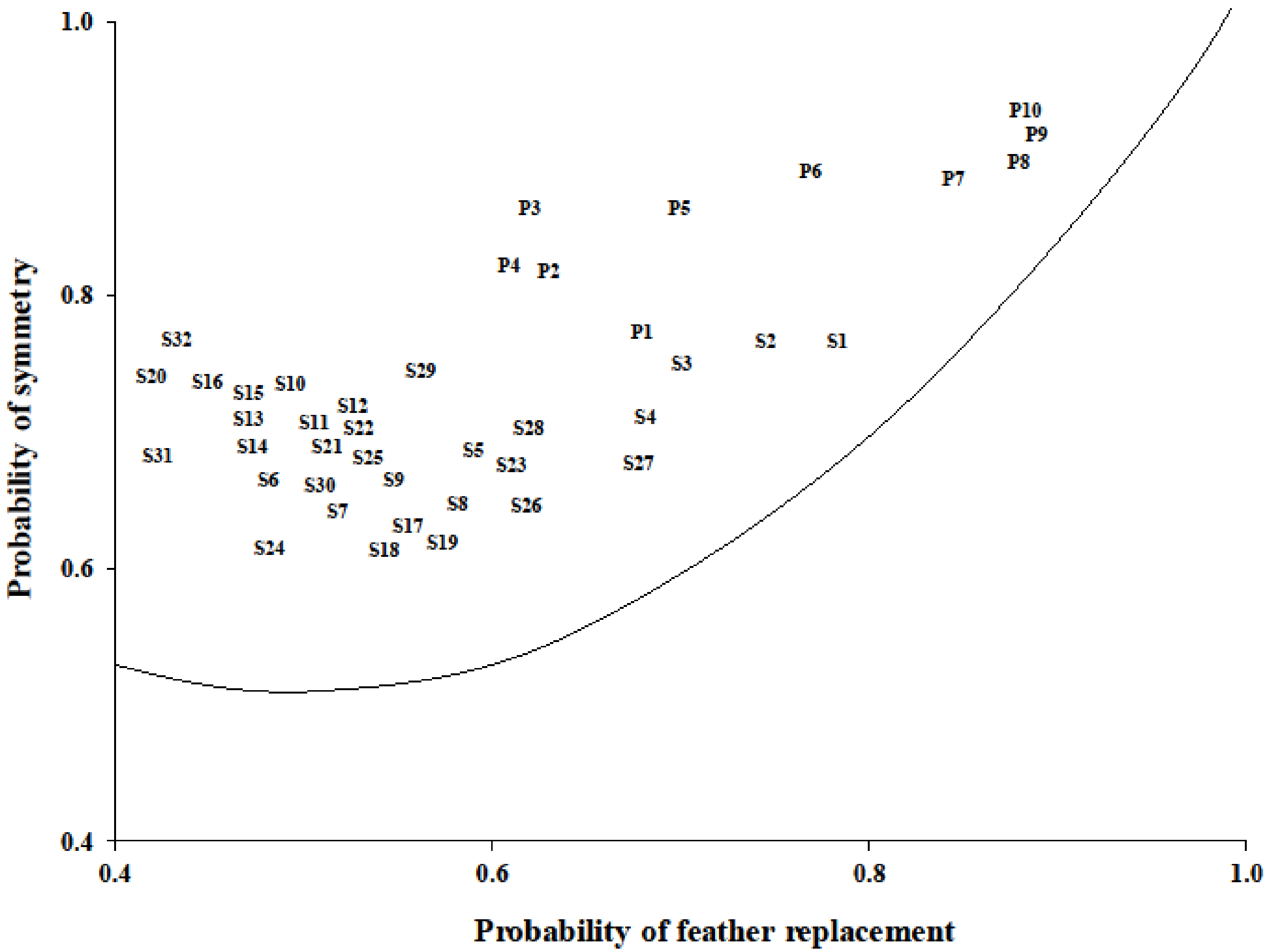


Figure 3.3: The probability that flight feathers are replaced symmetrically in Wandering Albatrosses in relation to the probability of replacement among primaries (P10-P1) and secondaries (S1-S32). The curve represents the null model assuming moult is random.

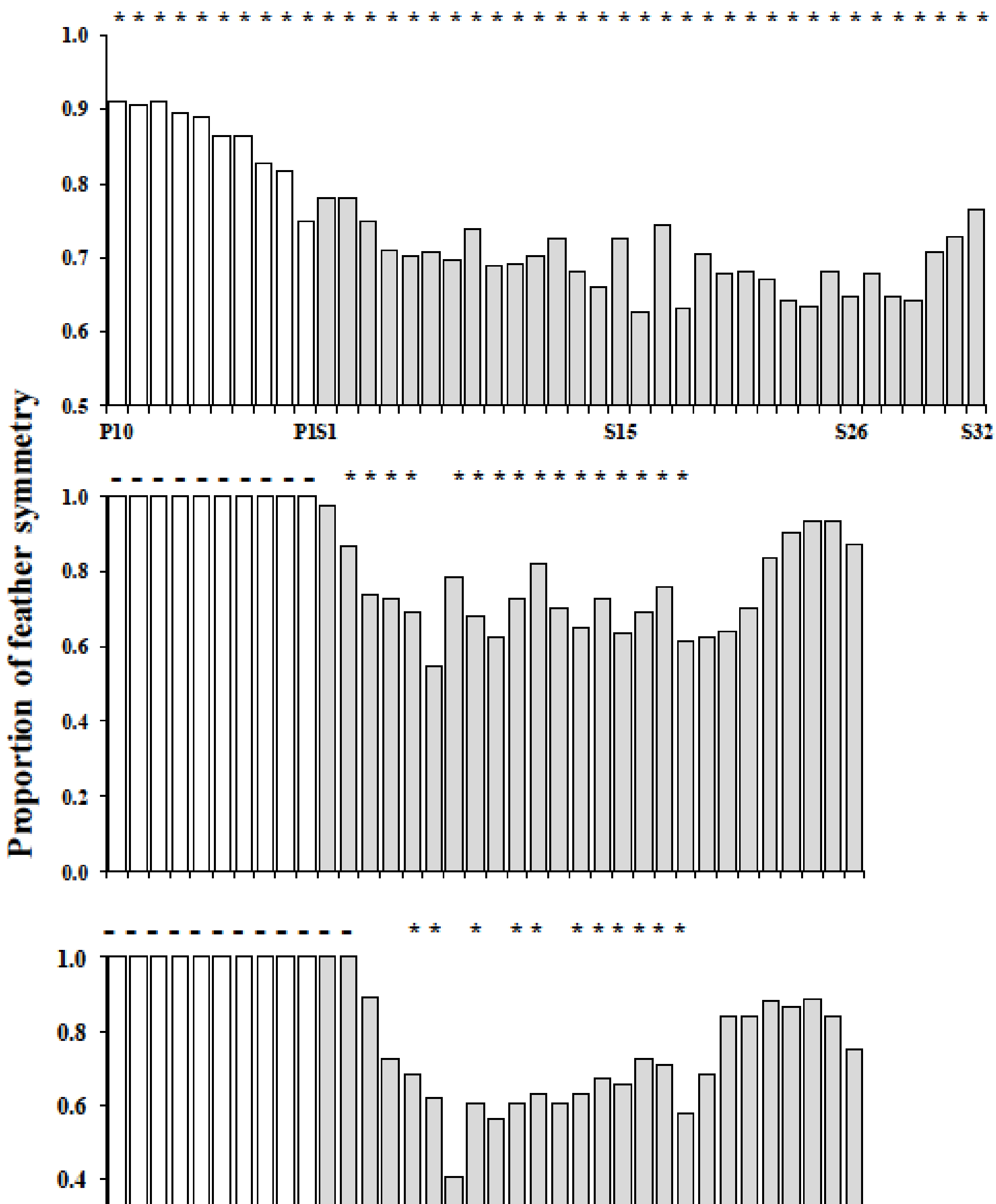


Figure 3.4: Symmetry of flight feather moult in adult Wandering Albatrosses (top, n=198) and Northern (middle, n=88) and Southern Giant Petrels (bottom, n=76) in primary (P) and secondary (S) feathers. Feathers marked above by an asterisk (*) were significantly more symmetrical than expected by chance, whereas no symbol indicates feathers not significantly different from random. Dashes (–) indicate feathers that were all replaced and thus had no possibility of being asymmetrical.

