Survival and reproduction in a biennially-breeding seabird, the Wandering Albatross

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Z. Vincent, MSc Zoology, University of Cape Town, August 2008

GENERAL ABSTRACT

I studied a long-term data set for Wandering Albatrosses *Diomedea exulans* collected at sub-Antarctic Marion Island to investigate adult survival, breeding biology and factors affecting reproductive success of this long-lived pelagic seabird. Until recently, the complex adult life cycle has caused biases in conventional mark-recapture modelling analyses that assume that recapture probability is equal for 'observable' and 'unobservable' states of the biennial adult life cycle. During 'sabbaticals' taken after successful and late-failed breeding attempts, the chances of resighting an adult Wandering Albatrosses are reduced, thus affecting estimated recapture rates. I applied a multi-state mark-recapture method to the colony breeding data from Marion Island (1987-2005). This method allows individual albatrosses to move through a network of breeding states according to previous breeding history using transition probabilities to estimate survival, breeding and breeding success probability. The best fit models in the multi-state analysis were those representing constant survival and independent breeding probabilities, suggesting that Wandering Albatrosses constrain reproductive investment to ensure long-term survival. I used the parameter estimates in a transition matrix to calculate the steady state equilibrium for the Wandering Albatross breeding population. For the first time I was able to estimate that approximately 3000 pairs of Wandering Albatrosses use Marion Island for nesting. I also describe the effects of age, sex and experience on Wandering Albatross reproductive success. Birds that were most successful began breeding at the mean age of first breeding and older and younger birds were less successful in 5/10 year periods after the onset of breeding. Disappearance from the population decreased with an increase of age of first breeding. I tested the selection and experience hypotheses on birds with 'complete' histories defined according to an imposed rule on recovery data. Males appeared to increase breeding success as a result of selective removal of low-quality individuals from the population (the selection hypothesis), whereas females appeared to improve their breeding success as a result of increased experience.

GENERAL INTRODUCTION

An important issue in life-history theory is the understanding of an organism's trade-off between investment in current breeding on the one hand and investment in self maintenance for survival and future reproduction on the other. For a provisioning parent, foraging during a breeding attempt must take into account the energetic costs related to self-preservation and those related to the successful rearing of its offspring, which may incur a cost to future survival and fecundity of the parent. The "costs of reproduction" highlighted by Williams (1966) are clear and suggest that the choice of breeding in a season should take into account residual reproductive value to maximize fitness. Life-time reproductive success (LRS), is defined as the total number of young raised by an individual during its life-time (Stearns 1992). Characteristics associated with higher probability of survival and reproductive rates are favoured by natural selection. An individual with a greater potential for genetic representation in future generations through increased survival, skill and reproductive success is said to have a relatively higher fitness (Clutton-Brock 1988, Charlesworth 1990). Fitness and life-time reproductive success are not the same by definition, but assuming that the probability of fledglings to recruit is not determined by parental investment, then LRS is a good proxy for fitness (Koenig and Albano 1987, Newton 1989, Bult and Lynch 1997). If reproduction was not costly, we would expect to see animals breeding from an early age and continuously (Golet et al 1998). For seabirds, it is predicted that the energetic requirements during the brooding phase are amongst the most constraining (Ricklefs 1983). When brood sizes were artificially increased for Glaucous-winged Gull *Larus glaucescens* and Black-legged Kittiwakes *Rissa tridactyla*, the females increased their effort, lost more mass and had lower survival to the next breeding season (Reid 1987). Therefore it has been suggested that long-lived birds have evolved a restricted level of investment in their young, to maximize their own survival (Sæther and Bakke 2000).

Certain demographic traits have greater influence than others on overall population growth (λ) across the "fast-slow" life-history continuum (Read and Harvey 1989). Species with a slow life-history are characterized by high survival rates, delayed maturity and low fecundity. Any decrease in adult survival will be more detrimental to overall population growth rate than to short-lived, highly fecund species, where reproduction is the primary driver of λ (Heppel et al. 2000). Juvenile survival to maturity is more critical to long-lived animal population growth than early breeding and quantity of offspring, with greater emphasis placed on good quality offspring (Sæther et al. 2000). For pelagic-feeding seabirds, the long commute between feeding and breeding areas means that that individual parents are absent from the nest for long periods. Successful reproduction therefore depends on well-coordinated bi-parental care. The slow provisioning rates result in slow growth and constrain brood size (Chaurand and Weimerskirch 1994). Slow growth, small brood size, bi-parental care, and deferred age of first breeding are seen as life-history strategies to reduce the costs of reproduction for adult breeders and to increase the probability of recruitment of inexperienced juvenile birds into the effective population. Pyle et al. (1997) showed higher annual mortality for Western Gulls *Larus occidentalis* that attempted their first breeding at younger ages as opposed to birds that delayed their first breeding one or two more years.

The risk of extinction for species is classified by the International Union for the Conservation of Nature (IUCN) Red List system in terms of population size, observed rates of decline or habitat loss (IUCN 2001). For conservation management, it is becoming increasingly important to understand the ecology of the species and how interspecific variation in demographic values affects the overall population response to perturbation. In this way, management plans can identify key life stages to protect based on their contribution to population growth rate. Wandering Albatrosses, *Diomedea exulans*, are classified as a 'Vulnerable' species which has suffered large population losses (>30%) within the last three generations (Birdlife International 2005). The adult life-cycle is complex, and at any time the population comprises of breeders and non-breeders in different stages of the biennial breeding life-cycle.

Identification of variation in demographic rates for birds within such complex life cycles can provide interesting and important information on their ecology and evolution. For "survivor" species on the extreme slow end of the "fast-slow" continuum, such as albatrosses, the difference between survival for a ten year old bird and an 11 year old bird are negligible but their difference in breeding probabilities can be substantial. The probability of breeding is determined by previous breeding status and is dynamic. In biennial breeding cycles, a bird that breeds successfully in year *i* has a very low probability of breeding in year $i + 1$, whilst any adult bird that does not breed or has a failed breeding attempt in year *i* has a much greater probability of breeding in year $i + 1$. This individual variation forms the basis of important animal ecology and evolutionary biology, but creates difficult methodological problems for field sampling. It also makes it difficult to accurately estimate population sizes.

Wandering Albatrosses are the largest albatrosses and the largest of all seabirds (Tickell 1968, Weimerskirch et al. 1987). They are a "slow" species characterized by delayed maturity, high adult survival and low fecundity, raising at most one chick every two years. They lay one large egg, and both parents take turns to incubate and provision for the chick until it fledges more than 10 months after laying (Tickell 2000). The adult breeding life-cycle is biennial, with most birds taking a year's temporary migration ('sabbatical') after a successful breeding attempt during which they molt primary feathers necessary for long distance flight (Prince et al. 1997). Thanks to the excellent efforts of seabird conservationists they are one of the most well studied birds and there are long-term data for these giant seabirds on several of the most important breeding colonies in the sub-Antarctic. I analyzed Wandering Albatross recapture data from Marion Island (47° S, 38° E) in the Prince Edward Islands, home to the largest Wandering Albatross breeding population (Nel et al. 2003). Monitoring of the island's colonies has resulted in long-term individual capture histories for albatrosses dating back as far as 1965. The data were scrutinized to give a broad understanding of the demographic characteristics and investigate the variation operating on the population as a whole, and at an individual level.

Chapter 1 introduces the background, study sites, materials and methods used in the thesis. I describe the Marion Island monitoring colony and the island populations. I provide nest counts within the colonies and compare population trends within the colonies to that of the entire island population. I also explain the 'disappearance' rule I use in chapter 3 as a proxy for mortality for Wandering Albatrosses. Empirical data were used to estimate the amount of time a Wandering Albatross must remain absent from the colonies before we can assume, with confidence, that it is dead. This work also contributes to chapter 2, as I estimate the proportion of successful breeders returning to breed again without 'sabbatical'. Although in theory the Wandering Albatross is considered an obligate biennial breeder (Tickell 2000), some successful breeders attempt to breed again without a 'sabbatical' year and I therefore had to justify the removal of such data for the multi-state mark recapture analysis. I also describe the individual variation in reproductive success inside the Marion Island Wandering Albatross colonies. This forms the backbone of my thesis, as I investigate the average breeding behaviour of Wandering Albatross in chapter 2 and take an individual, descriptive view of factors affecting breeding success in chapter 3.

In chapter 2, I use a dynamic, multi-state mark-recapture (MSMR) analysis to investigate the biennial life-cycle of adult, breeding Wandering Albatrosses. This approach to modelling allows the estimation of survival, breeding and breeding success probabilities in 'observable' and 'unobservable' states. MSMR analyses extend single-state mark-recapture estimations by breaking the life-cycles of organisms into distinct, behavioural states (Brownie et al. 1993, Schwarz et al. 1993). These states are represented by a life-cycle model and movement between the states is used to estimate demographic probabilities (Williams et al. 2002).

Wandering Albatrosses are excellent and interesting subjects for multi-state analysis. Breeding adults are easily captured, marked and because they have high site fidelity, they are easily recaptured (Weimerskirch and Jouventin 1987). They arrive at the colonies in November, lay eggs in December and by the end of January most nests are active and occupied (de la Mare & Kerry 1993, Prince et al. 1997). Early failed breeders (pre-July) are able to breed again the following year whilst successful breeders attempt their next breeding in the second season after success (Tickell 1968). However, some failed birds will also take a year off. This leads to an interesting set of ecological and biological questions: Does survival probability change in different life-cycle stages? What proportion of birds in different states attempt to breed again? How many of these breeders are successful according to their current breeding status? What is the proportion of the Wandering Albatross population breeding at an island each year? What is the per capita chick production of a Wandering Albatross? These questions can be answered theoretically using the MSMR approach.

Another reason to use the MSMR technique is that incomplete data due to temporary emigrations from open populations make estimations of "unobservable" states difficult and can cause bias in encounter probabilities (Kendall et al. 1997, Schaub et al. 2004). When adult Wandering Albatrosses leave the colonies after breeding successfully, there is little chance of recapture in the following year. Most are recaptured when they return to their colonies in subsequent breeding years. These 'sabbaticals' are similar for Grey Seals, *Halichoerus grypus*, right whales, *Eubalaena* spp., and for sea turtles that are marked only during breeding at nesting locations but then leave these areas between breeding events (Payne et al. 1990, Schwarz and Stobo 2000, Fujiwara and Caswell 2002a). This can lead to extreme heterogeneity in capture probability and bias in survival estimation (Fujiwara and Caswell 2002b). In MSMR analysis I can estimate important biological information even when certain states are unknown or "unobservable" by providing more information, or imposing deterministic, temporal constancy or state-specific survival constraints to the life-cycle model (Kendall and Nichols 2002).

Chapter 3 takes a descriptive look at the cause and effects of individual variation in reproductive success for the Wandering Albatross population on Marion Island. In contrast to chapter 2, where the 'average' demographic parameters are estimated for an 'average' bird in the colony, in this chapter I scrutinized the data to address questions relating to reproductive success on an individual level. Key questions addressed include how age, sex, and experience affect reproductive success? Individuals in populations differ from one another, with some individuals exhibiting greater fitness than others (Krüger and Lindström 1993). Fitness is a demographic characteristic based on births and deaths, and demography of a population is based on the foundation of those individuals within the population (Caswell 1989). By analyzing the long-term data on the Wandering Albatross, I attempt to expose the selective pressures on individuals and their evolutionary consequences. In this way I describe the strategies of a long-lived seabird that balance the costs of reproduction proposed by Williams (1966). I also test the two hypotheses used to describe the effects of age and experience on reproductive success, namely: the 'experience' and 'selection' hypotheses (Mauck et al. 2004).

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CHAPTER 1

Study sites, materials and methods

Abstract

Marion Island has the largest breeding population of Wandering Albatross of several breeding sites in sub-Antarctica, with some 1600 pairs nesting there each year. A summary of Marion Island Wandering Albatross data were made comparing the population trends inside the study colonies' to that of the population trends outside the study colonies across the entire island. Population trends were similar inside and outside the study colonies. The mean recruitment rate (1980-1990) into the study colonies was 36.1% with a cumulative, averaged recruitment rate of into the colonies of 38.1%. In the 1980s there was a drop in Wandering Albatross numbers according to census counts but since then the population has stabilized. As a proxy for mortality, which was vital to comparing individual variation in chapter 3, I calculated the length of time a Wandering Albatross must remain unsighted to assume with confidence that the albatross has died. Adult breeders that are successful seldom return to the colonies if they remain unsighted for 5 years, whilst breeding adults that fail to rear a fledgling rarely return if they remain unsighted for 4 years. There are also incidences of successful breeding Wandering Albatross attempting to breed without a sabbatical (1.3% of males, 1.8% of females). The modal chick output during the study period was 1 chick per adult, but there is a high degree of variation in reproductive success. 'Complete' histories show that in a 13 year interval some birds did not produce a single fledgling whilst a small percentage of breeders produced 7 fledglings.

Study site and global Wandering Albatross population

Sub-Antarctic Marion Island is home to the largest breeding population of Wandering Albatross, and together with Prince Edward Island, the Prince Edward Isles make up 44.1% of the global population (Table 1.1). This study made use of data collected from breeding colonies of Wandering Albatross, *Diomedea exulans*, located at three study sites on the north-eastern coast of Marion Island (280 km^2, 46°52'S, 37°51'E, Figure 1.1). Metal banding of Wandering Albatrosses on Marion Island started in 1965. In 1984 two colonies located at Macaroni Bay (average: 23 pairs/year) and at Sealer's Beach (average: 96 pairs/year), became established as annually monitored breeding colonies (Nel et al. 2003). In 1987 a third study colony was established at Goney Plain (average: 117 pairs/year) for annual monitoring. Nest densities for the three study colonies are 4.9, 5.7 and 8.0 nests per hectare, respectively (Underhill et al. 2003). These colonies account for around 15% of the total population of Wandering Albatrosses on the island.