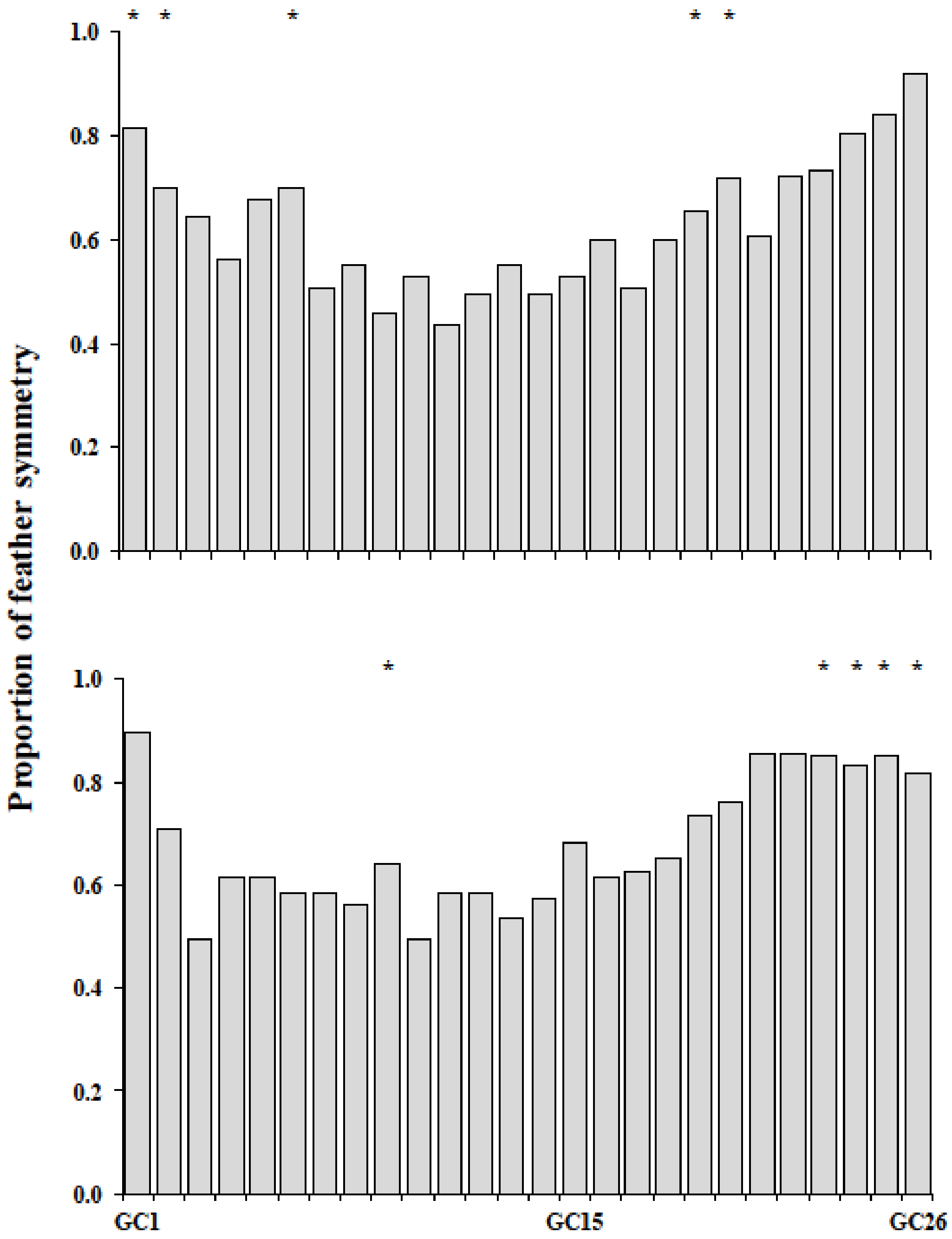


Figure 3.5 Symmetry of greater secondary covert moult in adult Northern (top: n=88) and Southern Giant Petrels (bottom; n=76) in (GC1-GC26). Feathers marked above by an asterisk (*) were significantly more symmetrical than expected by chance, whereas no symbol indicates feathers not significantly different from random.

Discussion

Probability of replacement of feathers varied across the wing; however, probability of replacement showed similar patterns in all three species and this is related to functional importance and exposure or wear rates on the wing (Zuberogoitia et al. 2013). Outer feathers such as primaries are more important for flight and are normally used for propulsion during flight (Hickman et al. 1993). Feathers that tend to wear faster are replaced more often (Zuberogoitia et al. 2016) and are usually outer feathers because they move faster through the air. Inner secondaries also experience high wear rates because they are most exposed to the sun (see Chapter 2, Zuberogoitia et al. 2013). Brommer et al. (2003) found that the probability of replacement among primaries was greater than the outer 10 secondaries, similar to my results in Wandering Albatrosses, where my results showed this pattern in the first five primaries and secondaries. Prince et al. (1997) found that Wandering Albatrosses preferentially replaced their outer primaries first. Zuberogoitia et al. (2016) also found adult Bearded Vultures tend to replace certain feathers more frequently than others, suggesting that some feathers are more important than others.

A consistent pattern of feather replacement and moult symmetry was observed across the wing among all three species. Greater probability of replacement was observed where greater moult symmetry occurred. Greater probability of replacement presumably indicates greater feather importance and therefore the symmetry pattern observed in this study supports the assumption that more important feathers that have a high probability of replacement are also most likely to be replaced symmetrically. Female Ural Owls have greater symmetry among the primaries than the secondaries (Brommer et al. 2003). My study found similar results in Wandering Albatrosses. The functional importance of the primaries may be the reason for greater moult symmetry among primaries than secondaries. The consistent pattern between feather replacement and moult symmetry indicates that both these indices can be used as a measure of feather importance. Thomas (1993) found that wing asymmetry reduces flight performance and therefore symmetrical wings are important for large birds due to their large wings.

Zuberogoitia et al. (2013) found high levels of asymmetric moult (60%) in Griffon Vultures (*Gyps fulvus*) and adult Bearded Vultures (Zuberogoitia et al. 2016), mainly in the secondaries. Brommer et al. (2003) and Zuberogoitia et al. (2016) found that asymmetry was greater in secondaries than primaries. My results agree with Brommer et al. (2003) and Zuberogoitia et al. (2016), where I have found that asymmetry among Wandering Albatrosses is greater in secondaries (outer ±20%; inner ±22%) than primaries (outer ±6%; inner ±18%). Brommer et al. (2003) found that asymmetry in primaries was related to reduced survivorship of female Ural Owls. They noted that asymmetry in primaries is more controlled compared to secondaries. Asymmetry is greatest in greater secondary coverts in Northern Giant Petrels (32%) and Southern Giant Petrels (37%) than secondaries in Northern Giant Petrels (25%) and Southern Giant Petrels (27%).

However, there is a relationship between moult symmetry and probability of replacement even if moult is random (Zuberogoitia et al. 2016). Brommer et al. (2003) found that moult was more symmetrical than chance among both primaries and secondaries in female Ural Owls. My study found similar results in Wandering Albatrosses. However, giant petrels showed asymmetry not significantly different from random in some secondaries and most greater secondary coverts. The more secondaries that are symmetrical compared to greater secondary coverts suggests that giant petrels selects for symmetry in functionally important feathers for flight.

This chapter has further shown the importance of assessing feather replacement, moult symmetry and asymmetry. Until recently, this has not been easy to assess for large-winged birds, but with recent technology advances in using digital photography it is possible to assess moult patterns relatively quickly and reliably. Therefore more data are needed from other species to see if this is a general pattern among birds.

Chapter 4

Does breeding outcome and sex have an influence on moult extent in adult Wandering Albatrosses and giant petrels?

Abstract

Many large birds such as albatrosses and giant petrels have evolved complex moult strategies, only replacing a subset of their flight feathers each year because they have insufficient time to breed and moult. Even immature albatrosses, which lack the obligations of breeding, typically only replace about half of their primary flight feathers (by mass) each year. The number of primaries replaced by adult albatrosses varies depending on the time available between successive breeding attempts. Among Wandering Albatrosses I found little difference between the sexes in the number of primaries replaced between breeding attempts by successful birds, which take a year off between breeding attempts (males 7.9±2.1 and females 7.3±2.2). Wandering Albatrosses that fail and return to breed the following year on average moult slightly fewer primaries, although the difference is greater for females (6.1±2.7) than for males (7.4±2.6). There is also a great variability in the extent of moult among these individuals. Males that failed also replaced almost as many secondaries (55%) as successful males (62%), whereas females that failed only replaced 36% of secondaries, compared to 48% in successful females. There was no evidence of a trade-off between replacing primaries and secondaries. General Linear Models (GLMs) showed that sex and time available to moult both influenced the number and mass of feathers replaced. Sex explained more variation in terms of number of feathers replaced (67%) than time available to moult (33%), but time available to moult explained 68% of the mass of flight feathers replaced. However, the model only accounted for 9.2% (number) and 11.9% (mass) of feathers replaced, due to marked inter-individual variation in the extent of moult. Giant petrels are annual breeders and are among the largest birds to undergo a complete primary moult every year. They do this by not only overlapping their moult and breeding, but also moulting multiple primaries at once. However, not all secondaries are replaced each year. Giant petrels replaced more secondaries (number and mass) when their breeding attempt fails,

giving more time to moult before the next breeding season. Following a successful breeding attempt, both sexes of Northern Giant Petrels replaced the same percentage of secondary feathers on average (males 65±15% and females 65±17%), whereas both sexes replaced similar greater secondary coverts (males 66±13%) and females 62±11%). Southern Giant Petrels typically replaced more secondaries (males 72±14% and females 67±11%) and more greater secondary coverts (males 80±13% and females 72±12%) following a successful breeding attempt than Northern Giant Petrels, and like Wandering Albatrosses showed a tendency for males to replace more feathers than females. When a breeding attempt fails, giant petrels have more time to moult, and replace more secondaries (but not secondary coverts) than successful breeders. Among failed breeders, males consistently replaced more secondaries (83±14% for Northern and 73±12% for Southern) than females (71±20% and 69±12%, respectively). Breeding outcome was the only variable that significantly influenced the mass of feathers replaced in Northern Giant Petrels, accounting for 14% of the variance in feathers replaced, while sex was the only variable in Southern Giant Petrels, accounting for 6% of variance. These results suggest that female albatrosses and petrels are under greater pressure to replace flight feathers than males, especially when time between breeding attempts is limited.

Introduction

In this chapter I discuss whether breeding outcome and sex have an influence on moult extent in Wandering Albatrosses and giant petrels. Most albatrosses do not moult while breeding (Harris 1973, Furness 1988, Prince et al. 1993). As a result, albatrosses have developed complex moult strategies to fit their protracted moult and breeding seasons into the year, even taking a year off between breeding attempts in some species (Tickell 1968, Weimerskirch 1991). The Wandering Albatross is the largest albatross species, and thus has a particularly severe problem in feather replacement because of its long wings that take a long time to grow individual flight feathers (Rohwer et al. 2009) and further has a long incubation and chick rearing period (Tickell 2000). Most Wandering Albatrosses only replace a subset of their primary feathers each year, with the number replaced by adults dependent on the amount of time between breeding attempts (Weimerskirch 1991, Prince et al. 1997).

Wandering Albatrosses are sexually dimorphic with females weighing approximately 80% to males (Tickell 1968). Adults return to their colonies in November, about a month before laying starts and chicks only fledge in November the following year (Tickell 1968, Jones et al. 2016). Because of the year-long breeding cycle, most adults only breed every other year when they are successful in fledging a chick. Adults that fail have 5 to 11 months between breeding attempts, depending on when failure occurs in the breeding cycle; however, some pairs that fail at late chick stage do not attempt to breed again the following season, and thus have more than a year to moult. If failure occurs during incubation (January-March) or early stages of chick-rearing, pairs usually attempt to breed again the following breeding season (Tickell 1968). Weimerskirch (1991) and Prince et al. (1997) found that the extent of primary moult in Wandering Albatrosses is related to the time between breeding attempts. Failed breeders that attempt to breed the following year (i.e. have 5-11 months between breeding attempts) replace fewer primaries (average 6.0) than successful breeders (7-8 primaries; Prince et al. 1997).

Because flight feathers differ in size, particularly among the primaries, Underhill and Zucchini (1988) argued that moult models should not only include the number of feathers replaced but also the mass. Therefore I explore both the number and mass of feathers replaced in both the primary and secondary feathers among different sexes in relation to the time available to moult since the last breeding attempt.

Studies investigating albatross moult patterns have mostly focused on primary flight feathers (Furness 1988, Weimerskirch 1991). Because of their very long wings, albatrosses have many more secondaries than primaries: 25-29 in the small albatrosses or mollymawks (*Thalassarche* and *Phoebetria* spp.) and up to 40 secondaries in the great albatrosses, like the Wandering Albatross (Ginn & Melville 1983). Replacing such large number of feathers likely poses an additional constraint (in addition to breeding) on these long-winged birds. Moult in secondaries have not been explored in breeding albatrosses, but Prince et al. (1997) reported that pre-breeding Wandering Albatrosses can have up to three generations of secondary feathers. Replacing secondaries is less important than primaries (Chapter 3), and so breeders would be expected to prioritise replacing primaries over secondaries.