Table 1.1. Populations of Wandering Albatross (breeding pairs per year) at all breeding sites.

Island	Population	Year of census
Bird Island	948	2004 (Poncet et al. 2006)
South Georgia	605	2004 (Poncet et al. 2006)
Marion Island	1869*	2001 (Crawford and Cooper 2003)
Prince Edward	1850	2001 (Crawford and Cooper 2003)
Crozets -		
Ile aux Cochons	1263	1981 (Tickell 2000)
Ile del la Possession	349	1995
Ile de l'Est	329	1982
Ilôts des Apotres	121	1981
Kerguelen	1094	1985-1987 (Weimerskirch et al. 1997)
Macquarie	10	1995 (Tickell 2000)
Total	8438	

*Marion Island accounts for 22.1% of the global population.

Figure 1.1. Map of Marion Island (46°52'S, 37°51'E) indicating the three Wandering Albatross colonies established as annually monitored study colonies in 1984 and 1987.

Population trends on Marion Island

Despite a drop in Wandering Albatross numbers on Marion Island during the 1970s and 1980s, presumably due to long-line induced mortality, the population is stable (Nel et al. 2003). This is in contrast to decreasing Wandering Albatross populations on Bird Island in South Georgia (Croxall et al. 1990) and Macquarie Island (de la Mare and Kerry 1994). Up until 1995, population trends on Marion Island and at the Crozet Islands were similar (Weimerskirch et al. 1997, Nel et al. 2003). Population numbers dropped drastically at both locations in the 1970s and only in the mid-1980s did they begin to increase. Three periods of population variation can be indentified on Marion Island (1974-2007; Figure 1.2). From 1974-1990 the population decreased by 23 pairs/yr ($P=0.044$), from 1991-1998 it increased by 74 pairs per year ($P<0.001$) and in the final period (1999-2007) the population has decreased on average by 16 pairs per year, but this was not significant (P=0.40). An estimate of trend from 1974-2007 could not be included due to gaps in data. The same pattern of increase over the last two decades can be seen inside the monitored colonies (Figures 1.3, 1.4 and 1.5). This suggests that the colonies are no different to the population on the island as whole and are subject to the same pressures.

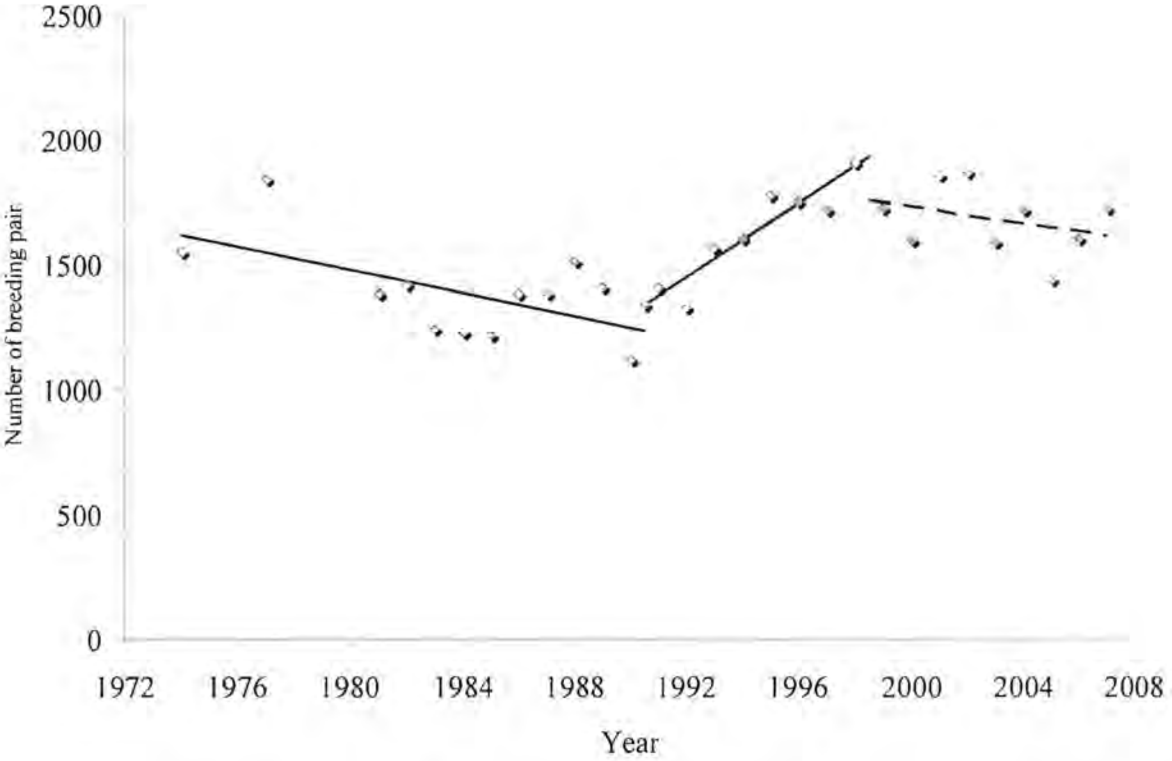

Figure 1.2. Annual census counts of Wandering Albatross at Marion Island for the entire island population (1974-2007; significant regression lines are solid, the dashed regression line is not significant).

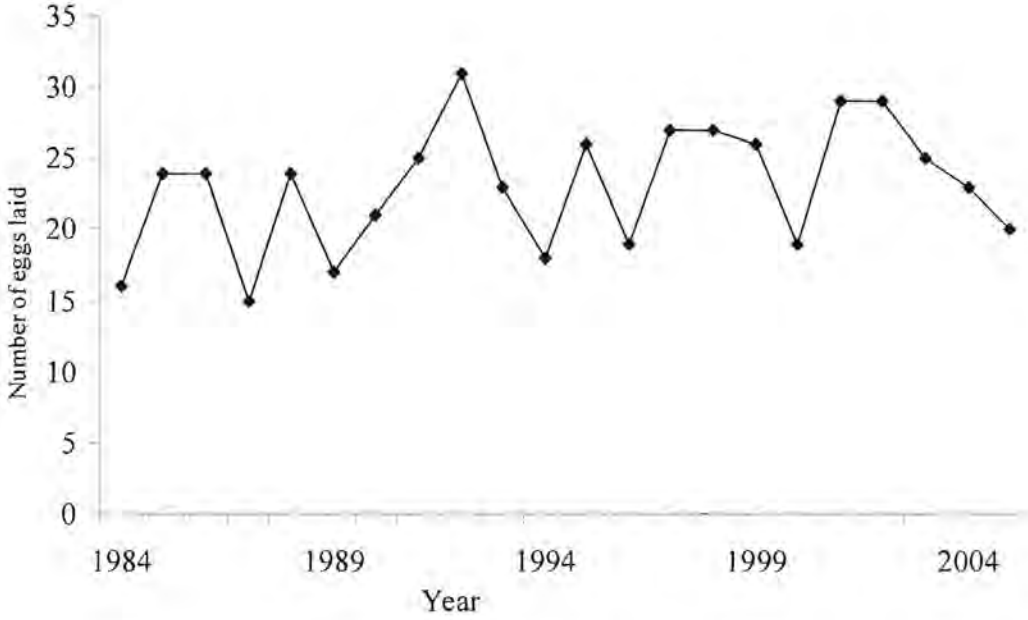

Figure 1.3. Annual number of eggs laid at Macaroni Bay colony 1984 – 2005.

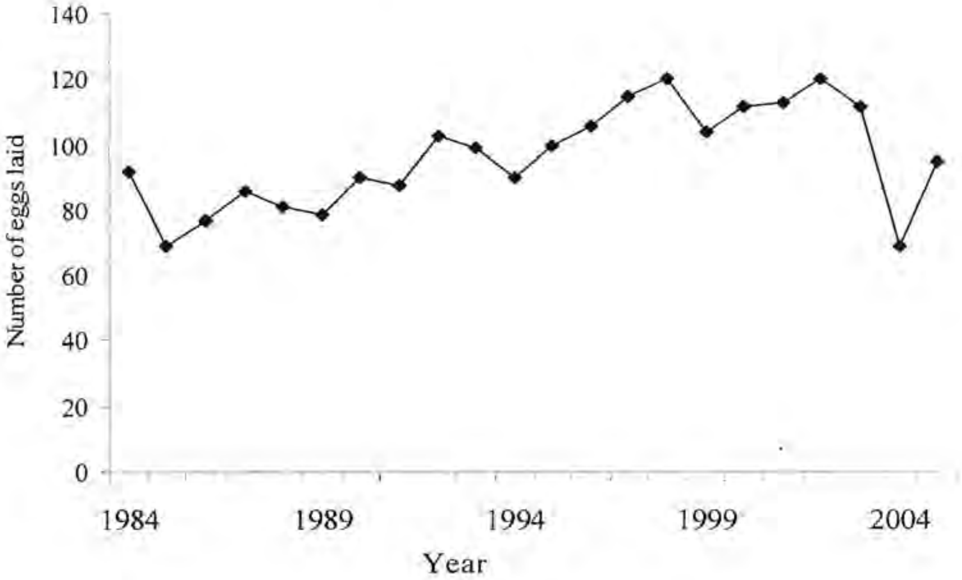

Figure 1.4. Annual number of eggs laid at Sealer's Beach colony 1984-2005.

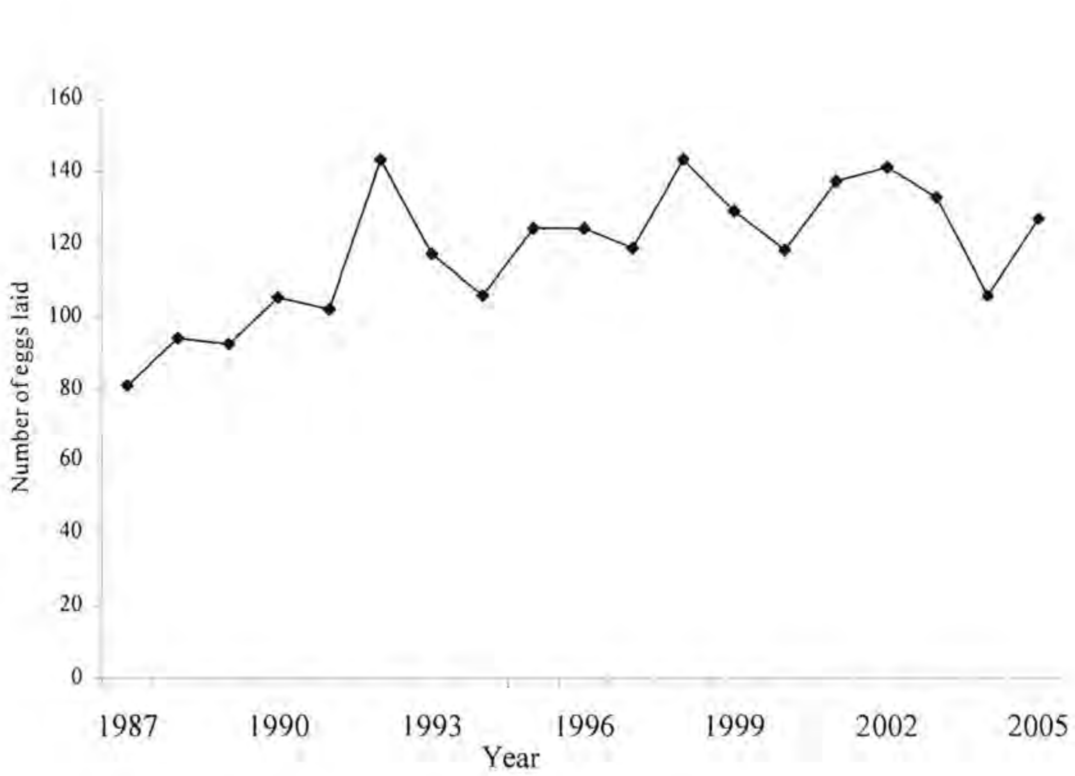

Figure 1.5. Annual number of eggs laid at Goney Plain 1987-2005.

Data collection and recruitment

The Wandering Albatross database for Marion Island is complex. Long-term, individual data have been recorded for each albatross and includes study colony, cohort and age at each breeding (if banded as a fledgling), metal band, colour band, sex, plumage, breeding nest site, breeding outcome, its partner and additional notes of interest. These records were all stored chronologically and in total, the Marion Island database has over 9500 primary captures with over 13500 recaptures. On average, around 240 pairs breed within the three colonies every year. Each fledgling and adult captured inside the colonies is banded with a metal band as its primary identification and breeders are additionally fitted with a plastic, alpha-numeric band for easy, non-invasive identification. Nest sites are marked as they become occupied by a pair in November and are then monitored regularly (every 10 days during incubation, every 2 to 3 weeks during chick-rearing) to identify both partners at all nests and to assess the outcome of each breeding attempt. Eggs are laid mid-December and hatched chicks that survive are banded in July of the next year.