Giant petrels are able to overlap moult and breeding and can also moult several primaries at once (Hunter 1984a). Hunter (1984a) suggested that this overlap is due to the abundant and easily available food supplies during breeding season. Like the smaller albatrosses, giant petrels have 26-29 secondaries and most individuals do not start secondary moult until they are at least halfway through their primary moult (Hunter 1984a). Hunter (1984a) showed that adult giant petrels did not moult all their secondaries within a year and found at least two generations of feathers in most birds. He also found no specific sequence of secondary moult in either species.

Both species of giant petrels are annual breeders that lay a single egg, and like all Procellariiformes, raising a chick requires both parents (Conroy 1972). Northern and Southern Giant Petrels are the most sexually dimorphic procellariiforms, with males averaging 25% heavier than females (Hunter 1984b, Copello et al. 2006). At Marion Island, Northern Giant Petrels start breeding in early August, about 6 weeks before Southern Giant Petrels. The chicks of Northern Giant Petrels hatch from mid-October whereas Southern Giant Petrels hatch from late November to early December (Hunter & Brooke 1992). This difference in breeding biology reduces competition due to the similarities in the diet and foraging ranges (Cooper et al. 2001).

Hunter (1984a) reported that among both giant petrels breeding on Bird Island, South Georgia, the males started primary moult before females. Southern Giant Petrel males start primary moult at the same time of egg laying, whereas the females start near hatching time. Northern Giant Petrels moult somewhat later in the breeding cycle, with most males only starting to moult around the time the eggs hatch (although a few males start midway through incubation), whereas females only start moulting three weeks after hatching. Hunter (1984a) also reported that during late chick period both sexes of Northern Giant Petrels started rapid moult; however, no data for Southern Giant Petrels were available. Male and female Southern Giant Petrels start to moult earlier than the Northern Giant Petrels and primary moult also start more rapidly. Birds that failed, not only moulted earlier, but also moulted more feathers and at a faster rate than successful birds (Hunter 1984a). When breeding failure occurred, birds started moulting immediately (Hunter 1984a).

Furness (1988) showed that Atlantic Yellow-nosed Albatrosses (*Thalassarche chlororhynchos*) that breed successfully replaced fewer primaries than failed or non-breeders. Furness (1988) suggested that time, nutrients or energy available between breeding attempts constrains moult. Furness (1988) also found no difference in primary moult between sexes. Atlantic Yellow-nosed Albatrosses (Furness 1988) and giant petrels (Hunter 1984a) are both annual breeders; however, Atlantic Yellow-nosed Albatrosses do not replace all their primaries within a year (Furness 1988).

I test whether the pattern in primary moult among Wandering Albatrosses at Marion Island is the same as populations studied at the Crozets (Weimerskirch 1991) and Bird Island, South Georgia (Prince et al. 1997). This difference may be due to various factors such environmental factors and different foraging zones (Pardo et al. 2017). I predict that the number and mass of feathers replaced should be directly related to sex and time between successive breeding attempts, and time between successive breeding attempts should be greater for successful breeders than those that fail early and try to breed again the following year. However, birds that fail late and then still skip a year should have the most time for moulting and thus replace the most feathers. I further predict that time between successive breeding attempts should have greater influence than sex on the number and mass of feathers replaced. I also predict that females should replace fewer feathers than males, and females will replace even fewer primaries when failure occurs. This may be influenced by competition between sexes and females investing energy in reproductive activities (Weimerskirch et al. 1997). I expect similar results in the secondaries compared to primaries in both sexes and breeding attempts. In giant petrels I test whether the moult patterns are similar to other annual breeders (seabirds) as discussed in Furness (1988) and Harris (1973), I predict that both giant petrel spp. show similar moult patterns. I expect that failed breeders should have more time to moult and therefore replace more feathers (number and mass) than successful breeders. Lastly, I predict, like Wandering Albatrosses, males replace more feathers (number and mass) than females.

Materials and Methods

Moult data were collected by photographing the spread wings of adult Wandering Albatrosses and giant petrels incubating in long-term study colonies on Marion and Gough Islands (Chapter 2). Nests were checked regularly from the onset of laying to identify individuals attempting to breed. Breeding information for Wandering Albatrosses in these study colonies has been recorded annually since the 1980s, with about 300 pairs monitored annually (Jones et al. 2014). Sex of Wandering Albatrosses is assigned based on size (males average larger than females); plumage development (males average paler than females) and behavioural observations (copulation events, timing of arrival at colonies and incubation shifts [males take the first long incubation shift]); this combination of methods is 100% accurate when compared with birds sexed using genetic markers (Jones et al. 2012). Further checks occur until the chicks fledge or the breeding attempt fails (Jones et al. 2016).

Average masses of primaries (n = 6) and secondaries (n = 4) were obtained from adult Wandering Albatrosses found dead at Marion Island (n = 5) or killed accidentally by longline fishing vessels (n = 1). The masses of secondaries and greater secondary coverts were obtained from an adult Northern Giant Petrel found dead at Marion Island; additional secondary masses were obtained from four giant petrels killed on longlines (not idenditifed to species because of the loss of soft-part coloration). I used the same mass estimates for both species. Feathers were oven dried at 30 ºC for 24 hours, measured (total length and vane length) to the nearest 1 mm, and weighed to the nearest 1 mg. I used the average mass of these feathers (Appendices 4.1 and 4.2) to calculate the mass of feathers replaced in the most recent moult cycle (all feathers with scores of 1, assumed to have been replaced in the most recent inter-breeding interval, see Chapter 2). Feathers (primaries and secondaries) were grouped together to calculate the average mass of all primaries and secondaries, separately. Although males are larger than females in both Wandering Albatrosses (Tickell 1968) and giant petrels (Hunter 1984b, Copello et al. 2006), the importance of using mass of feathers is to indicate the relative energy needed to replace different feathers (Underhill and Zucchini 1988), and this is likely to be more in males than females.

For Wandering Albatrosses, the past breeding history was known for all birds and therefore I could calculate the time available for moult since the last breeding attempt. Male Wandering Albatrosses arrive at their colonies at Marion Island on average four days earlier (~17 November) than females (~21 November; Jones et al. 2016). These return dates were used to estimate the time available to moult for birds returning the following season, because returning birds have completed flight feather growth (Tickell 1968, Furness 1988). Among successful pairs, the average date of fledging at Marion Island is 6 December (based on chick departure dates inferred from successive colony checks, which averaged 10-15 days apart towards the end of the chick-rearing period). Therefore, assuming both sexes continue to provision the chick until fledging, and moult only commences after the chick fledges, the average time a successful bird would spend at sea potentially available for moulting would be ~346 days for males and 350 days for females. For pairs that lose their egg or chick, the date of breeding failure was assumed to be the midpoint between the two colony checks when the failure occurred. These checks typically are 5-15 days apart, depending on the stage of the breeding season. The inferred failure date was used as the start of the period potentially available for failed breeders to moult before the next breeding attempt.

Breeding information for Northern Giant Petrels at Marion Island has been recorded annually since the 1980s (Cooper et al. 2001), whereas the demographic long-term study of Southern Giant Petrels breeding at Gough Island was only initiated in 2010/11 (Cooper & Parker 2011), although many Southern Giant Petrels had been metal banded since 1989 (Cuthbert & Sommer 2004, Cooper & Parker 2011). Sex was assigned on size (males have distinctly larger and heavier bills than females), and behavioural observations (copulation events) (Cooper & Parker 2011). Monitoring methods for giant petrel breeding colonies (Cooper et al. 2001, Cooper & Parker 2011) are similar to those for Wandering Albatrosses. Both species of giant petrels were photographed during the 2014/15, 2015/16, 2016/17 breeding seasons, with Southern Giant Petrels also photographed in 2017/18. See Chapter 2 for methods used to score moult in both Wandering Albatrosses and giant petrels. The previous breeding history was known for all birds and this was used to test if there was a difference in feather replacement between successful and failed breeders.

Statistical Analyses

In order to assess whether number and mass of feathers replaced in Wandering Albatrosses is influenced by the time available between breeding attempts, I used a General Linear Model (GLM). Both the number and mass of feathers replaced were used as response variables: Giant petrels initiate wing moult while breeding, with males starting several weeks before females (Hunter 1984a) therefore I used breeding outcome (failed versus successful) rather than time available for moulting in the GLM model for giant petrels. Sex was again included as a possible explanatory variable. Feathers were grouped this way because it was easier to score and identify them. The GLM models were used to assess the effects of time and sex interaction on the number and mass of feathers replaced in Wandering Albatrosses. In giant petrels it was used to assess the effects of breeding outcome and sex interaction on number and mass feathers replaced.

Wandering Albatrosses: Number/mass of feathers replaced ~ Time available + Sex

Northern Giant Petrels: Number/mass of feathers replaced ~ Breeding Outcome + Sex

Southern Giant Petrels: Number/mass of feathers replaced ~ Breeding Outcome + Sex

The GLM was run together with a Gaussian distribution and then compared using Akaike's Information Criterion (AIC, Crawley 2008). The data were explored visually and normality tested through inspection of qq-plots and histograms; the testing of assumptions and the statistical tests were completed in R-Studio (R Development Core Team 2010) and Microsoft Office Excel 2007. Statistical significance (α) was set at 5% and only significant predictors were included in the final model to explain number and mass of feathers replaced.

Results

Wandering Albatrosses on Marion Island replaced more flight feathers (number and mass) following a successful breeding attempt than when they fail and attempt to breed again the following year (Figure 4.1), and males replaced more primaries and secondaries than females, especially among failed birds (Figure 4.1).

Both species of giant petrels replaced more secondaries (number and mass) following a failed breeding attempt compared to a successful breeding attempt, except for greater secondary coverts in Southern Giant Petrel females (Figures 4.2 and 4.3). My results showed that across all three species females replaced less feathers (Wandering Albatrosses: primaries and secondaries; giant petrels: secondaries), with Southern Giant Petrels having a smaller difference, especially when time available for moult is limited. Furthermore, I compare my results of Wandering Albatrosses to other populations breeding at the Crozet Islands and South Georgia (Table 4.1) and found that they are somewhat similar with females always replacing fewer feathers, especially when breeding attempt fail.

There was large inter-indvidual variation in number and mass of primaries and secondaries replaced independent of the time available for moult in Wandering Albatrosses (Figure 4.4). Among Wandering Albatrosses, both sex and time available to moult influenced the number and mass of feathers replaced. The pseudo coefficient of determination (R^2) that is used to explain the final model for number and mass of feathers replaced showed 9.2% and 11.9% respectively (Table 4.2). The R^2 values represent the total deviance explained by the final model, which gives a measure of the goodness-of-fit for the model. The GLM model that was performed using data from Northern Giant Petrels showed that only breeding outcome had an influence on the mass of feathers replaced and accounted for 14% of the variance while sex was the only variable that had an influence on mass of feathers replaced in Southern Giant Petrels, accounting for 6% of variance (Table 4.3).

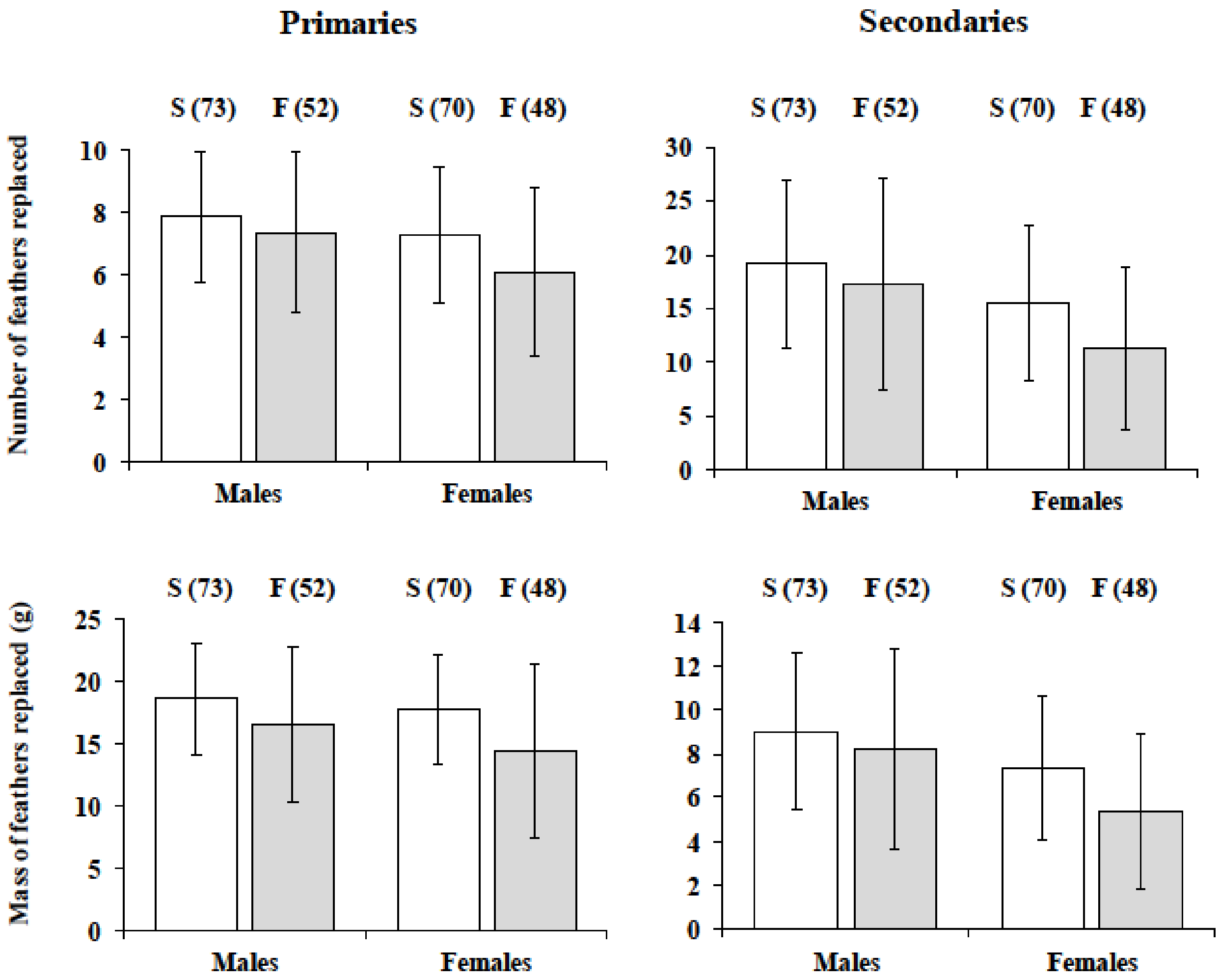
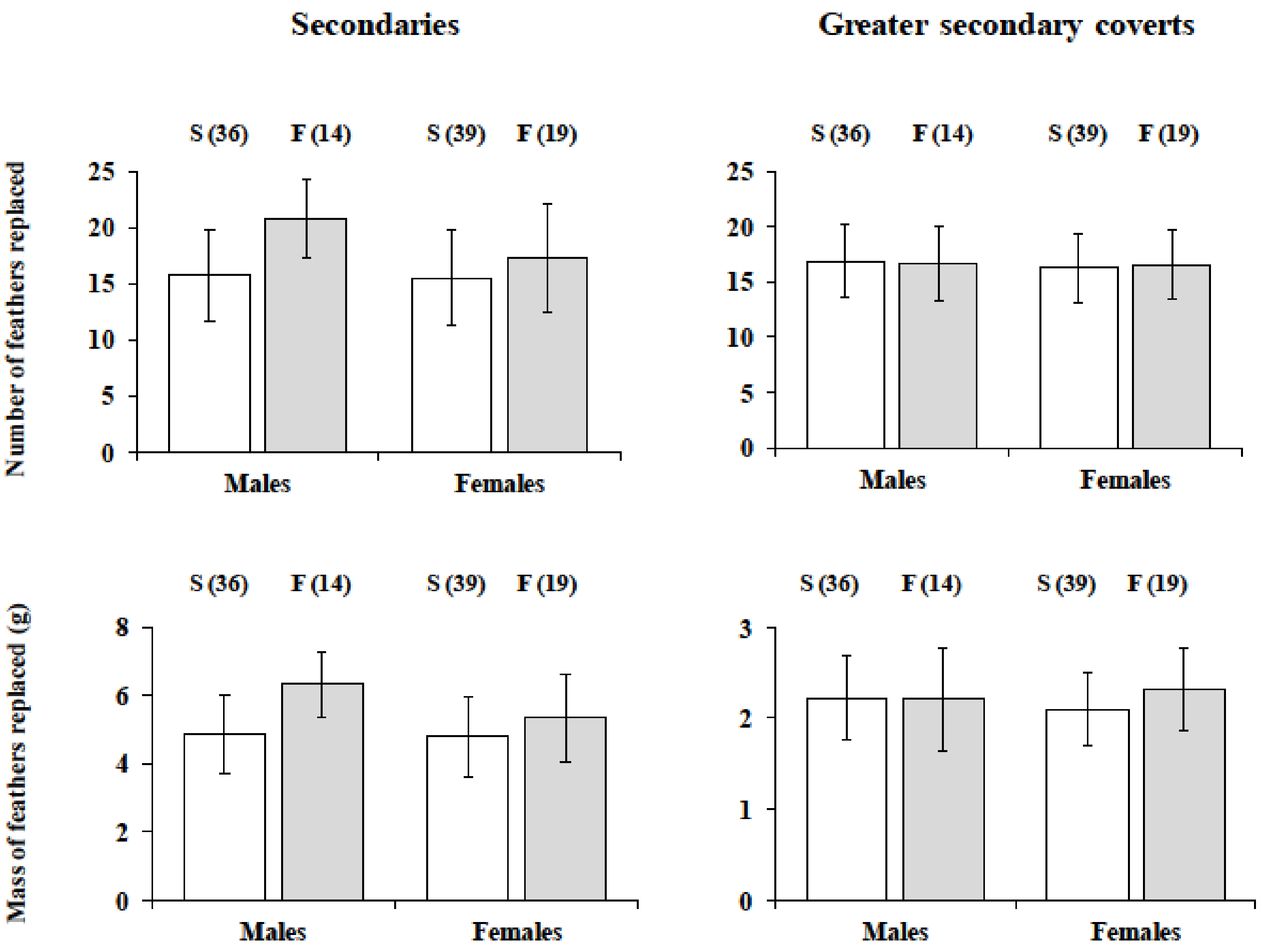


Figure 4.1: Average number and mass of primaries and secondaries replaced in failed (F) and successful (S) male and female Wandering Albatrosses (n=243) at Marion Island. Error bars show ± 1 standard deviation.


Secondaries

Greater secondary coverts

Figure 4.2: Average number and mass of secondaries and greater secondary coverts replaced in failed (F) and successful (S) male and female Northern Giant Petrels (n=108) at Marion Island. Error bars show ±1 standard deviation.

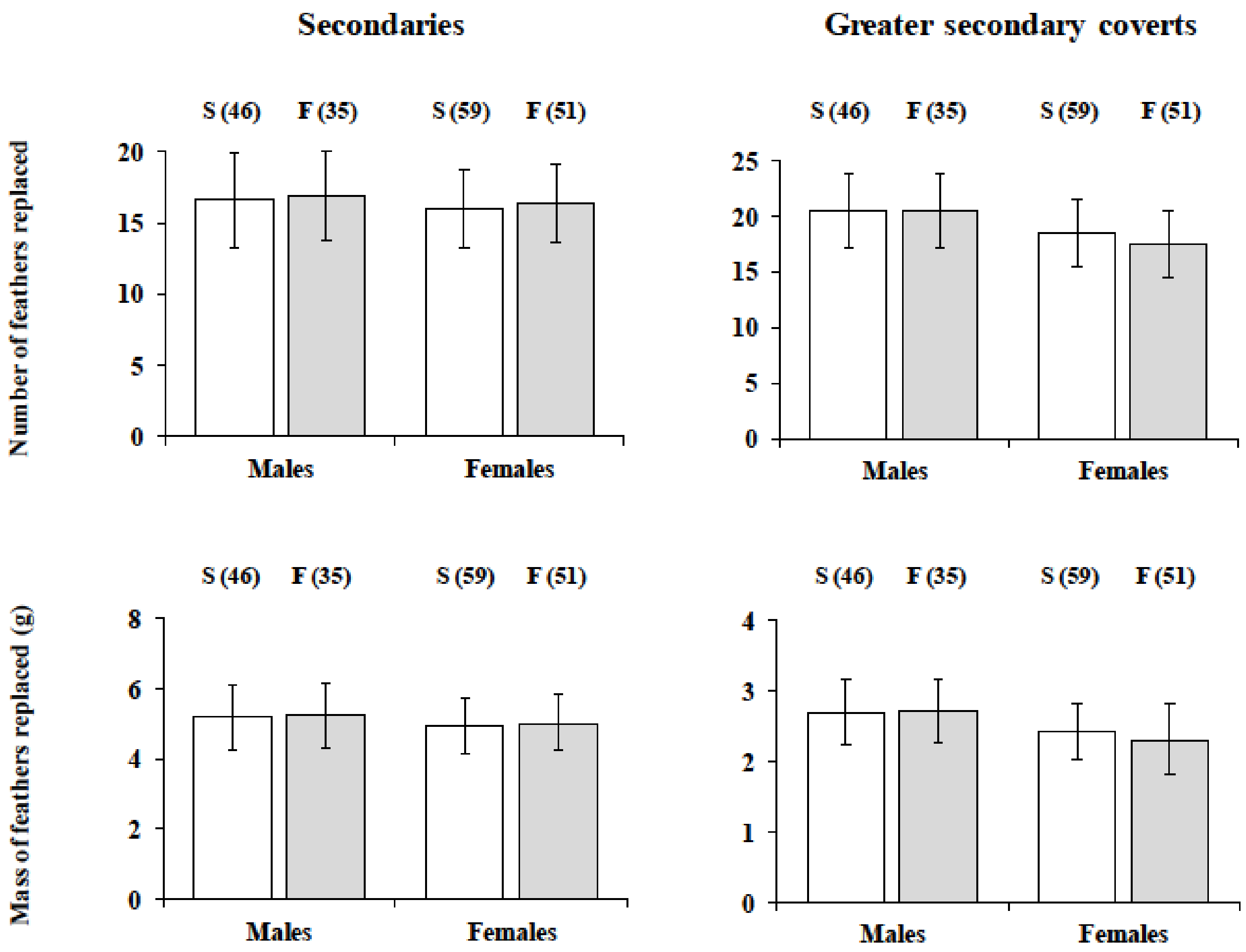


Figure 4.3: Average number and mass of secondaries and secondary coverts replaced in failed (F) and successful (S) male and female Southern Giant Petrels (n=191) at Gough Island. Error bars show ±1 standard deviation.