Almost all chicks recruit to their natal colony (Inchausti & Weimerskirch 2002), thus chicks are recaptured if they survive to recruit in later years. In this way we were able to analyze age of first return to colony and age of first breeding. Albatrosses, once paired, are sexed according to size (males are larger with deeper bills), plumage (females being the darker mate) and behaviour (observations of displays and copulations) (Tickell 2000). Every year an island census of all incubating birds takes place to increase the chance to detect recruits outside the breeding colonies. Recruitment rate is the percentage of fledglings banded inside the colonies that were recaptured as breeding adults in later seasons inside the study colonies. This is a minimum estimate as some fledglings do settle outside of the study areas (Table 1.2). Average yearly recruitment rate was 36.1% (1980-1990). The cumulative recruitment rate was calculated by pooling all fledglings banded and all recruits across years as a way to assess the effect of incomplete recruitment. Table 1.2 suggests that cohorts banded after 1990 probably had not completely recruited by the end of the study period..

A proxy for mortality

The thesis deals with demographic understanding of the adult breeding life cycle and variation in reproductive success of Wandering Albatrosses. In chapter 3 the effects of sex, age and experience on reproductive success and survival are investigated. I will return to discuss the problems facing chapter 2 as these follow on from this discussion. Bands from dead albatrosses are very seldom recovered. We seldom know when or where they die. I set up a proxy for the presumed death of a Wandering Albatross: I estimated the length of time an albatross must remain unobserved before we can assume it has died. The intervals are the periods between breeding attempts when the bird remains absent from the colonies and unobserved. An interval of 1 yr implies an attempt was made the following year. I used all the breeding event data in the established colonies up to 1995, allowing birds that disappear up to ten years to return. The maximum interval observed was 7 years (Tables 1.3 & 1.4), but >99% of all absences were ≤5 years. I then calculated the proportion of breeders that return after each of these unobserved interval lengths and the 99% cut-off point. This results in a time period within which the majority of breeding Wandering Albatross will return to colonies to breed again with a high level of certainty (95% return within so many years). For males and females, I estimated that if a bird is absent for at least 5 years after a breeding attempt that it can be presumed to have died.

Table 1.2. Summary of bandings of Wandering Albatrosses on Marion Island (1965-2005). For 1980-1990: average recruitment rate = 36.1 ± 7.2 % (SD; N = 1095 fledglings from 11 cohorts).

Year	Chicks banded	Adults banded	Chicks banded inside colonies	Chicks from colonies that recruited	Recruitment (%)	Cumulative Recruitment
1965	12	1	12	9	75	-
1976	440	46	52	19	36.5	-
1978	296	4	-	22		-
1979	93	66	-	16		-
1980	61	126	61	23	37.7	37.7
1981	229	6	15	7	46.7	39.5
1982	242	0	84	38	45.2	42.5
1983	316	14	84	36	42.9	42.6
1984	329	148	101	39	38.6	41.4
1985	97	110	72	18	25	38.6
1986	335	31	90	23	25.6	36.3
1987	347	230	132	43	32.6	35.5
1988	177	431	157	55	35	35.4
1989	171	78	135	48	35.6	35.4
1990	365	133	164	52	31.7	34.9
1991	404	87	155	43	27.7	34.0
1992	388	90	166	38	22.9	32.7
1993	284	217	195	42	21.5	31.3
1994	223	206	160	24	15.0	29.9
1995	247	70	193	22	11.4	28.1
1996	190	9	181	24	13.3	26.8
1997	226	58	193	25	13.0	25.6
1998	215	27	215	19	8.8	24.2
1999	197	11	197	2	1.0	22.6
2000	186	17	185	0	0	-
2001	208	35	208	0	0	-
2002	167	24	167	0	0	-
2003	215	13	215	0	0	-
2004	139	19	139	0	0	-
2005	194	19	194	0	0	-
Total	7260	2330	3922	687		

Table 1.3. Gaps between breeding events for female Wandering Albatross on Marion Island based on adult breeding data up to 1995 from within the study colonies.

Years after breeding	Post success	Post success %	Cumulative %	Post failure	Post failure %	Cumulative %
1	23	1.8	1.8	382	82.5	82.5
2	1135	87.2	89.0	57	12.3	94.8
3	113	8.7	97.6	13	2.8	97.6
4	22	1.7	99.4	7	1.5	99.1
5	5	0.4	99.8	4	0.9	100.0
6	1	0.1	99.8	0	0.0	100.0
7	2	0.2	100.0	0	0.0	100.0
8	-	-	-	-	-	-
9	-	-	-	-	-	-
10	-	-	-	-	-	-
Total	1301	Gaps > 5yr	0.2	463	Gaps > 5yr	0.9

Table 1.4. Gap between breeding events for male Wandering Albatross on Marion Island based on adult breeding data up to 1995 from within the study colonies.

Years after breeding	Post success	Post success %	Cumulative %	Post failure	Post failure %	Cumulative %
1	16	1.3	1.3	338	81.8	81.8
2	1068	85.9	87.14	51	12.3	94.2
3	76	6.1	93.25	20	4.8	99.0
4	53	4.3	97.51	3	0.7	99.8
5	16	1.3	98.79	1	0.2	1
6	9	0.7	99.52	-	-	-
7	4	0.3	99.84	-	-	-
8	2	0.2	100.0	-	-	-
9	-	-	-	-	-	-
10	-	-	-	-	-	-
Total records	1244	Gaps > 5yr	1.3	413	Gaps > 5yr	0.0

Once I estimated the cut-off point in years that breeders took returning to colonies I could test the effects of age of first breeding on survival and compare the reproductive success of those birds that survived to those that presumably died.

Individual variation in reproductive success

The best way to show variation in individual reproduction is by drawing a frequency histogram of the number of chicks produced across the population. Once the cut-off point in unobserved length of time was estimated, I could express the variation in reproductive success for the Marion Island Wandering Albatross population in terms of 'incomplete' and 'complete' histories (Figure 1.6). This investigation ran between 1984 and 2006 using the colony data. Using the 5 year cut-off, all individuals that were either already breeding at the start of the monitoring of the study colonies, or were still present and breeding post-2001 were considered to have 'incomplete histories'. Complete histories are for those we are reasonably certain have started and ended their breeding careers with our study period. Those birds that were either banded as fledglings or recruited post-1989 and were not present in the last 5 years of the study were considered to have 'complete histories'. Incomplete histories represent those individuals that may have bred before the study or may still breed in the future. Both males and females are included in the figure, because not all partners were identified each year.

The modal chick output of Wandering Albatrosses on Marion Island is 1 chick per adult, both for birds with complete and incomplete histories. Average per capita chick output for complete histories was 2.4 ± 1.3 chicks, whereas for birds with 'incomplete' histories it was 3.8 ± 2.3 chicks. The great variation in chick output implies great individual variation within birds studied. In the period analysed (1984 - 2006), the maximum output for a biennial breeder would be 12 fledglings. None attained this level of production, but four birds out of 1774 individuals raised 11 chicks. Complete histories could only span 13 years (1989 - 2001) and only 1 individual of a possible 568 managed 7 successful attempts in this period. Thus, <1% of the population studied reproduced at the maximum possible level throughout the study period.

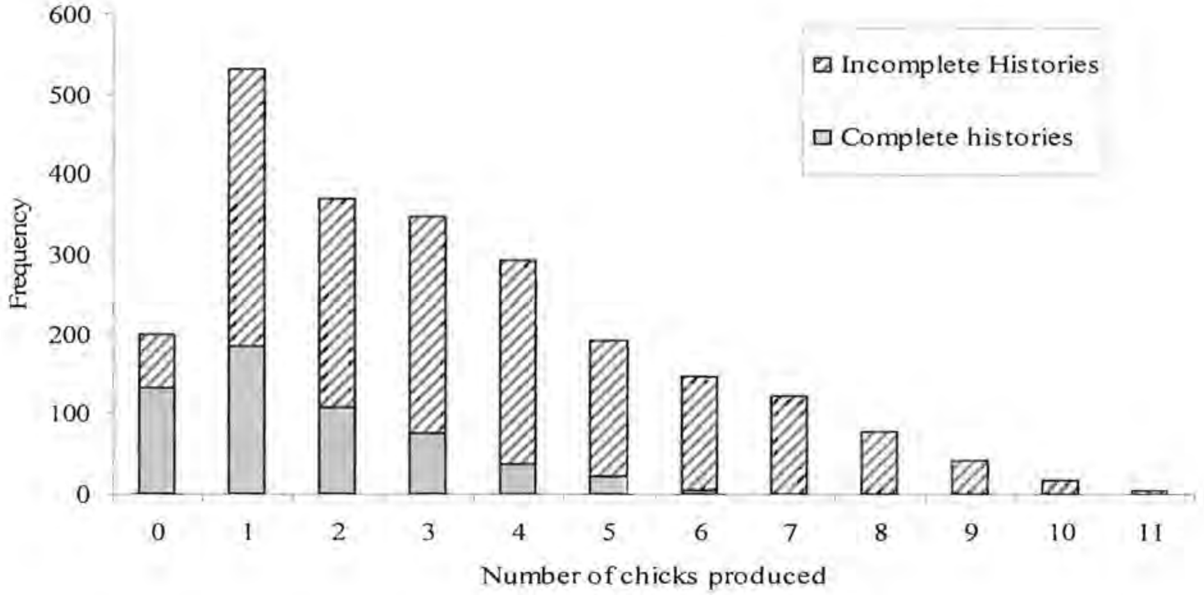

Figure 1.6. Frequency histogram of the number of adult Wandering Albatrosses rearing different numbers of chicks on Marion Island (1984-2006).

Multi-state mark-recapture analysis: issues and approach

In chapter 2, I address the issues biennial breeding life cycles present to conventional mark-recapture methods. Post-breeding sabbatical years cause a bias in survival estimation as conventional mark-recapture analyses assume that recapture is equal in all years (Kendal et al. 1997). To address this bias, I applied a 'multi-state' mark-recapture (MSMR) analysis to Wandering Albatross recapture data from Marion Island. In order to gain an understanding of the mark-recapture analyses I travel led to the U.S.A. and France and learn from the Albatross Demography Workgroup, comprised of mathematical biologists, naturalists and ornithologists. At the workgroups, different albatross datasets from various sub-Antarctic Islands were analyzed and models were tested for biennial and annual breeding albatrosses, whilst it also provided a platform to discuss issues.

The major issue concerning Wandering Albatross is the biases caused by unobservable, post-successful breeding states. In nature, some Wandering Albatrosses return to the colonies during 'sabbatical' years either to "loaf" and or occasionally to breed. The rate of consecutive annual success in Wandering Albatrosses is extremely low (Tickell 1968, Tickell 2000, Jouventin and Dobson 2002). On Marion Island the rate of repeated breeding after a success without sabbatical is 1.3% for female and 1.8% for male breeders in the Goney Plain study colony (Table 1.3 and 1.4). Of the post-successful breeding attempts (N = 39) without sabbatical, 43.6 % were successful and 56.41 % failed. This may influence individual life-time reproductive success, but whether it has a great effect on population growth is debatable (Ryan et al. 2007). In order to deal with this problem I had to check all the data for instances of post-successful observations during sabbatical years. Based on the Albatross Demography Workgroup forums and discussions with Hal Caswell and Christine Hunter, it was decided that I approach the Wandering Albatross MSMR analysis by modelling the characteristics of an obligate, biennial breeding life-cycle of the 'average' Wandering Albatross according to those biological qualities expressed by most birds in the global population (Warham 1990). Each individual Wandering Albatross record had to be converted into numerically coded strings representing the breeding history. For example: 0010101200 is a hypothetical 10-yr individual adult history data string, where '0' indicates that the bird was unobserved, '1' represents a successful breeding attempt producing a fledgling and '2' implies a failed breeding. In the case of post-successful breeders that bred and failed, the post-successful attempt was removed and replaced with a '0' (giving 0010101000). Where breeding was successful, an extra year was added (thus 101100101 became 101010101 and 10110101 became 101010101) to avoid biasing against high-quality breeders. By simplifying the model we reduced the number of parameters to be estimated, placing fewer demands on the data. We are continuing our progress to address this issue in future models.

The Marion Island Wandering Albatross data set provides an excellent opportunity for the demographic analysis and study of a long living vertebrate. When such data are available, the combination of matrix models and mark-recapture statistics is one of the best methods of parameter estimation and can be efficiently used to address evolutionary theory and conservation ecology (Fujiwara and Caswell 2002, Lebreton 2006). MSMR analysis can address variation in the breeding population by breaking the life cycle into breeding states, and estimating the probability of movement amongst states (Caswell 2001). Important biological information even when certain states are unobservable and unknown can be estimated by providing more information, or imposing deterministic, temporal constancy or state-specific survival constraints to the life-cycle model (Kendall and Nichols 2002). The data also provided a platform from which to test scientific hypotheses such as the effect of age, sex and experience on reproductive success. By using the rules I set for the data, such as the disappearance interval of 5 years, I could compare the outcomes of individual breeders even though the data set is not long enough to estimate life-time reproductive success.