Table 4.1: Comparison of number of primaries replaced in male and female Wandering Albatrosses in relation to breeding success on Marion, Crozet Islands and South Georgia. Values are mean ±SD (N), range. Data from South Georgia do not include range of number of primaries replaced.

Breeding success	**Marion Island**		**Crozet Island**		**South Georgia**	
	Males	**Females**	**Males**	**Females**	**Males**	**Females**
Successful	7.9 ±2	7.3±2	8.8±1.2	8.1±1.6	8.6±1.4	7.1±7.7
	(46) 0-10	(59), 2-10	(142), 5-10	(162), 3-10	(180)	(168)
Failed	7.4±2.8	6.1±2.9	8.3±1.9	6.5±2.2	7.2±2.4	5.2±2.4
	(35) 0-10	(51), 0-10	(53), 2-10	(57), 3-10	(109)	(110)

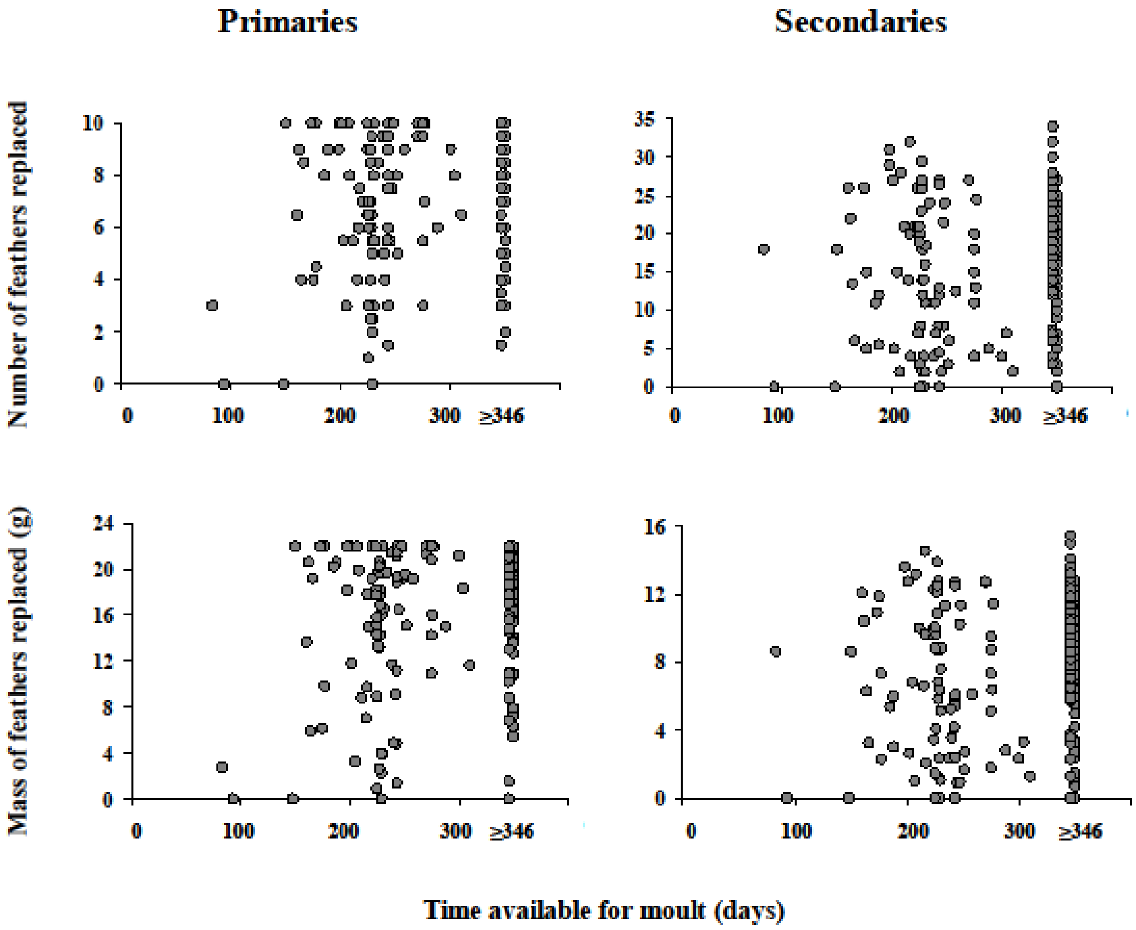


Figure 4.4: Number and mass of primaries and secondaries replaced of breeding male (125) and female (118) Wandering Albatrosses in relation to time available to moult (days).

Table 4.2: GLM with significant predictors of number and/or mass of feathers (primaries and secondaries) replaced in Wandering Albatrosses.

	Degrees of freedom	**% Explained**	**P-value**
Number of feathers			
Sex	138	67.4	0.0001
Time available for moult	137	32.7	0.008
AIC:1605.7			
R^2: 9.22			
Mass of feathers			
Sex	223	32.1	0.002
Time available for moult	222	67.9	0.00001
AIC: 4660			
R^2: 11.93			

Table 4.3: GLM with significant predictors of mass of feathers (secondaries and secondary coverts) replaced in giant petrels.

Northern Giant Petrels	**Mass replaced**		
	Degrees of freedom	**% Explained**	**P-value**
Breeding Outcome	137	100	0.0337
AIC:1605			
R^2: 14.17			

Southern Giant Petrels	**Mass replaced**		
freedom	**Degrees of**	**% Explained**	**P-value**
Sex	223	100	0.002
AIC: 4660			
R^2: 6.44			

Discussion

Moult is challenging for birds, especially large birds that take more time to grow long flight feathers (Rohwer et al. 2009). Moult in birds is an important constraint that could compete with breeding success (Weimerskirch 1991). My results agree with previous studies of Wandering Albatrosses from the Crozet Islands and South Georgia where I have found that the the primary moult patterns between sexes are somewhat similar (Table 4.1; Weimerskirch 1991, Prince et al.1997). However, females on South Georgia appear to replace fewer feathers, especially if they fail, and thus might be under more stress than populations from the Indian Ocean (Marion and Crozet Islands). This may be related to the contrasting population trends that show increases in the Indian Ocean populations such as Marion (Ryan et al. 2009) and Crozet (Weimerskirch et al. 2018) islands over the last few decades, but an ongoing decrease in the South Georgia population (Pardo et al. 2017).

Weimerskirch (1991) argued that sexes not only differ in morphology but also behaviour and life history. Weimerskirch and Jouventin (1987) found that males and females forage in different oceanic water masses; males prefer colder Antarctic waters whereas females mostly forage in sub-Antarctic and sub-tropical waters. Food availability and weather conditions, including wind speed, differ between these zones (Jouventin and Weimerskirch 1990), resulting in structural differences between the sexes in terms of wing loading linked to the stronger winds typically experienced farther south, where males tend to range (Shaffer et al. 2001). Such factors might affect both the rate of resource acquisition needed to fuel moult, and the degree to which wing area can be compromised through moult, helping to explain the sex-specific differences in moult extent (Weimerskirch 1991).

When provisioning chicks, males have a higher foraging efficiency than females, delivering higher energy content food more regularly than females (Weimerskirch et al. 1997). During incubation and brooding period females fly farther than males (Salamolard and Weimerskirch 1993). It appears to be more costly for females to raise offspring than for males, and females also stop feeding their offspring earlier than males (Weimerskirch et al. 2000). Previous studies by Weimerskirch and Jouventin (1987) and Weimerskirch (1992) also found that males have higher survivorship and age at breeding. This agrees with my results where I have found that male Wandering Albatrosses replace more feathers than females.

Prince et al. (1997) investigated secondary moult in non-breeding Wandering Albatrosses; however, my study investigated secondaries in breeding birds. My results showed a similar pattern to the primaries, with females replacing on average fewer secondaries than males, especially after a failed breeding attempt. Prince et al. (1997) found that among non-breeding individuals, males of all ages moult more secondaries than females, resulting in females having more older secondaries compared to males.

Weimerskirch (1991) found that the extent of moult in breeding birds was directly related to the time available between breeding attempts in females, but not in males. Prince et al. (1997) also argued that the time available between successive breeding attempts in both sexes is most likely to be the main constraint on the number of primaries moulted. I found that there is a significant difference in the mass of feathers replaced between failed and successful breeding attempts. Both sex and time available to moult influenced the number and mass of flight feathers replaced, with sex explaining more variation in terms of number of feathers replaced (67%) but time available to moult explaining 68% of the mass of flight feathers replaced. However, there was marked inter-individual variation in number and mass of primaries and secondaries replaced independent of the time available for moult (Fig. 4.4). This suggests that other factors such as age and experience may affect feather replacement. By comparing adult and immature birds Weimerskirch (1991) and Prince et al. (1997) showed that age and experience affect the amount of feather replacement while Zuberogoitia et al. (2013) suggested that foraging experience could influence moult in Griffon Vultures (*Gyps fulvus*). Younger and less experience birds replace fewer feathers than older and more experience birds (Prince et al. 1997). Inexperience in foraging, especially in adverse weather conditions can lead to not having enough energy in excess for moulting (Zuberogoitia et al. 2013). All these factors show how it can influence moult.

In contrast to Wandering Albatrosses, giant petrels are annual breeders and overlap breeding and moult (Hunter 1984a). Although they overlap breeding and moult, the intensity varies throughout the breeding cycle, e.g. moult rate increased as parental investment decreased (Hunter 1984a) and therefore breeding outcome is expected to influence the number of feathers moulted. Among annual breeders such as Atlantic Yellow-nosed Albatrosses (Furness 1988) and Waved Albatrosses (*Phoebastria irrorata,* Harris 1973), failed breeders replace more feathers than successful breeders because they have more time to moult before the onset of the next breeding season than do birds that fledge a chick.

My results for giant petrels agree with Hunter (1984a), where I have found that giant petrels species replaced more secondaries (both by number and mass) when a breeding attempt fails, giving them more time to moult before the following breeding season. The signal was less convincing for greater secondary coverts, with no significant effect noted among male Northern and female Southern Giant Petrels. Grissot et al. (2019) suggested that moult duration in Northern Fulmars (*Fulmarus glacialis*) is the same, irrespective of whether their breeding attempt fails or not. However, this species is appreciably smaller than the giant petrels, and thus might be less constrained to complete its moult within the annual cycle.

I found that, like Wandering Albatrosses, females replaced fewer feathers than males. This was most marked in the number of secondaries replaced by Northern Giant Petrels following a successful breeding attempt. Hunter (1984a) found that males of both giant petrels start their primary moult before females and he further reasoned that this may be due to females attending to reproductive activities (e.g. egg formation). Female Northern Giant Petrels at Marion Island spend more time incubating than males (Cooper et al. 2001). Females having a greater investment in breeding could be one of the reasons for fewer feathers being replaced. This chapter has highlighted the importance of moult patterns in the Wandering Albatross and giant petrels. Therefore continued annual collection of moult data for this long-term monitoring species is needed to give researchers a better understanding of moult patterns of breeding albatrosses and petrels at Marion and Gough Islands.

Chapter 5:

Synthesis and Conclusions

This chapter explores the importance of my findings and gives a better understanding of moult patterns in three large seabird species, Wandering Albatrosses and Northern Giant Petrels at Marion Island and Southern Giant Petrels at Gough Island. I explored the use of digital photography as a method to study moult patterns rather than scoring moult the old fashioned way (in the hand). Using this method I was able to collect extensive moult data efficiently from large numbers of birds with minimal disturbance, and compare moult patterns to other island populations. I conclude this chapter with recommendations for future research.

Key Findings

Chapter 2 reports on using digital photography as a method to study moult patterns in upperwings of known breeding albatrosses and giant petrels. The technique works best for dark feathers, where enhancing image saturation makes it easier to detect wear contrasts between adjacent feathers. This method of photography has highlighted not only its own pitfalls, but also pitfalls of previous methods used to score moult e.g. in the hand (Hunter 1984a, Furness 1988) and in doing so improved both these methods. This method can help to create a permanent archive of photographic images that can be used for future research. Using repeat photography of known birds in successive years allows the opportunity to track the rate of feather wear over time. This approach indicated that inner secondaries (and their coverts) wear much faster than the central feathers. This chapter also showed photographing the extended wings of albatrosses and petrels incubating eggs had no impact on hatching success, making this method a convenient and reliable way to investigate moult patterns.

A major advantage of the photographic technique is that images can be obtained quickly and then scored afterwards. It thus made it much easier to score the moult pattern in both the secondaries as well as the primaries, and even in the coverts, without having to handle the birds for any longer than it might take to score the primaries directly in the hand. Also, both wings can be photographed with little added disturbance. Most moult studies assume that feathers are symmetrical in both wings and therefore only use one wing to study moult pattern (Harris 1973, Hunter 1984a, Furness 1988, Rohwer et al. 2011, Bugoni et al. 2014, Vieira et al. 2017). Chapter 3 explores how symmetrical moult is in the three study species, and how this relates to the probability of feather replacement. Symmetry has been used as a measure of the importance of a feather, whereby more 'important' feathers (in terms of aerodynamics and propulsion in flight) are expected to show greater symmetry in the pattern of replacement (Zuberogoitia et al. 2013). Adult Wandering Albatrosses prioritise replacing the outer primaries (P10-P7), outer secondaries (S1-S3), and inner secondaries (S25-S27). Giant petrels also preferentially replaced the inner and outer secondaries and the inner and outer greater secondary coverts, and feather symmetry was greatest in these feathers. These results support the hypothesis that symmetry correlates with the 'importance' of specific flight feathers whereby some wing feathers are more important than others and also some feathers may be more exposed than others (Zuberogoitia et al. 2013).

All three species showed some asymmetry in all feathers that had an incomplete annual moult. As expected, Wandering Albatrosses exhibited greatest moult symmetry in the outer flight feathers, especially the outer primaries compared to less distal flight feathers. However, the pattern of increasing asymmetry towards the body was not consistent; the inner primaries showed less symmetry than the outer secondaries, and the central secondaries were less symmetrical than the inner secondaries. However, such a pattern is expected simply because there is more scope for assymmetry as the probability of replacement approaches 50% (from both lower and higher replacement values). Comparing the observed values to a random null model, I found that the amount of asymmetry in Wandering Albatrosses always was significantly less than expected by chance, indicating selection for moult symmetry across the wing. This is similar to data from female Ural Owls (Brommer et al. 2003), which is the only other species for which this character has been critically assessed. By comparison, asymmetry in giant petrels was less marked, with the replacement of some secondaries and most secondary coverts not significantly different from random. This suggests that giant petrels selects for symmetry/asymmetry in functionally important feathers. Data from other species are needed to assess the generality of these patterns across species, and to test which factors might account for the symmetry differences observed among species.

Chapter 4 investigated how number and mass of feathers replaced by large seabirds are affected by their breeding phenology and sex. Specifically, I assessed how the time between breeding attempts and sex affect moult extent in adult Wandering Albatrosses (primaries and secondaries) and giant petrels (secondaries and greater secondary coverts). To date, studies of moult in these species (Hunter 1984a, Weimerskirch 1991, Prince et al. 1997) only considered the number of feathers replaced. However, particularly among the primaries, size differences among feathers make it important to consider not just how many feathers are replaced, but also the size of those feathers (Underhill and Zucchini 1988). Accordingly, I included mass of feathers replaced in my study. Previous studies also have focused only on the primaries (although Prince et al. 1997 did examine secondaries of non-breeding Wandering Albatrosses); however, I expanded my studies to secondaries in breeding adults.

General Linear Models (GLMs) indicated that sex and time available to moult both influenced the number and mass of feathers replaced in Wandering Albatrosses. Sex explained more variation in the number of feathers replaced (67%), whereas time available to moult explained 68% of the mass of flight feathers replaced. However, there was considerable inter-individual variation not accounted for by these factors; the final model only accounted for 9.2% (number) and 11.9% (mass) of feathers replaced. Further studies of birds with known breeding histories might begin to tease apart some of the other factors (e.g. age, experience and individual ‘quality’, measured by historical breeding performance and/or body condition both before and after the moulting period) that might help to explain this large individual variation in moult extent. It is striking that some individuals can replace all primaries in less time than it take other birds to only replace a few primaries (Figure. 4.4).

As expected, primary moult patterns from Wandering Albatrosses breeding on Marion Island were similar to those reported from the Crozet Islands (Weimerskirch 1991) and Bird Island, South Georgia (Prince et al. 1997). There was little difference between sexes in the number of primaries replaced following a successful breeding attempt, when birds have a full year to moult between breeding attempts. However, following a failed breeding attempt, the number of primaries replaced decreased. South Georgia birds generally replaced fewer primaries than birds breeding in the southwest Indian Ocean, which might reflect generally better conditions for Wandering Albatrosses from the latter colonies (reflected in the contrasting population trends between these regions). Females replaced fewer primaries than males, irrespective of breeding site. At Marion, they also moulted fewer secondaries than males. Interestingly, males that failed replaced a similar number of secondaries as successful males, whereas females that failed replaced fewer secondaries than successful females. Overall, females appear to be less capable of replacing flight feathers than males, especially when the time available for moult is constrained (i.e. when a breeding attempt fails), despite the fact that they average slightly smaller, and thus if anything should be able to moult faster than males. This might reflect a later onset of moult or poorer feeding conditions for females, which generally forage farther north than males (Shaffer et al. 2001).

Among giant petrels, only breeding outcome significantly influenced the mass of feathers replaced in Northern Giant Petrels, accounting for 14% of the variance in feathers replaced, while only sex had a significant influence in Southern Giant Petrels, accounting for 6% of variance. Giant petrels replaced more feathers (number and mass) when breeding attempts fail (Hunter 1984a). When giant petrels fail a breeding attempt, they have more time to moult, and replace more secondaries (but not secondary coverts) before returning to breed again than after a successful breeding attempt. Like Wandering Albatrosses, male giant petrels that fail their breeding attempt, consistently replace more secondaries than females, even though they average 25% larger (by mass) than females (Hunter 1984b, Copello et al. 2006). This might simply be a consequence of starting moult earlier than females (Hunter 1984a), or because males can afford to moult more rapidly than females (i.e. replace more feathers at once) given their greater propensity to scavenge on or close to land, whereas females mainly forage at sea (Hunter 1983, Hunter & Brooke 1992).

Recommendations for future research

This study demonstrates the benefits of using photography to record wing moult in breeding seabirds, and has given some novel insights into the moult of flight feathers in large procellariiform seabirds. It has also provided some interesting novel insights into how large birds are able to cope with the challenges of moult. I recommend that long-term breeding studies of these birds consider recording upperwing patterns every year, to detect possible changes in moult extent and pattern over time, while also increasing sample sizes to try to understand the factors that might explain the large inter-individual differences in moult extent (e.g. age, experience and individual quality). Such data might also allow us to address other, more challenging questions. For example, what impact does the accumulation of old feathers have on future breeding success? What are the impacts that limited time available to moult has on feather quality? What other negative impacts do breeding adults experience when failure occurs, especially females?