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CHAPTER 2

A MULTI-STATE MODEL OF SURVIVAL AND BREEDING PERFORMANCE AMONG ADULT WANDERING ALBATROSSES AT MARION ISLAND

Abstract

I applied a multi-state mark-recapture analysis to interpret the adult breeding life cycle of Wandering Albatross, *Diomedea exulans,* to data captured on Marion Island from 1987 to 2005. Estimation of demographic parameters for biennial breeding birds, such as the Wandering Albatross, can be difficult because of yearly 'sabbaticals' taken after successful or late unsuccessful breeding attempts. Conventional mark-recapture methods can lead to bias as they assume recapture probability is equal for 'observable' and 'unobservable' states. I broke the adult breeding life cycle into 4 possible states: successful and unsuccessful breeders, post-successful and post-failed non-breeders. I measured the probabilities of survival, breeding, and breeding success for movement between these states. My best models had survival being equal for all states, with breeding probabilities independent. This suggests that Wandering Albatrosses adapt their breeding decisions to maintain a high survival rate. For the period investigated (1987-2005), survival probability was 0.928 ± 0.002; 0.7% lower than conventional recapture methods. Next season breeding probability for failed breeders was 0.93 ± 0.009, for post-successful non-breeders 1.00 ± 0.0, and for post-failed non-breeders 0.168 ± 0.043. Breeding success was lowest for failed breeders (0.576 ± 0.012) in their next attempt but similar for post-failed (0.689 ± 0.094) and post-successful non-breeders (0.704 ± 0.007) that took 'sabbaticals'. Although failed breeders had lower probabilities of success (>10%) without taking a break, they generally attempted to breed without a 'sabbatical'. If failed breeders are successful in their next attempt without taking 'sabbatical'; they potentially make up for their first attempt failure by still producing one chick in two years. We applied our best model to individual colonies to investigate possible differences. Survival rates were similar, but breeding probabilities differed. The smallest colony had much higher breeding probabilities (> 3 times) for post-failed non-

breeders than the other large colonies and conversely, the lowest breeding probability for failed breeders. I used the estimates in a transition matrix to model average life-time chick output for individuals (2.6 chicks) and found that in order to keep population growth rate stable ($\lambda = 1$), a recruitment rate of 38% is necessary. The multi-state mark recapture method is not only an effective tool for parameter estimation but allows the user to study the life cycle of biennial breeders in depth.

Introduction

The Wandering Albatross, *Diomedea exulans,* is a well-studied, long-lived, socially monogamous seabird that endures a harsh life in sub-Antarctic environments (Warham 1990, Tickell 2000). They are the largest species of the order Procellariiformes (albatrosses and petrels) and the largest of all seabirds (Tickell 1968, Weimerskirch et al. 1987, Jouventin and Dobson 2002). Ecologically, they can be described as a "survivor" species, on the extreme right of the "fast-slow" continuum (Read and Harvey 1989, Stiling 1999). Their life history characteristics include: delayed maturity (5 - 19 years), high adult survival (>90% annual survival) and extremely low reproductive output (max 1 chick every two years) (Pickering 1989, Croxall et al. 1990, Stearns 1992, Tickell 2000, Jouventin and Dobson 2002). They have been the subject of extensive demographic research due to their dimorphism, philopatry, their lack of fear of humans, their ease of capture and the need to protect this species, which is classified as 'Vulnerable' by Birdlife International (Weimerskirch et al. 1987, Croxall et al. 1990, de la Mare & Kerry 1994, Moloney et al. 1994, Nel et al. 2003, Mills and Ryan 2005, Birdlife International 2005).

The nature of Wandering Albatross biology still presents distinct challenges for demographic investigations due to unavoidable gaps in data. Individuals can only be marked as chicks, immatures (pre-breeders) or adults during breeding seasons at nesting sites. After fledging, juvenile Wandering Albatrosses leave the colonies for a period of time ranging from 2-12 years (mode 6 years; see chapter 3) until they return to the colonies to find potential mates (Pickering 1989, Croxall et al. 1990, Weimerskirch 1992, Jouventin et al. 1999). During this period before returning to colonies, the juveniles cover great distances at sea and recapture is highly unlikely

(Tickell 2000). Once mature, breeding is typically biennial, with successful and some late failed breeders taking a 'sabbatical' year off to molt flight feathers and recover the high costs of rearing large chicks (Jouventin and Dobson 2002). Although some adults return to the colonies during sabbatical years, recapture is greatly reduced. These "immature-emigration" and "inter-birth emigration" processes or 'sabbaticals' are similar for other albatross species, such as Royals (*Diomedea epomophora/sanfordi*) and most Grey-headed Albatrosses (*Thalassarche chrystosoma*), as well as whales, seals and sea turtles (Payne et al. 1990, Robertson 1993, Schwarz and Stobo 2000, Fujiwara and Caswell 2002b, Ryan et al. 2007). The resulting gaps in data due to 'unobservable' states during immaturity and during 'sabbatical' years lead to biases in survival estimation when recapture rates are assumed to be equal for 'observable' and 'unobservable' states, as is the case in the assumptions of the most commonly used Jolly-Seber mark-recapture models (Seber 1982, Pollock et al. 1990, Lebreton et al. 1992, Kendall et al. 1997, Fujiwara and Caswell 2002b).

In this study I applied a multi-state mark-recapture analysis to the Wandering Albatross recapture data from three study colonies on Marion Island for the period 1987 - 2005. The analysis was based on a 4-state adult breeding life cycle; and estimates survival, breeding and breeding success probability for adults in 'unobservable' and 'observable' states of the life cycle. I then took the estimates and used them to estimate the population state distribution, life time reproductive output and recruitment rate to keep the population growth rate stable. The best model was applied to the three colonies separately to identify possible differences in parameters.

Methods

For study sites and data collection methods inside the study colonies see chapter 1. Individual histories were converted into coded strings according to breeding outcome. Multiple recaptures of a breeding individual in one year are given a single digit code to represent the year breeding outcome. As a result, in the period 1987-2005, we had 653, 911 and 1009 individual histories of breeding Wandering Albatrosses at Macaroni Bay, Sealer's Beach and Goney Plain, respectively, which include 4579 successful and 1311 unsuccessful breeding attempts. Records of successful breeders attempting to breed again without 'sabbaticals', were left out of the analysis, due to the biennial model constraints (see chapter 1).

Model Structure and Model Notation

I followed the three main steps of the MSMR method as stated by Fujiwara and Caswell (2002a): construction of a life stage structure, expressing the transitions in the form of likelihoods in terms of parameters and finally finding the best parameter estimates using maximum likelihood tests. In order to derive the projection matrices for the breeding Wandering Albatrosses I needed to build the adult breeding life-cycle graph as described by Caswell (2001). In describing the adult breeding life-cycle of Wandering Albatrosses I chose a 4-state model based on their current breeding status which distinguishes between breeding and non-breeding birds, and those that are successful or unsuccessful (failed) breeders (Albatross Demography Work Group 2005 pers. com.). A successful breeding attempt results in a fledgling.

The four states are :

1) Successful breeder, - an individual that breeds successfully;

2) Failed breeder – an individual that breeds, but fails to fledge a chick;

3) Post-successful non-breeder - a non-breeding individual taking a 'sabbatical' after breeding successfully the previous year;

4) Post-failed non-breeder – a non-breeding individual taking a 'sabbatical' after breeding unsuccessfully the previous year (Figure 2.1). In the model, the non-breeding states (3 and 4) are unobservable due to temporary emigration ('sabbaticals') in the biennial breeding cycle.

In the multi-state model, individuals may move amongst the four states or can die between discreet time intervals (Lebreton et al. 1992) and in our case only one transition is possible in any given year. Arrows between the states in Figure 2.1 represent the possible transitions that can occur. Movements between the 4-states are described as transitions (φ_{ij}), where i is the state of departure and j the state of arrival. Each transition has a probability of survival (σ_i), breeding (β_i) and breeding success (γ_i) estimated for the current breeding state of the albatross (Table 2.2). These probabilities depend on whether the most recent breeding status was successful or failed.

As the model only takes the adult life cycle into account, age and time since recruitment have no influence. Again in nature these do have an effect (Weimerskirch 1992, see chapter 3).

Greek notation is used to define parameter estimates. Survival (σ), breeding (β), and breeding success (γ) probabilities are followed by the number of the state the estimate represents. Thus σ_2 is survival of birds in state 2, β_3 is the breeding probability of albatrosses in state 3, and γ_4 is the breeding success probability for albatrosses attempting to breed in state 4. Time variation on parameters can be specified in order to estimate changes in parameter estimates over time. Additive variation on parameter estimation tests for links amongst the states (Hastie and Tibshirani 1987). I used the following notation to express time variation on parameters for the 12 models. Variation can be applied to model estimation of probability of survival, breeding or breeding success to test for better fit. A is for additive, C for constant and T for time variation. For example, M8ACT refers to model 8 with additive variation on survival, constant breeding probabilities and time variation on breeding success probabilities. For the biennial 4-state model, at any time, a successful breeder (state 1) cannot breed again in the following year, thus they have a zero probability for breeding (β_1) and breeding success (γ_1).

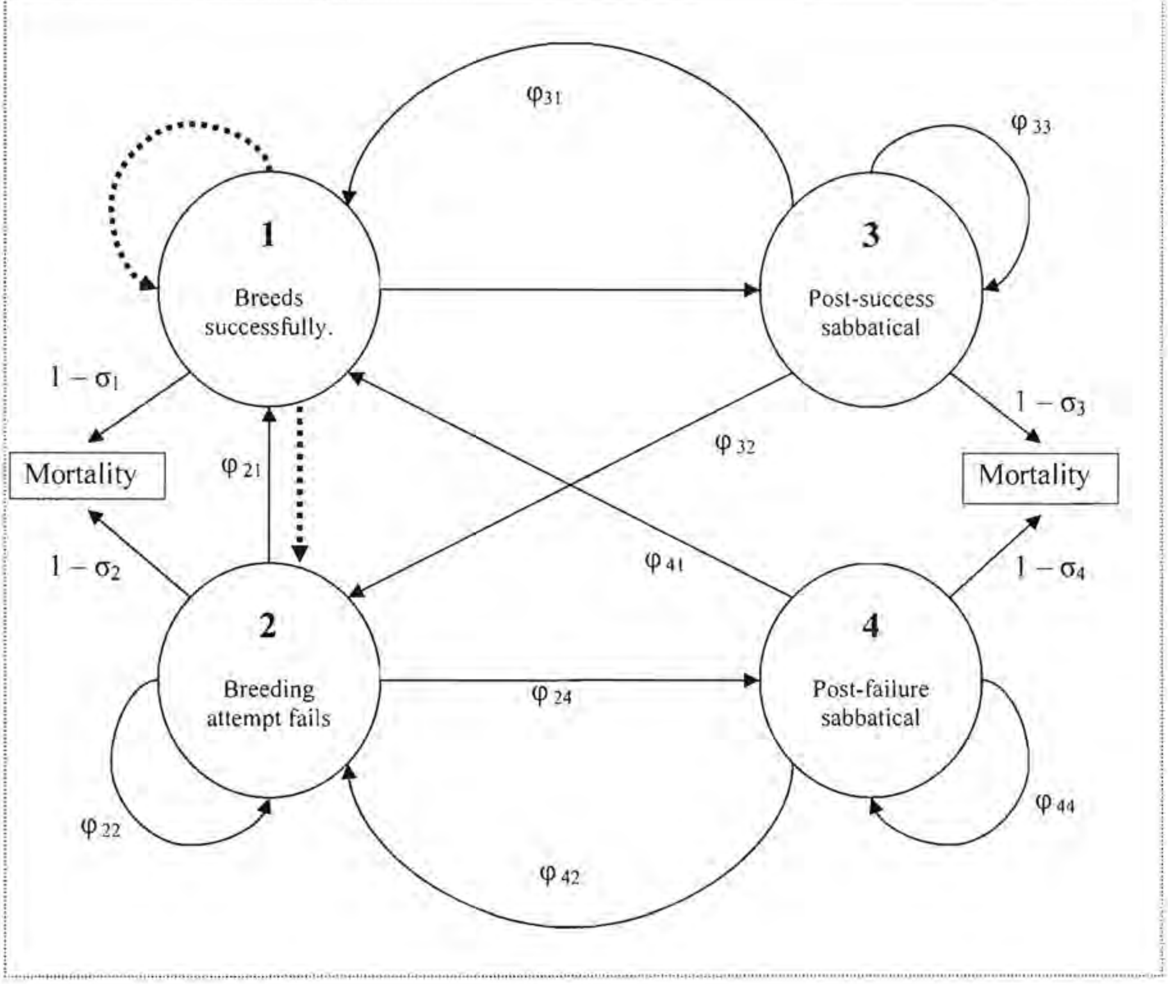

Figure 2.1: Four-state adult breeding life-cycle structure for Wandering Albatross. Breeding states are successful breeder (1), failed breeder (2), post-successful non-breeder (3), and post-failed non-breeder (4). Transitions are indicated by φ_{ij} where *i* is the state of departure and *j* is the state of arrival. Successful breeders very rarely attempt to breed again the following year (dashed lines) so these probabilities were excluded from the model.

Table 2.2. Transition probabilities (φ_{ij}) for the biennial 4-state adult breeding life-cycle model (Figure 2.1). Notation: σ = survival, β = breeding and γ = breeding success probability. Note that due to the biennial nature of the species the model assumes all successful breeders take a sabbatical ($\varphi_{11} = \varphi_{12} = 0$).