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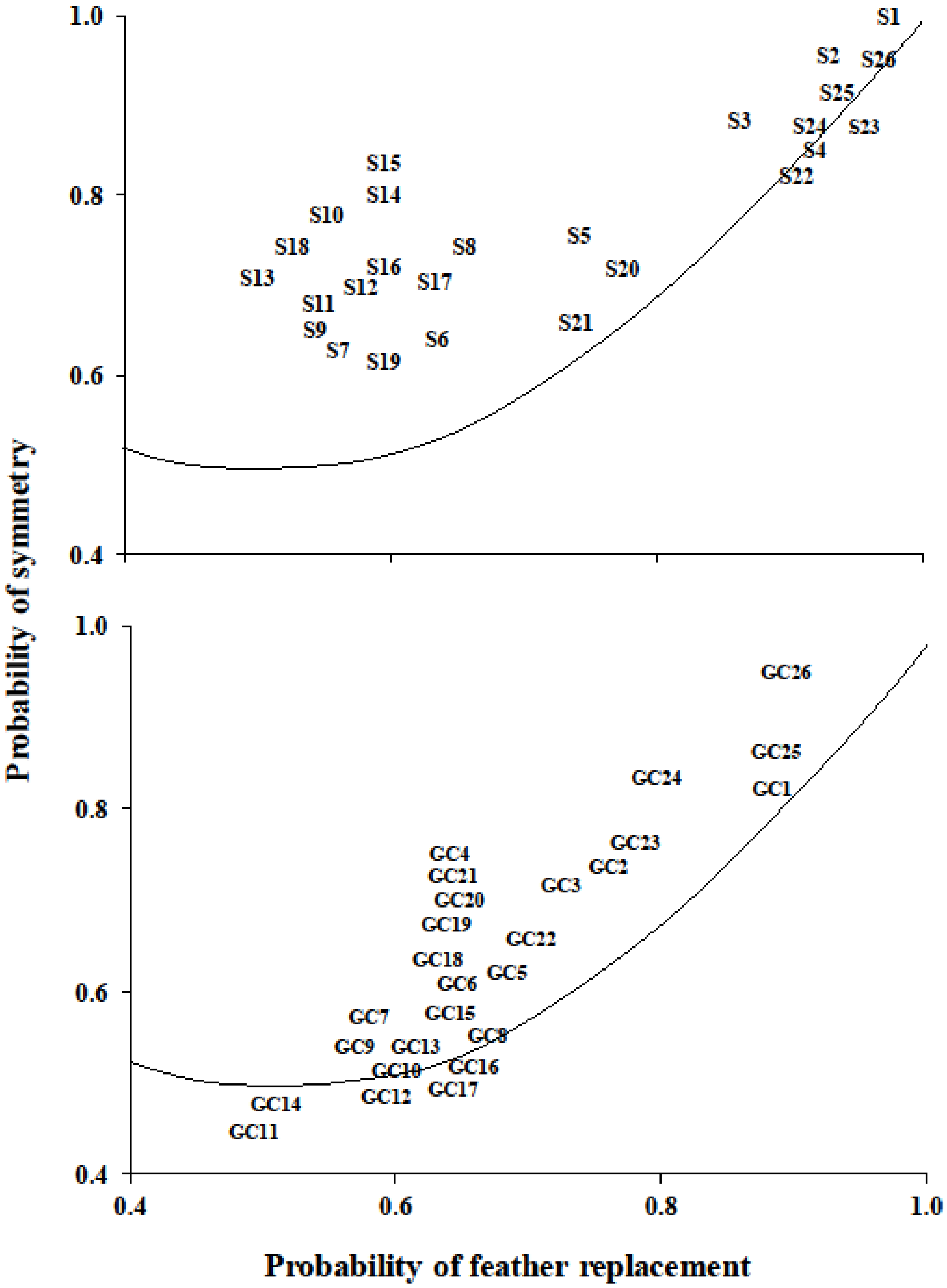
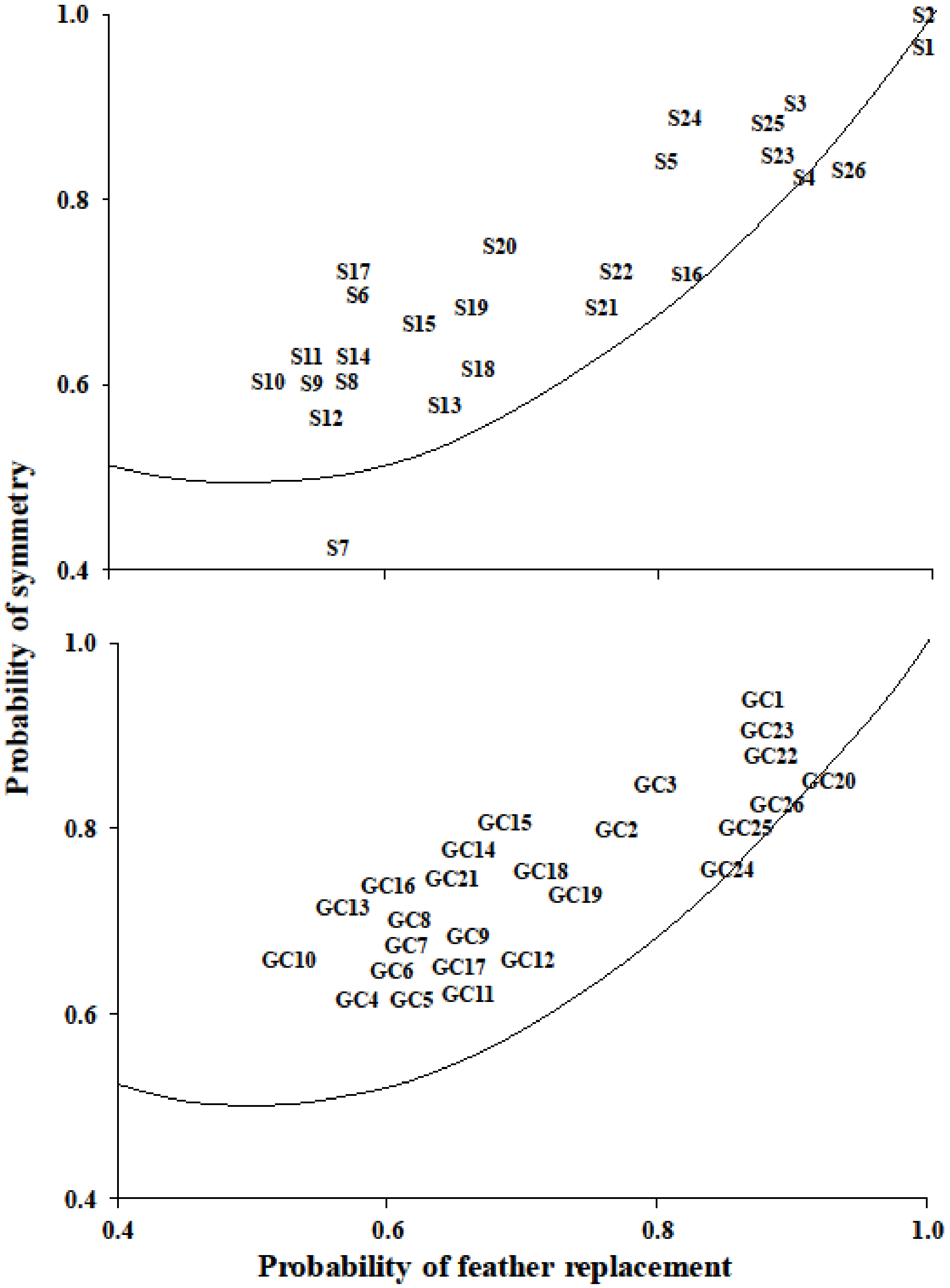
Appendix 3.1: The relationship between the probability of feathers replaced and feathers replaced symmetrically of Northern Giant Petrels in secondaries (S1-S26) and greater secondary coverts (GC1-GC26). The curve represents a null model assuming moult is random.



Appendix 3.2: The relationship between the probability of feathers replaced and feathers replaced symmetrically of Southern Giant Petrels in secondaries (S1-S26) and greater secondary coverts (GC1-GC26). The curve represents a null model assuming moult is random.



Appendix 3.3: Frequencies at which feathers of different symmetry/asymmetry combinations (new/new; new/old; old/old) showing Chi-square results in primaries and secondaries of Wandering Albatrosses. Significance codes: *** P<0.001, ** P<0.01, * P<0.05, NS = P>0.05

	Probability of replacement	**Expected asymmetry**	**Observed asymmetry**	**Chi-square**	**N**
Primaries					
P10	0.86	0.24	0.01	50.26***	188^{+}
P9	0.86	0.24	0.01	47.88***	188
P8	0.87	0.23	0.01	45.46***	188
P7	0.84	0.27	0.01	59.11***	188
P6	0.74	0.39	0.02	98.39***	188
P5	0.69	0.43	0.03	110.40***	188
P4	0.65	0.45	0.03	122.63***	188
P3	0.65	0.46	0.07	100.83***	188
P2	0.66	0.46	0.05	103.00***	188
P1	0.70	0.42	0.06	81.70***	188
Secondaries					
S1	0.73	0.39	0.21	26.89***	198
S2	0.71	0.41	0.22	28.89***	198
S3	0.70	0.42	0.24	25.40***	198
S4	0.64	0.46	0.28	23.82***	196
S5	0.55	0.50	0.30	29.25***	195
S6	0.52	0.50	0.29	33.23***	192
S7	0.50	0.50	0.30	28.34***	189
S8	0.47	0.50	0.25	44.24***	185
S9	0.43	0.50	0.30	26.01***	180
S10	0.46	0.50	0.30	26.40***	180
S11	0.41	0.49	0.28	25.94***	177
S12	0.43	0.49	0.27	32.35***	171
S13	0.42	0.49	0.31	19.90***	168
S14	0.43	0.49	0.33	15.81***	164
S15	0.45	0.49	0.27	30.62***	162
S16	0.44	0.49	0.37	9.60***	159
S17	0.45	0.50	0.25	34.82***	152
S18	0.48	0.50	0.37	9.74***	148
S19	0.46	0.50	0.29	23.28***	142
S20	0.47	0.50	0.32	17.32***	139
S21	0.49	0.50	0.32	17.23***	134
S22	0.50	0.50	0.32	16.40***	130
S23	0.53	0.50	0.36	9.26***	122
S24	0.47	0.50	0.36	7.67**	115

S25	0.49	0.50	0.31	14.68***	110
S26	0.50	0.50	0.35	8.58***	99
S27	0.55	0.49	0.03	10.86***	90
S28	0.53	0.50	0.35	6.59***	79
S29	0.43	0.49	0.35	5.77**	70
S30	0.42	0.49	0.29	8.53**	58
S31	0.34	0.45	0.24	6.21**	44
S32	0.32	0.44	0.22	6.53**	32

$^{+}$Primaries not photographed on some individuals

Appendix 3.4: Frequencies at which feathers of different symmetry/asymmetry combinations (new/new; new/old; old/old) showing Chi-square results in secondaries and secondary coverts of Northern Giant Petrels. Significant codes: *** P<0.001, ** P<0.01, * P<0.05, NS = P>0.05