Transition	**Description**	**Probability**
φ_{13}	Breeding success to sabbatical	$\sigma_1 \cdot 1^*$
φ_{11}	Consecutive breeding success	$\sigma_1 \cdot 0$
φ_{12}	Breeding success to failed attempt	$\sigma_1 \cdot 0$
φ_{21}	Breeding failure to breeding success	$\sigma_2\beta_2\gamma_2$
φ_{22}	Repeated breeding failure	$\sigma_2\beta_2(1-\gamma_2)$
φ_{24}	Breeding failure to sabbatical	$\sigma_2(1-\beta_2)$
φ_{31}	Post-success sabbatical to breeding success	$\sigma_3\beta_3\gamma_3$
φ_{32}	Post-success sabbatical to breeding failure	$\sigma_3\beta_3(1-\gamma_3)$
φ_{33}	Repeated post-success sabbatical	$\sigma_3(1-\beta_3)$
φ_{41}	Post-failure sabbatical to breeding success	$\sigma_4\beta_4\gamma_4$
φ_{42}	Post-failure sabbatical to breeding failure	$\sigma_4(\beta_4)(1-\gamma_4)$
φ_{44}	Repeated post-failure sabbatical	$\sigma_4(1-\beta_4)$

*By definition, all successful breeders return as post-successful non-breeders.

Model Constraints

In order to make parameters estimable for the observable and unobservable states I had to apply certain constraints to the parameters estimated by the models. These constraints also serve as biological hypothesis testing tools as the models with the best fit will indicate how the albatross life cycle is constrained according to survival and breeding probabilities. Twelve models were described each with a different set of constraints on survival and breeding probabilities between the states (Table 2.3).

Table 2.3. Constraints on survival and breeding probabilities for the 4-state biennial breeding model. [Mz] represents the model number that incorporates the constraints of survival and breeding probabilities.

	Survival Constraints		
Breeding Probability Constraints	Survival Constant $[\sigma_1 = \sigma_2 = \sigma_3 = \sigma_4]$	Successful breeders $\neq$ Failed breeders $[\sigma_1 = \sigma_3, \sigma_2 = \sigma_4]$	Breeders $\neq$ Non-Breeders $[\sigma_1 = \sigma_2, \sigma_3 = \sigma_4]$
$\beta_2 = \beta_3 = \beta_4$	[M1]	[M5]	[M9]
$\beta_2 = \beta_4$	[M2]	[M6]	[M10]
$\beta_3 = \beta_4$	[M3]	[M7]	[M11]
β_3, β_4	[M4]	[M8]	[M12]

Model Selection

Rather than selecting a general model with full time dependence ($\varphi^t p^t$) where p is the probability of recapture, and then comparing models of reduced time constraints against this general model using likelihood ratio (Lebreton et al. 1992), I used a different approach due to the limitations of using biennial data. I started with constant probabilities for survival, breeding and breeding success and then added time constraints to parameters to check if this improved the model fit.

I used MUSE (Choquet pers. Comm.), an update of program M-SURGE (Choquet et al. 2003), for running our MSMR models. Within MUSE, transition probabilities were broken down into three pattern matrices for survival, breeding and breeding success probabilities respectively. In order to estimate these parameters I needed to incorporate encounter probabilities (p). These probabilities were either "not seen", "seen in state 1" or "seen in state 2". States 3 and 4, for non-breeders are unobservable. Very recently Muse was updated to program E-Surge (Choquet et al. 2008).

Akaike's Information Criterion (AIC), the deviance of the model plus twice the number of parameters estimates, was used as an index of model fit (Akaike 1973). The model with the lowest AIC value was taken to be the best model. Other models were compared to the best fit model using difference in AIC (ΔAIC). I used a spreadsheet to generate random initial encounter probabilities for each model required to estimate demographic parameters. I calculated AIC values for all 12 constant models and selected the three best fitting models. I then added time and additive variation to survival, breeding and breeding success probabilities for models deemed estimable and ran those models with 10 new sets of random initial encounter parameters. I then selected the best model to apply to the grouped colony effect to see whether the colonies differed with respect to their demographic characteristics. I then compared estimates of Wandering Albatross survival from the MSMR model to a conventional CJS mark-recapture analysis in MARK (White and Burnham 1999) using the same input data for all colonies combined. However, due to biases being most pronounced in the first year and last two years in the MARK CJS method (Rothery and Prince 1990) the estimates in these years were removed. As a result I compared the MSMR and CJS models over the period 1989 - 2003.

Weighted Average Model

The parameter estimates from the best models were combined into the weighted average model, which provided the best overall picture of the demographic parameter change from 1987-2005 at Marion Island. After all possible models were completed I selected the best models with a cumulative weight of 1 in order to create a weighted average model across the range of parameter estimates. The models were ranked from lowest to highest according to their Δ AIC value.

The average model was represented by the equation:

$$M_A = w_i M_i + \ldots\ldots + w_n M_n;$$

where $i = 1$ to n (n = the number of models included) and M represents the matrix of parameter estimates for Models i to n, and

$$w_i = e^{-1/2\,\Delta\,AIC_i} / \Sigma_j e^{-1/2\Delta\,AIC_j} \;;\ \text{for } j = 1,2\ldots.n;$$

is the weight coefficient for each model according to its Δ AIC. We used MATLAB to construct the average model and map the demographic parameter estimates for the time period 1987-2005.

Goodness of Fit

To test whether the data adequately obey the assumptions of the mark-recapture model, I used UCARE V2.02 (Choquet et al. 2003) for goodness-of-fit (GOF) tests (Pradel et al. 2003). Similar to single-state GOF, the individual histories need to be checked for independence and transience. If the data do not adequately fit the MSMR model, deviance will tend to be inflated, favouring the selection of over-parameterized models leading to erroneous biological conclusions (Pradel et al. 2005). UCARE Global Test 3 compares the future history of encountered individuals with respect to previous capture history and encompasses an adequate test of transience, that is, individuals who pass through the colony and are encountered on route to other locations. I tested GOF for data independently for the colonies and the combined histories of all colonies using $\hat{c}$ as an indication of fit. Formal GOF tests are available for all multi-state models and should be used as a guide more than an ultimate description of the data (Pradel et al. 2003). For my study a $\hat{c} \leq 2$ indicates an acceptable goodness-of-fit. GOF results were adequate and suitable for all data sets based on Global Test 3 of UCARE (Table 2.1). It is important to note that GOF tests for multi-state analysis are as yet not advanced so we generally accept the GOF tests to be acceptable if $\hat{c} \leq 2$.

Table 2.1. Goodness of fit results for datasets used in this analysis.

Data Set	$\hat{c}$
Goney Plain	1.72
Sealer's Beach	1.33
Macaroni Bay	0.92
Combined Colonies	1.67
All Males	1.57
All Females	1.89

Population projections

Once all the estimates for adult survival, breeding and breeding success probability were calculated for the breeding states, I created a 5-state transition projection matrix that included mortality (Caswell 2001). I modelled the average per capita chick production and state distribution for 1000 individuals entering the adult breeding cycle with first time breeding success separately set to observed success rates, successful first and failed first attempts. I ran the model until >95% of the population was dead. This took 40 years. The oldest banded Wandering Albatross at the Prince Edward Islands was estimated to be approximately half a century old (Cooper et al. 2003). Individual longevity was thus truncated to 40 years within the adult life cycle. I then used the per capita chick production to calculate the recruitment rate necessary to ensure population growth remains stable. I also set up a 4-state projection matrix to estimate the steady state equilibrium.

Results

Best models that describe the data.

M4CCC had the best fit, followed closely by M8CCC and M12CCC. Other models failed to provide a good fit to the data (Table 2.4). Once I selected M4, M8 and M12 as our basis for further investigation, I ran these models with time variation and additive variation on the parameters (Appendix 1. A). Model 4CCC (AIC = 21079.49) remained the best fitting model followed by M4CCT (ΔAIC = 1.29; time variation on breeding success). Variation in breeding success across the years showed the best fit for time variation in any parameter. Breeding probability showed no time variation and remained constant for the best fitting models. Despite reducing model deviance due to the greater number of parameters, adding time or additive variation failed to improve AIC. Including a colony effect into model 4CCC decreased the deviance (21006.9 from 21027.5), but added 14 more parameters, thus resulting in a larger AIC (ΔAIC = 7.43).

Table 2.4. Results for the 4-state constant models with constraints on survival and breeding from program MUSE (R. Choquet pers. comm.). The models with the lowest AIC are considered to be the best fitting. Δ AIC indicates the difference in AIC between the best fitting model.

Constraint Model	*Number of Parameters*	*Deviance*	*AIC*	*Δ AIC*
M4CCC	26	21027.49	21079.49	-
M8CCC	27	21027.48	21081.48	1.98
M12CCC	27	21027.48	21081.48	1.98
M7CCC	26	21161.07	21213.07	133.57
M11CCC	26	21161.09	21213.09	133.56
M10CCC	26	21161.48	21213.48	133.98
M9CCC	25	21173.99	21223.99	144.49
M2CCC	25	21174.05	21224.05	144.56
M5CCC	25	21174.65	21224.65	145.15
M3CCC	25	21174.88	21224.88	145.39
M1CCC	24	21191.21	21239.21	159.71
M6CCC	26	23990.90	24042.90	2963.41

Survival

My estimate for adult survival (Table 2.5) from our best fit model is slightly lower than the previous estimate (94.2% ± 0.008%) for the same colonies over the period 1984-2001 using a Cormack-Jolly-Seber (CJS) mark-recapture model (Nel et al. 2003). The estimate of average adult survival ($\sigma_{average}$= 0.936 ± 0.03%, Appendix 1.D) derived from my conventional mark-recapture model in MARK (White and Burnham 1999) for the same data set was also higher (0.7%) than that obtained from the MSMR model (Appendix 1.A). Interestingly, the time-varying survival model had the lowest AIC (best fit model: σ (t) p (t): AIC = 24544.2) in the MARK analysis, followed by the constant survival model (Δ AIC = 31.29). Despite the CJS survival estimates having higher standard deviation, the patterns that emerges is similar to those of the MSMR model except for the last two years (Figure 2.4). Based on the extremely high adult survival estimates in MARK, I assume this increase is due to biases in recapture estimation. Model 8CCC (Table 2.6) and 12CCC (Table 2.6) suggest that there is no difference in survival between successful and failed breeders, but difference between breeders and non-breeders (0.5%). Survival probabilities showed similar patterns amongst the states over time with respect to increases and declines between observable and unobservable states with closer relationships for breeders (Figure 2.2) and non-breeders respectively (Figure 2.3). Survival for unobservable states showed less extreme fluctuations in comparison to those for birds in observable states. During the period of the study, survival rates increased very slightly (<1%) for all states except post-successful non-breeders which experienced a decrease (<1%). Survival was similar for all colonies, though slightly higher at Goney Plain (Table 2.7).

Table 2.5. Parameter estimates for best model M4CCC. Survival is constrained for all states equal, breeding and breeding success probabilities are estimated separately for states 2, 3 and 4. σ =Survival, β=breeding probability, and γ = breeding success.

Parameter	Probability ± SE [95% Confidence Limits]
Adult Survival (σ)	0.928 ± 0.003 [0.923 0.933]
Breeding probability (β):	
Failed breeders (β_2)	0.930 ± 0.009 [0.909 0.947]
Post-successful non-breeders (β_3)	1.000 ± 0.000 [1.000 1.000]
Post-failed non-breeders (β_4)	0.168 ± 0.043 [0.099 0.270]
Breeding success (γ):	
Failed breeder (γ_2)	0.576 ± 0.011 [0.553 0.599]
Post-successful breeder (γ_3)	0.704 ± 0.007 [0.689 0.718]
Post-failed breeder (γ_4)	0.689 ± 0.094 [0.484 0.840]

Table 2.6. Survival parameter estimates of observable and unobservable states from M8CCC and M12CCC (σ_3 and σ_4 are unobservable non-breeding states).

Model	Parameter	Probability ± SE [95% Confidence Limits]
M8CCC	$\sigma_1 = \sigma_3$	0.928 ± 0.003 [0.923 0.933]
	$\sigma_2 = \sigma_4$	0.929 ± 0.008 [0.912 0.944]
M12CCC	$\sigma_1 = \sigma_2$	0.931 ± 0.023 [0.870 0.964]
	$\sigma_3 = \sigma_4$	0.926 ± 0.025 [0.860 0.962]

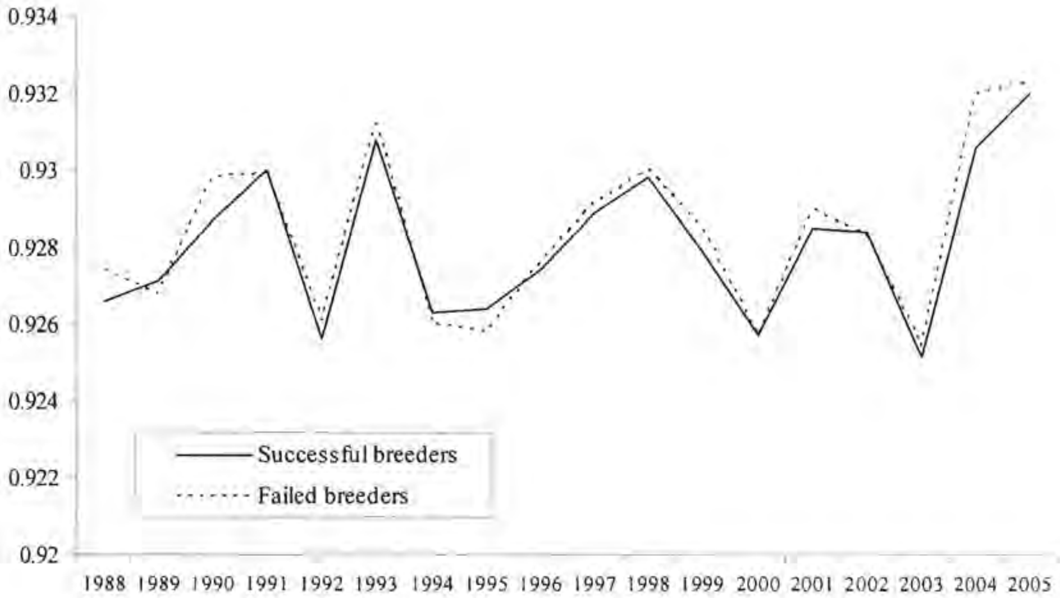

Figure 2.2. Survival probability for Wandering Albatross in 'observable' breeding states according to the weighted average MSMR model.