	Probability of replacement	**Expected asymmetry**	**Observed asymmetry**	**Chi-square**	**N**
Secondaries					
S1	0.98	0.02	0.02	0.11 NS	88
S2	0.87	0.22	0.14	3.03*	88
S3	0.74	0.38	0.26	4.815*	88
S4	0.61	0.47	0.27	13.53***	88
S5	0.63	0.47	0.31	8.31**	88
S6	0.63	0.46	0.46	0.002 NS	88
S7	0.58	0.49	0.22	24.53***	88
S8	0.65	0.45	0.32	5.60**	88
S9	0.61	0.47	0.30	2.91*	88
S10	0.61	0.47	0.27	13.52***	88
S11	0.61	0.48	0.19	29.00***	88
S12	0.59	0.40	0.30	11.71***	88
S13	0.58	0.49	0.35	5.72**	88
S14	0.04	0.50	0.27	16.64***	88
S15	0.59	0.48	0.36	4.59**	88
S16	0.55	0.50	0.31	11.69***	88
S17	0.59	0.48	0.24	19.80***	88
S18	0.58	0.49	0.39	3.19*	88
S19	0.66	0.47	0.38	1.50 NS	88
S20	0.73	0.39	0.36	0.19 NS	84
S21	0.79	0.33	0.30	0.26 NS	84
S22	0.91	0.15	0.17	0.03 NS	78
S23	0.95	0.09	0.10	0.00 NS	72
S24	0.95	0.09	0.06	0.28 NS	64
S25	0.94	0.10	0.06	0.35 NS	47
S26	0.87	0.22	0.13	0.36 NS	16
Coverts					
SC1	0.18	0.30	0.18	5.05**	87
SC2	0.65	0.45	0.30	7.61**	87
SC3	0.68	0.43	0.36	1.75 NS	87
SC4	0.64	0.46	0.44	0.09 NS	87
SC5	0.65	0.49	0.32	1.73 NS	87
SC6	0.06	0.48	0.30	10.25***	87
SC7	0.52	0.50	0.49	0.00 NS	87

SC8	0.58	0.49	0.54	0.37 NS	87
SC9	0.55	0.49	0.54	0.58 NS	87
SC10	0.59	0.48	0.47	0.01 NS	87
SC11	0.48	0.50	0.56	1.16 NS	87
SC12	0.60	0.48	0.51	0.19 NS	87
SC13	0.54	0.50	0.45	0.60 NS	87
SC14	0.54	0.50	0.51	0.00 NS	87
SC15	0.59	0.50	0.59	0.01 NS	87
SC16	0.63	0.46	0.40	1.01 NS	87
SC17	0.61	0.47	0.49	0.07 NS	87
SC18	0.61	0.47	0.40	1.49 NS	87
SC19	0.63	0.47	0.35	4.58*	87
SC20	0.67	0.44	0.28	8.12**	85
SC21	0.68	0.43	0.39	0.37 NS	84
SC22	0.76	0.36	0.28	2.10 NS	83
SC23	0.79	0.34	0.28	1.09 NS	82
SC24	0.87	0.31	0.33	0.07 NS	81
SC25	0.88	0.21	0.16	0.89 NS	75
SC26	0.92	0.14	0.80	1.12 NS	62

Appendix 3.5: Frequencies at which feathers of different symmetry/asymmetry combinations (new/new; new/old; old/old) showing Chi-square results in secondaries and secondary coverts of Southern Giant Petrels. Significant codes: *** P<0.001, ** P<0.01, * P<0.05, NS = P>0.05

	Probability of replacement	Expected asymmetry	Observed asymmetry	Chi-square	N
Secondaries					
S1	1	0	-	-	76
S2	1	0	-	-	76
S3	0.93	0.12	0.11	0.09 NS	76
S4	0.7	0.34	0.28	1.10 NS	76
S5	0.55	0.49	0.32	9.04***	76
S6	0.58	0.49	0.38	2.87*	76
S7	0.55	0.49	0.59	2.60*	76
S8	0.52	0.50	0.40	2.88*	76
S9	0.57	0.49	0.43	0.72 NS	76
S10	0.46	0.50	0.40	2.77*	76
S11	0.50	0.50	0.37	4.75**	76
S12	0.42	0.49	0.40	2.26 NS	76
S13	0.44	0.49	0.37	4.34**	76
S14	0.44	0.49	0.20	7.53**	76
S15	0.47	0.50	0.34	6.83**	76
S16	0.57	0.49	0.20	12.98***	76
S17	0.58	0.49	0.29	11.15***	76
S18	0.59	0.48	0.42	0.93***	76
S19	0.79	0.33	0.32	0.03 NS	76
S20	0.90	0.17	0.16	0.00 NS	76
S21	0.92	0.15	0.16	0.02 NS	76
S22	0.91	0.16	0.12	0.56 NS	76
S23	0.89	0.18	0.15	0.42 NS	69
S24	0.87	0.23	0.12	3.05*	58
S25	0.76	0.36	0.16	2.58 NS	19
S26	0.63	0.48	0.40	0.14 NS	19
Coverts					
SC1	0.92	0.15	0.11	0.68 NS	75
SC2	0.77	0.35	0.29	0.84 NS	75
SC3	0.65	0.45	0.51	0.67 NS	75
SC4	0.62	0.47	0.39	1.82 NS	75
SC5	0.58	0.49	0.39	2.64 NS	75
SC6	0.60	0.48	0.41	0.98 NS	75

SC7	0.55	0.49	0.41	1.65 NS	75
SC8	0.62	0.47	0.44	0.18 NS	75
SC9	0.50	0.50	0.36	5.33**	75
SC10	0.56	0.49	0.51	0.01 6NS	75
SC11	0.63	0.46	0.41	0.59 NS	75
SC12	0.62	0.47	0.41	0.79 NS	75
SC13	0.62	0.47	0.47	0.00 NS	75
SC14	0.65	0.45	0.43	0.11 NS	75
SC15	0.74	0.38	0.32	0.85 NS	75
SC16	0.75	0.37	0.39	0.02 NS	75
SC17	0.69	0.43	0.37	0.62 NS	75
SC18	0.72	0.40	0.38	0.75 NS	75
SC19	0.76	0.37	0.27	2.70 NS	75
SC20	0.84	0.27	0.24	0.18 NS	75
SC21	0.88	0.20	0.15	1.06 NS	75
SC22	0.88	0.20	0.15	1.06 NS	75
SC23	0.85	0.24	0.15	3.11*	74
SC24	0.81	0.30	0.17	5.13**	71
SC25	0.81	0.31	0.15	7.63**	68
SC26	0.83	0.28	0.15	3.90*	54

Appendix 4.1: Feather mass (mg) and length (mm) of primary and secondary feathers of Wandering Albatrosses.

	Mass			**Length**		
Primaries (n=6)	**Mean**	**95%**	**CI**	**Mean**	**95%**	**CI**
P10	3812.9	3446.1	4179.7	442.3	428.5	456.2
P9	3803.5	3425.0	4182.0	450.5	437.1	463.9
P8	3300.0	2934.2	3665.8	441.6	430.0	453.1
P7	2844.3	2623.8	3064.7	411.0	399.9	422.1
P6	2309.2	2104.1	2514.2	372.3	360.7	383.8
P5	1790.5	1683.2	1897.7	333.8	325.3	342.3
P4	1355.7	1247.5	1463.9	296.3	288.9	303.8
P3	1066.0	998.3	1133.7	263.4	256.5	270.3
P2	911.9	844.1	979.6	239.2	233.0	245.3
P1	816.7	777.1	856.3	222.5	216.8	228.2
Total	**22010.4**			**3472.9**		
Secondaries (n=4)						
S1	713.2	630.9	795.5	213.0	203.1	222.9
S2	594.5	424.9	764.1	199.5	183.6	215.4
S3	548.8	389.0	708.6	192.3	175.1	209.4
S4	491.2	357.6	624.7	193.3	178.9	207.6
S5	462.3	353.2	571.4	193.3	179.9	206.6
S6	425.9	330.2	521.5	188.0	172.7	203.3
S7	453.4	331.4	575.4	192.5	181.0	204.0
S8	430.9	346.0	515.8	190.5	179.6	201.4
S9	432.4	343.9	520.8	191.8	180.9	202.6
S10	413.5	342.7	484.2	192.3	184.7	199.8
S11	406.9	331.2	482.7	193.0	184.6	201.4
S12	403.6	329.5	477.6	192.5	180.4	204.6
S13	408.4	344.7	472.0	193.3	182.4	204.1
S14	405.8	332.2	479.3	194.3	184.2	204.3
S15	408.0	345.2	470.8	195.3	184.6	205.9
S16	410.5	336.9	484.1	195.3	184.0	206.5
S17	414.7	337.6	491.8	196.5	187.2	205.8
S18	410.9	349.0	472.9	196.8	186.0	207.5
S19	413.0	335.7	490.4	198.0	186.9	209.1
S20	414.2	360.2	468.3	198.0	187.9	208.1
S21	423.5	373.8	473.1	200.5	192.4	208.6
S22	418.1	357.0	479.2	200.0	188.9	211.1

S23	424.6	360.2	489.1	201.0	189.6	212.4
S24	426.5	358.0	495.0	196.3	174.6	217.9
S25	444.0	391.3	496.6	203.3	191.0	215.5
S26	446.5	385.5	507.5	204.5	193.8	215.2
S27	460.6	395.2	526.1	204.0	193.5	214.5
S28	476.2	390.1	562.3	207.3	197.2	217.3
S29	492.2	382.7	601.7	206.5	194.8	218.2
S30	504.3	369.5	639.0	208.0	190.0	226.0
S31	519.7	335.3	704.1	190.8	118.5	263.0
S32	639.7	478.3	801.1	221.0	207.0	235.0
S33	667.3	566.7	767.9	226.0	214.0	238.0
S34	624.9	538.7	711.1	216.5	197.5	235.5
Total	**16030.1**			**6784.5**		

Appendix 4.2: Feather mass (mg) and length (mm) of secondaries and secondary coverts of giant petrels.

Secondaries (n=5)	Mass Mean	Length Mean	Coverts (n=1)	Mass Mean	Length Mean
S1	478	194	SC1	98	93
S2	414	183	SC2	160	123
S3	353	175	SC3	168	124
S4	333	173	SC4	185	133
S5	304	169	SC5	102	98
S6	282	167	SC6	186	133
S7	267	158	SC7	156	127
S8	260	164	SC8	112	114
S9	257	164	SC9	154	118
S10	255	164	SC10	148	126
S11	241	164	SC11	148	125
S12	256	165	SC12	139	123
S13	257	164	SC13	147	124
S14	255	165	SC14	131	123
S15	253	166	SC15	116	108
S16	258	166	SC16	135	117
S17	261	167	SC17	130	121
S18	267	168	SC18	109	114
S19	282	171	SC19	111	108
S20	286	172	SC20	108	114
S21	299	171	SC21	121	113
S22	311	172	SC22	122	115
S23	326	174	SC23	112	106
S24	345	175	SC24	124	112
S25	354	174	SC25	116	99
S26	326	174	SC26	122	106
S27	304	173	SC27	112	105
S28	248	162	SC28	87	89
S29	198	151	SC29	75	87
Total	**8530**	**4905**	**Total**	**3734**	**3298**