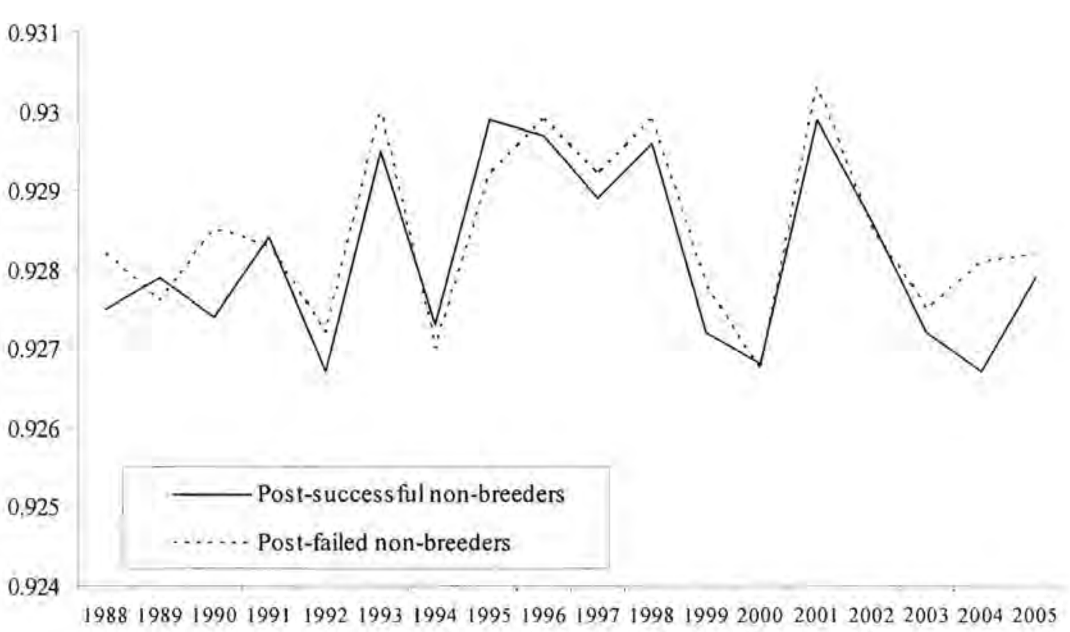

Figure 2.3. Survival probabilities for Wandering Albatross during 'unobservable' sabbatical years according to the weighted average MSMR model.

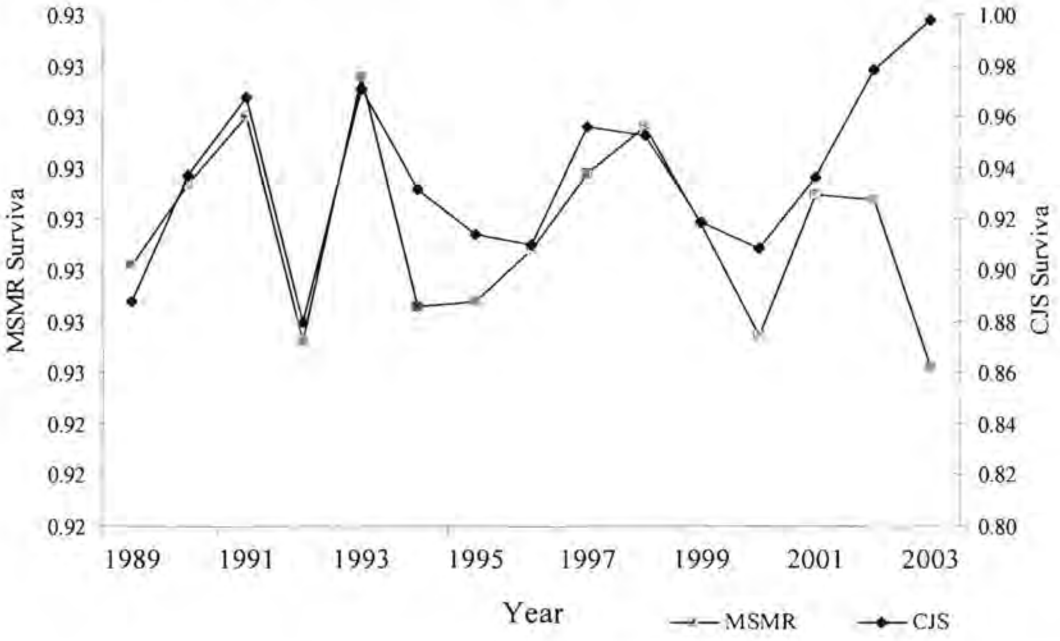

Figure 2.4. Survival probability for adult breeding Wandering Albatrosses on Marion Island as measured using a Cormack-Jolly-Seber and MSMR method (White and Burnam 1999).

Breeding and breeding success

Probability of breeding (β) and breeding success (γ) showed distinct variation for failed, post-successful and post-failed birds. Breeding success probabilities were consistently 10-15% greater for adults that had bred successfully two years prior (post-successful non-breeders returning from sabbatical to breed), than for birds that failed their previous breeding attempt (Figure 2.5). The majority of failed breeders attempted to breed in the following year with far fewer attempting to breed again after a year sabbatical (Figure 2.6). Post-failed non-breeders showed erratic success rates but for years 1987-1993 where probabilities were remarkably stable; this may be the result of smaller sample sizes. Failed and post-successful breeding success probabilities fluctuated synchronously but were relatively stable in comparison to post-failed success. Actual probability estimates are given in Appendix 1.C.

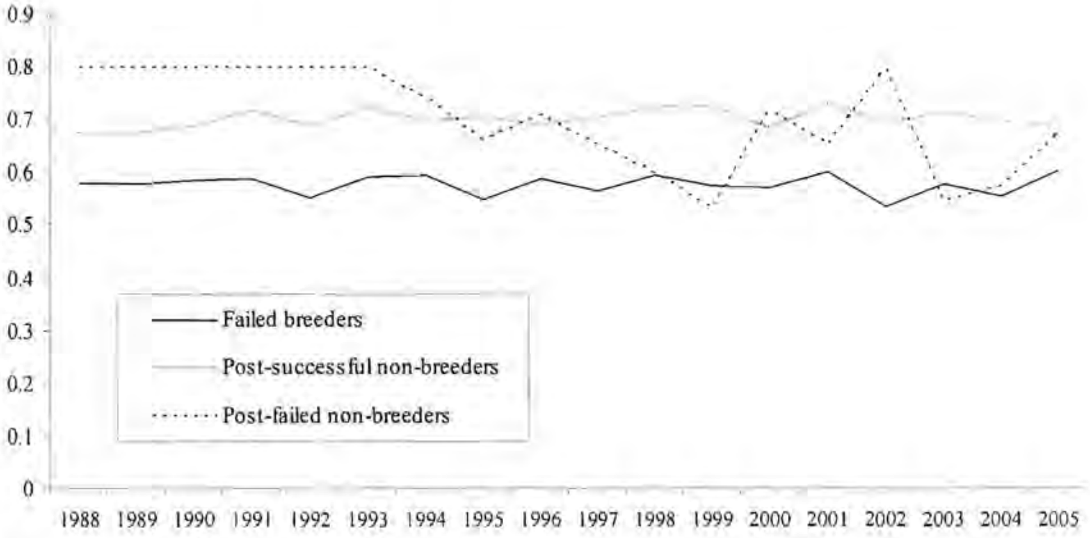

Figure 2.5. Breeding success probability for failed breeders and post-successful, non-breeding Wandering Albatrosses on Marion Island.

Post-failed non-breeders from Macaroni Bay were more than three times more likely to breed than similar birds from the other two colonies (Table 2.7). However, failed breeders at Macaroni Bay were less likely to breed again without a sabbatical. For all colonies, breeding success was lowest for failed breeders that attempt to breed again in the next season, suggesting that success is more likely to occur if a breeder takes a year off, survives and then breeds after sabbatical. However, the probability of a failed breeder breeding after a sabbatical is very low.

Table 2.7. Parameter estimates of the best fit model (M4CCC) with the colony group effect on Marion Island (1987-2005). Survival (σ) is constant for all states, breeding (β) and breeding success (γ) probabilities are estimated for states 2, 3 and 4. Reported as: estimate ± SE.

	Marion Island Colony (1987-2005)		
Parameter Estimated	Sealer's Beach	Goney Plain	Macaroni Bay
σ	0.927 ± 0.004	0.931 ± 0.004	0.922 ± 0.008
β_2	0.938 ± 0.014	0.923 ± 0.013	0.877 ± 0.044
β_3	1.000 ± 0.000	0.992 ± 0.011	1.000 ± 0.000
β_4	0.133 ± 0.059	0.135 ± 0.046	0.456 ± 0.132
γ_2	0.604 ± 0.018	0.564 ± 0.164	0.545 ± 0.038
γ_3	0.698 ± 0.011	0.724 ± 0.013	0.663 ± 0.024
γ_4	0.816 ± 0.149	0.621 ± 0.124	0.679 ± 0.176

Transition probabilities for breeding Wandering Albatrosses

Combining the parameter estimates from the best fit model (Table 2.4) results in transition probabilities (Figure 2.6). The parameters all make good biological sense, except for $\beta_3 = 1.0$. which implies that all successful birds breed after a year off. This is not supported by the observed data, and suggests a problem with the estimation of this parameter.

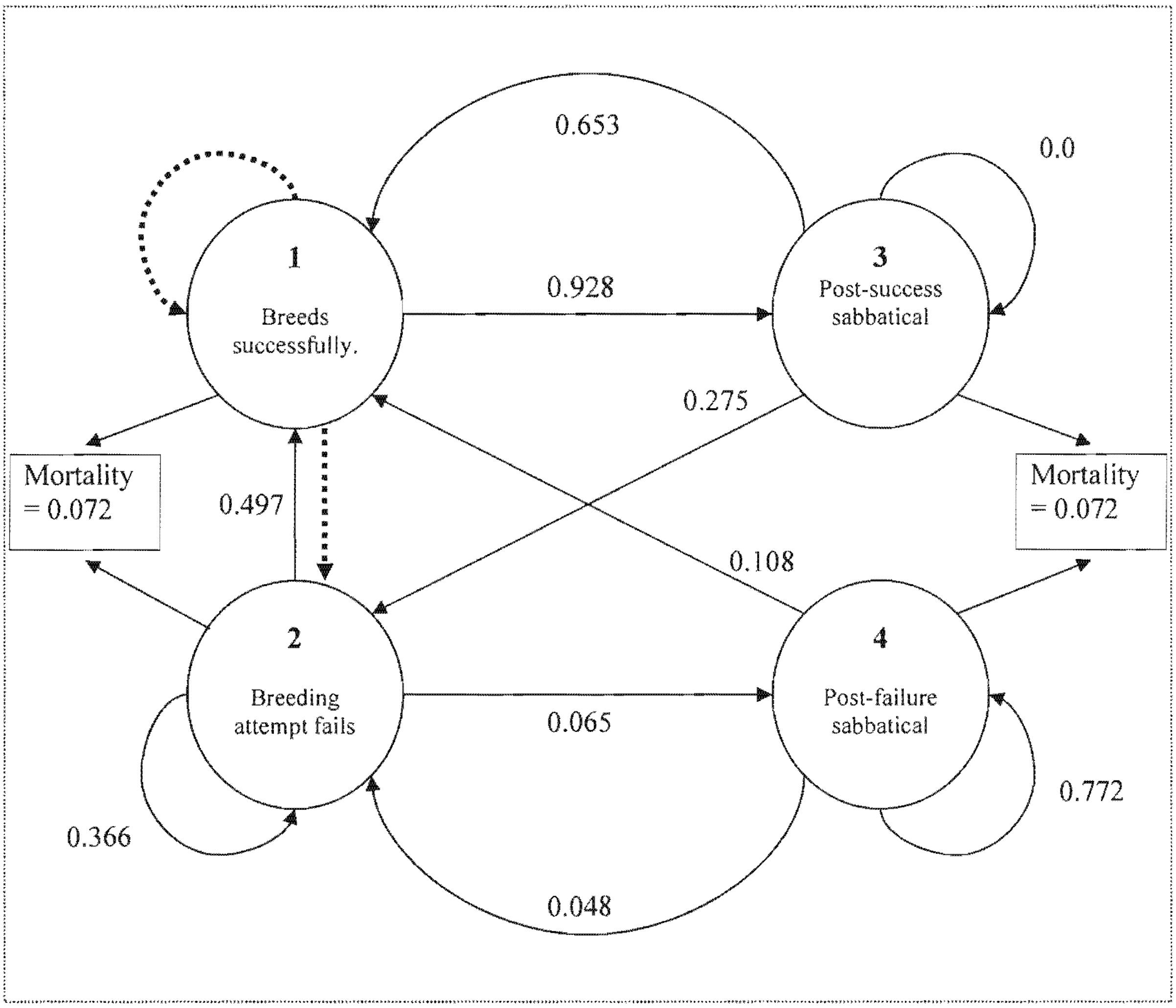

Figure 2.6. Transition probabilities estimated for adult Wandering Albatross in the 4-state, breeding life-cycle. Dashed lines represent very rare transitions excluded from the model.

Transition matrix projections

Average projected life-time chick production for each adult entering the breeding population was 2.6 chicks under observed initial success rates (74.5% successful first breeding attempt; see chapter 3). In order for the population to be stable, this requires 38.4% of chicks to recruit to the breeding population. The per capita chick production is highest when first breeding attempts are successful (2.7 chicks) compared to breeders that initially fail (2.2 chicks). The model shows that 95% of the breeding population would have died within 40 years of recruitment. The population state distribution (Table 2.8) shows that 55.4% of the population will be breeding in a given year, suggesting that a population of around 3000 Wandering Albatrosses use Marion Island as a breeding ground.

Table 2.8. Population state distribution of breeding Wandering Albatross on Marion Island (1987-2005).

State	Percentage of population
Successful breeder	36.8
Failed breeder	18.7
Post-successful non-breeder	36.8
Post-failed non-breeder	0.78

Discussion

This is first multi-state mark-recapture model analyses of Wandering Albatrosses. The 4-state breeding life-cycle model suggests that survival does not vary significantly among states, but breeding probabilities show clear independence in states 2, 3 and 4. M4, M8 and M12 were similar in their model constraint definitions in that they estimate breeding probabilities independently for states 2, 3 and 4 and were clearly the best fitting models in the constant model set. Despite their different constraints on survival, there was little variation in survival rates amongst the states.

M4CCC was the best model, indicating constant survival but independent breeding and breeding success probabilities for Wandering Albatrosses depending on their most recent breeding history. Constraining survival across the states has no effect on overall fit of the model. This indicates that breeding history has little effect on survival for adult Wandering Albatrosses, supporting suggestions that long-lived species limit their breeding effort to enhance their survival (Williams 1966). In fact, my survival estimates indicate that non-breeders have lower survival than breeders. This implies that there is no cost of breeding or that non-breeders suffer a greater risk of dying when not breeding. This may be linked to foraging zones of non-breeders where they may interact with long-line fishing vessels (Weimerskirch & Jouventin 1987, Nel et al. 2003).

The importance of survival in Wandering Albatross fitness can not be underestimated because breeding success and adult survival are highly correlated (Weimerskirch et al. 1987). Survival is the key driver of population growth rate in long lived organisms (Read and Harvey 1989). Although survival varied on a fine scale (between 92% and 94%), this detail is actually of great importance because overall albatross population growth is sensitive to any change. At an individual level, a breeding adult Wandering Albatross could only compensate a decrease of 1% in adult survival rate for by an advancement of first breeding of 6.5 years (Weimerskirch et al. 1987, Croxall et al. 1990). Our estimates for survival were lower than previous investigations on Marion Island (Nel et al. 2003) and Bird Island (Croxall et al. 1990) but similar for breeding Wanderers on the Crozet Islands (Weimerskirch et al. 1987) (Table 2.9).

Table 2.9. Comparison of survival estimates at various Wandering Albatross colonies using CJS mark-recapture methods in comparison to our multi-state method (Marion Island, 1987-2005).

Colony	Years	Survival Estimate	Source
Possession Island, Crozét	1966-1969	89.7 ± 1.200	Weimerskirch et al. 1987
	1968-1983	92.2 ± 0.005	
	1986-1993	95.6 ± 0.300	Weimerskirch et al.1997
Bird Island, South Georgia	1976-1984	94.8 ± 0.600	Croxall et al. 1990
Marion Island (CJS)	1984-2001	94.2 ± 0.008	Nel et al. 2003
Marion Island (MSMR)	1987-2005	92.8 ± 0.002	This study.

Conventional CJS models that assume equal probability of recapture each year can cause bias in parameter estimation (Henle 2001, Fujiwara and Caswell 2002b, Pledger et al. 2003). The higher survival estimate, obtained by the conventional CJS model of the same data used in this MSMR model, presumably reflects this bias. A comparison of MSMR and conventional model estimates for the biennial-breeding Grey-headed Albatross *Thalassarche chrysostoma* at Marion Island found the MSMR estimate to be 0.5 % lower than the MSMR estimate (Converse et al. in press), similar to the difference between the CJS and MSMR (0.7%). This suggests that previous demographic models of Wandering Albatross populations have been somewhat optimistic. These errors of parameter estimation are due to underestimation of recapture rates caused by post-fledging and inter-birth sabbaticals and are most pronounced in the first and last two years of analyses (Rothery & Prince 1990). This has led to some investigations leaving these years out completely to compensate (Weimerskirch et al 1997). Some have argued that such bias in estimation is insignificant if it falls within the range of the standard error for the actual estimate (Henle 2001). However, in our case, the difference of 0.7% falls outside the standard errors for MSMR survival.

Successful breeders invariably attempt to breed after a sabbatical. However, we may expect some deviance from the rule. It does not include any room for the small proportion of birds that may experience a 'divorce' or the greater likelihood of not breeding because of a mate loss (Jouventin et al. 1999). Consecutive successful breeding attempts for Wandering Albatrosses without sabbatical have been reported on Marion Island data but these were not allowed in the model (see chapter 1). Other instances of biennial breeding albatross breaking the pattern have been recorded (Waugh et al. 1997). How important these extraordinary occasions are to population growth is debatable but nonetheless interesting (Tickell 2000). More intriguing is the effect of these consecutive successes on life-time reproductive success (Ryan et al. 2007).

Breeding success was influenced by previous breeding performance and indicates strong variation for individuals in different reproductive states. According to our results, breeding success (γ) was similar for birds that, regardless of success or failure, took a year off between breeding events. Failed birds that attempt to breed the following year risk higher probabilities of failure. However, if they are successful without a sabbatical they will exhibit no loss in reproductive output due to the 'catch up' year allowed in biennial breeding cycles. For those birds that failed but take a year off, they maximize the probability of being successful in their next attempt if they survive.

Colonies may act as "information centres" and the larger a colony becomes, it is assumed the mean age of breeders becomes older and thus probably more experienced (Ward & Zahavi 1973, Warham 1996). Larger, denser colonies also seem to attract more pre-breeders and widowed birds (Wiemerskirch & Jouventin 1987). There is little evidence of colony effects on demographic rates. Demographic research on two colonies at Crozet also showed no significant differences in survival (Weimerskirch et al. 1987). However, there were greater differences in breeding and breeding success probabilities. The greatest difference was in the estimated probability of breeding for post-failed breeders. Macaroni Bay post-failed non-breeders showed a significantly higher likelihood of returning to breed compared to the larger colonies (3:1). At Macaroni Bay, failed birds that take a sabbatical exhibit higher breeding success in the year of breeding than the group that does not take sabbatical. Failed breeders that take a sabbatical may have higher breeding success if they do breed, but paradoxically they have much lowerprobability of actually breeding after the sabbatical. I calculated the actual breeding success from the colony data and Sealers beach had the highest breeding success rate (78.4% compared to 75.7% for Goney Plain and Macaroni Bay). According to the MSMR results, failed breeders from Sealer's Beach colony are more likely to return to breed, and to breed successfully without a year break than the other two colonies.

Twelve Wandering Albatrosses were banded as chicks in 1965. The oldest bird from this cohort bred in 2006 at an age of 41 years. My longevity estimate suggests few birds live beyond 50 years of age, that is, if you take the modal age of first breeding to be 10 years (see chapter 3). The model suggested it is possible for these giant birds to live beyond 80 years. We will only be able to truly justify this after at least another 4 decades of recapture monitoring; such is the study of albatrosses. The recruitment rate estimated is acceptable; of chicks banded between 1980 and 1993 I calculated a recruitment rate of 36% (see chapter 1). Together with those recruits from outside the breeding colonies, the 38.4% threshold to ensure stable growth rate ($\lambda \geq 1$) is a good estimate of total recruitment into the effective population.

The MSMR method is modern and may open doors to further analysis of other biennial breeding albatrosses. Certain assumptions were made to suit the analysis, for instance, sex and adult age are not accounted for, and both have been shown to have an affect on breeding effort and success in Wandering Albatrosses (Weimerskirch et al. 2000; see chapter 3). However, I set out to develop a method to identify key states in the adult breeding life-cycle, provide insight into the overall breeding decisions and their consequences for the average, adult breeding Wandering Albatross. I suggest comparative analyses of Wandering Albatross populations on Bird Island and the Crozet Islands. These will help address the biases highlighted by this project and give conservationists a broader idea about survival of Wandering Albatrosses on the islands. Further analysis could test for sensitivities of population growth and help identify key areas to protect which are frequented by breeding or non-breeding adults.

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CHAPTER 3

THE EFFECTS OF AGE, SEX AND EXPERIENCE ON BREEDING SUCCESS AND SURVIVAL OF WANDERING ALBATROSSES

Abstract

I investigated the effects of age, sex and experience on the reproductive success of Wandering Albatross, *Diomedea exulans*, on Marion Island. The average age of first breeding for all birds fledged between 1980 and 1988 was 9.9 ± 1.9 y (N = 378) with 95% of males and females breeding by the age of 14 and 12 years, respectively. Females first bred significantly earlier (9.6 ± 1.3 years; N = 178) than males (10.3 ± 1.9 years; N = 200). Most females first returned to the colony to find mates 3.1 ±1.6 years (N = 144) before first breeding whereas males spend more time in this pre-breeding stage (3.4 ± 1.9 years, N = 180). Males that bred for the first time at ages younger than 8 years were the most likely to disappear from the breeding colonies within the first 10 years of recruitment. Female disappearance within the first 10 years of recruitment decreased with increasing age of first breeding until 11 years of age, then increased for females >11 years. The success of the first breeding attempt was affected by age with highest initial success recorded for birds that first bred at ages older than 11 years.. I analysed the number of chicks produced in the first 5 and 10 breeding years after an individual bred for the first time. For both sexes, the average number of chicks produced in 5-and 10-year intervals increased up to birds that first bred at age 11, but decreased for birds that only bred for the first time after 11.. Age versus breeding success produced a bell-shaped response in males but female success remained relatively stable across the age groups. Of the birds that disappeared during the first 5/10 years of breeding after recruiting, most were lost after their first breeding year suggesting high costs of initial breeding. When age was controlled for and experience was analysed, breeding success was constant until it started to decrease after 10 breeding attempts. I tested the 'selection' hypothesis against the 'experience' hypothesis and both seem evident in the males, whereas only experience effects emerged in females. The results provide empirical support for deferred maturity in this long-lived species, with significant costs in terms of reduced survival

for early breeders, especially among males. The results also indicate that the most productive birds start breeding at the mean age of first breeding.

Introduction

By studying the behaviour and life-cycles of animals, life history theory can reveal the mechanisms that act on a species at an individual level, which ultimately lead to a complex pattern of traits to maximise selection and fitness (Stearns 1992). Fitness summarizes births and deaths, and is thus a demographic concept (Caswell 2001). Individual fitness properties are bound to have an effect on overall population growth because demography of a whole population relies on the properties of the population's individuals (de Kroon et al. 2000). Individuals differ widely in the number of offspring they produce in their life-time (Krŭger & Linstrŏm 1993). Some population modelling methods, for instance those based on the logistic equation; assume that all individuals are identical (Lomnicki 1980, Caswell 1989). However, ecological systems based on individual dynamics are more complex (Uchamski and Grimm 1996). Life history traits, such as age at maturity and reproductive effort directly influence reproduction and survival. They may vary between the sexes and are bound by trade-offs including costs of current reproduction versus future survival and reproduction (Lack 1968, Williams 1966, Stearns 1992, Erikstad et al. 1998). Thus, it is imperative to understand the species on an individual level and this need is bolstered by the fact that identifying changes in behaviour can bring to light pressures acting on the population as a whole.

Reproductive success increases with age and experience in many species of birds (Saether 1990, Pyle et al. 1991, Cam and Monnet 2000, Pyle et al. 2001). This may be due to an increase in skill and foraging efficiency, increased skill in displaying and pairing behaviour, increased reproductive effort exerted by older birds as their reproductive value decreases or selective removal of poor quality birds (Lack 1968, Pugesek 1981, Lequette and Weimerskirch 1990). Younger parents and first-time breeders may have smaller egg or clutch sizes, reduced chances of pairing, or lack the skill necessary to fledge chicks (Curio 1983, Weimerskirch 1990, Croxall et al. 1992). Experienced and older Wandering Albatross, *Diomedea exulans,* arrive later to breed than young breeders and thus require a shorter time span to reproduce successfully

(Weimerskirch 1992). Food delivery to chicks is more synchronised for older breeders, resulting in chicks gaining weight faster (Weimerskirch et al. 2000). Thus, parental age and experience of a breeder has a significant influence on albatross fecundity.

One reason why young birds may invest less in reproduction, or defer reproduction entirely, is that breeding has intrinsic costs to future survival (Williams 1966). Pyle et al. (1997) showed higher annual mortality for Western Gulls, *Larus occidentalis,* which attempted breeding at younger ages than birds that delayed breeding for 1-2 more years. For long-lived species such as Wandering Albatross, with very high residual reproductive value, survival is the driving force of population increase (Read and Harvey 1989). Delayed maturity is an evolutionary adaptive strategy that allows the individual to achieve a threshold body condition capable of withstanding the costs of reproduction, decreases the probability of mortality and in the long run, increases fecundity (Stearns 1992). Even experienced birds may not breed in a given year when resources are limited as they cannot achieve this threshold (Chastel et al. 1995). The decision when to start breeding may have a great influence on the number of chicks produced in a long-lived individual's lifetime (Newton 1989).

Three hypotheses may explain the effect of age and experience on reproductive success: experience, effort and selection (Mauck et al. 2004). Briefly, the experience hypothesis argues that older birds are more efficient foragers, and are thus able to reduce the costs of reproduction on survival through increased parental co-ordination and ability to maximise reproductive output. The effort hypothesis suggests that older birds invest more per breeding attempt because their residual reproductive value decreases with age, thus reducing the value of ensuring future survival (and thus for future breeding attempts). The selection hypothesis suggests that as a cohort ages, low quality birds die off, resulting in a bias towards birds with higher reproductive success, raising the average success rate. Rarely can any one hypothesis fully explain the effect of age and experience on reproduction of a species; usually it is a combination of two of more of these factors (Weimerskirch 1992).

The ideal candidate species for studying reproductive success can be marked at birth and readily observed in its breeding cycle, so that each breeding attempt can be documented (Clutton-Brock 1988). Wandering Albatross are excellent subjects and have been studied extensively (Croxall et al. 1990, Weimerskirch 1990, 1992). However, due to their very long life-spans (with known records of breeding beyond 40 y of age), life-time reproductive success is still difficult to measure as the sample size of complete histories is small. In this study I address reproductive success according to age, experience and sex. I also attempt to measure and compare, instead of life-time reproductive success, reproductive performance in measured units of time.

Studies have shown that younger birds tend to incur higher mortality when breeding for the first time, that breeding success increases with age and experience, but that individual quality may mask these phenomena so that distinguishing amongst the three hypotheses stated can be difficult (Bradley et al. 1989, Weimerskirch 1990, Wooler et al. 1990). I expect to see differences in reproductive traits between the sexes for a number of reasons: males are larger and bring more food for chicks than females, and males and females feed with different success in different feeding zones (Weimerskirch et al. 2000). Also, populations are biased towards males due to greater mortality of females from long-line fishing (Weimerskirch et al. 2005). Although it may seem that the costs of reproduction are greater for males, it may prove more costly for females as they often feed less successfully and further away from the colonies than males (Weimerskirch 2000).

Methods

For details on the data collection and study sites see Chapter 1. For this investigation I used different subsets of the Wandering Albatross database from Marion Island. I combined all data from chicks banded from 1980 to investigate the age and timing of events leading to the first breeding. Few (if any) birds from these cohorts would have started breeding before the monitored colonies were established in 1984 (no chicks were banded at the Goney Plain colony prior to 1987, so only the 1987 and 1988 cohort were used from this colony). I included only birds that fledged within the study colonies and that were subsequently recaptured and sexed as adult pre-breeders and breeders. All fledglings banded from 1980-1990 were analysed to measure age of first breeding. This gave chicks at least 16 years to recruit until 2006, the last year of data used in the study. Some birds may have recruited outside the study areas and later moved into the study areas. However, all nests outside colonies are checked during incubation, so at least half of all breeders outside colonies are checked for bands each year. Any bird recorded breeding outside a colony was discarded from other analyses.

Despite the study running for more than 20 years, it was not feasible to measure life time reproductive success for such long lived birds. As a proxy, the number of attempts and the numbers of chicks produced in the first 5 y and 10 y of breeding was recorded for each aged bird. Analyses were conducted for males and females separately and combined. Breeding success is calculated as number of fledglings produced out of total breeding attempts and alternatively as number of chicks produced in 5 and ten year periods. To assess the importance of experience, I controlled for age by aligning all the breeding records from first to last attempt and removing gaps from sabbatical years. I then measured breeding success for sequential breeding attempts and compared the averages for the first three attempts to the next three attempts and so on.. I used all breeding records from aged birds in the Wandering Albatross file to assess the age versus breeding success of the Marion Island colonies.

I analyzed the effect of age of first breeding on survival, restricting all birds to ten year post first-breeding histories. I then calculated the number of birds that were not observed for an interval greater than or equal to the cut-off point. Of the number that died I recorded how many years it happened post first breeding attempt and whether or not the first attempt was successful or failed.

To estimate male and female survival statistics for the aged histories being used, I ran a Cormack-Jolley-Seber model in MARK using the coded data history strings for each aged, individual (White and Burnham 1999). I ran 4 preset models which use AIC to calculate the best fit model. Models were straight forward binomial models using only 1 and 0 to estimate survival. To test for significance of the experience effect, I used data for birds that survived at least ten years of breeding. I compared their breeding success per attempt for the first five years to their breeding success in the second 5 years. To test for selection, I compared the breeding success of survivors in their first five years of breeding, to those birds that died within a ten year period. The effort hypothesis is difficult to test for as it must take into account foraging ecology.

Results

The effect of age on breeding success

The age effect on breeding success for Wandering Albatrosses on Marion Island has already been reported (Nel. et al. 2003). I present an updated version of this report which shows the same pattern with a larger sample size, longer history and split into sexes (Figure 3.1). The youngest birds did the worst; with males showing evidence of decreased breeding success with age (senescence) but this was not obvious in females.

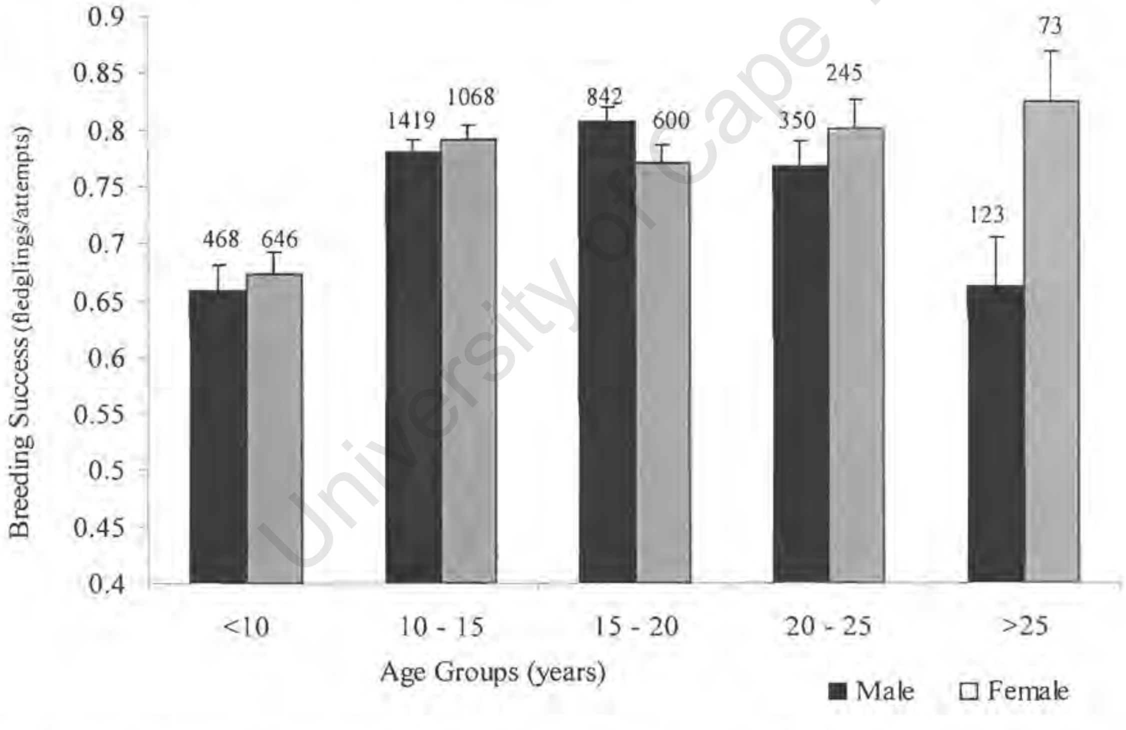

Figure 3.1. Breeding success (fledglings/attempts) measured for aged Wandering Albatross on Marion Island.

The return to colonies

Male and female albatrosses differed significantly in the age at which they return to colonies as pre-breeders and age of first breeding (Table 3.1). Females returned and bred at younger ages and spent a shorter time in the pre-breeding stage. Most females first bred at 9 years with 95% breeding by 12, whereas most males first bred in their tenth year with 95% breeding by 14 years of age (Figure 3.2). The youngest recorded breeding was for a 3 year old male that bred successfully at Sealer's Beach in 1996. There was a decrease in age of first breeding for cohorts fledged from 1980 until 1990 (Figure 3.3).

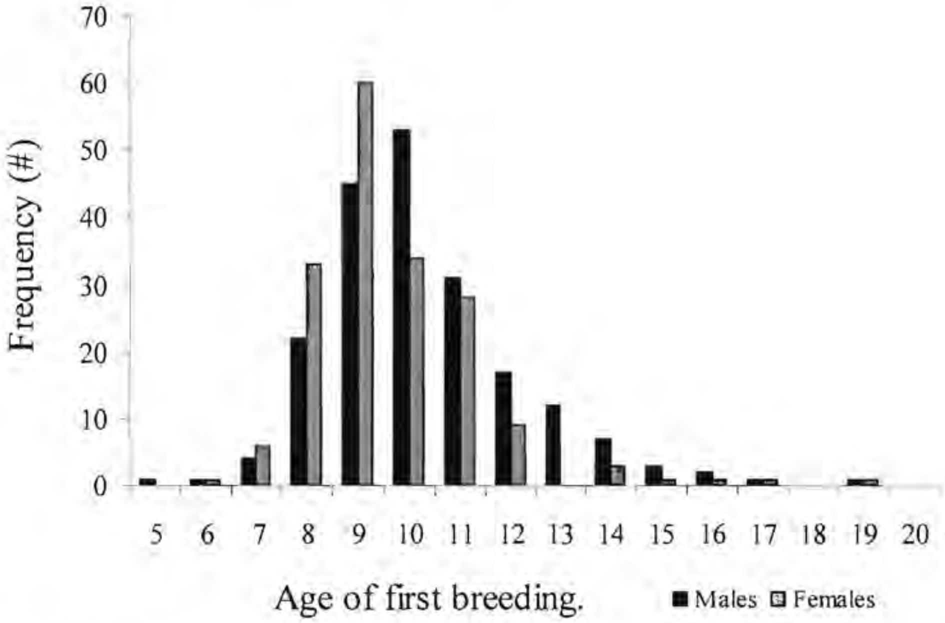

Figure 3.2. The age of first breeding for Wandering Albatrosses that fledged on Marion Island (1980-1988). Males are represented by black and females by grey bars.

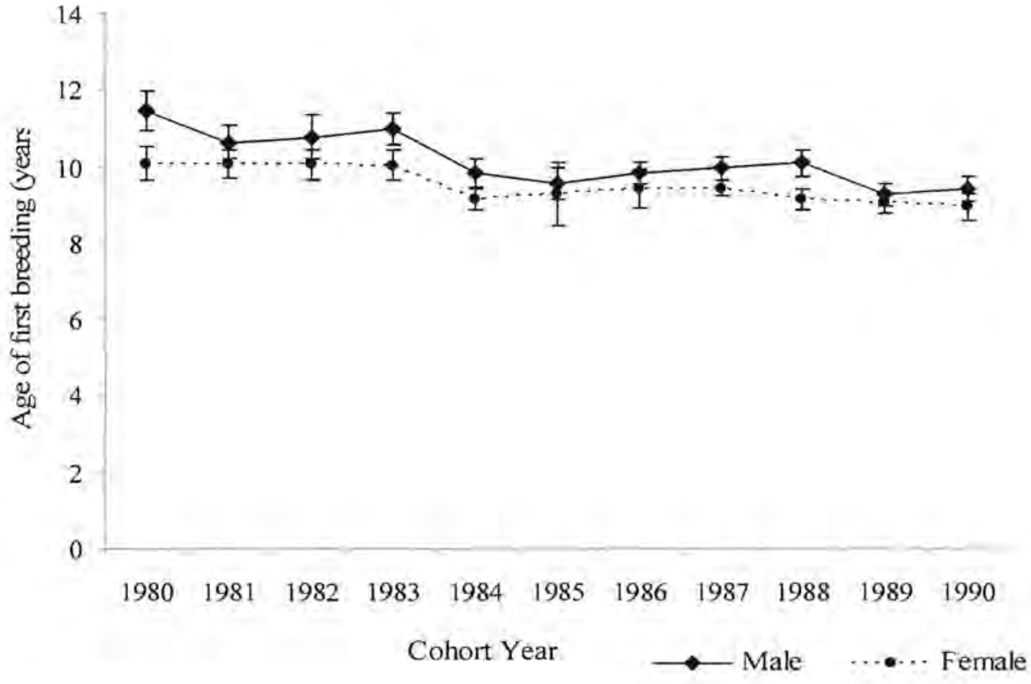

Figure 3.3. Age of first breeding for Wandering Albatross cohorts 1980-1990.

Table 3.1. Results for analysis of immature Wandering Albatrosses' return to colonies and onset of breeding for cohorts fledged between 1980 -1988 on Marion Island. [Years = yrs]

	Mean ± SD	**Mode**	**Range**	**Significance**
Age of first return:				
Males (n = 188)	6.28 ± 1.90 yrs	5 yrs	2 - 12 y	t = 2.63; P = 0.009
Females (n = 143)	5.74 ± 1.73 yrs	4 y	2 - 11 yrs	
Pre-breeding duration:				
Males (n = 143)	3.31± 1.74 yrs	3 yrs	1 - 11 yrs	t = 2.17; P = 0.031
Females (n = 125)	2.89 ± 1.35 yrs	2 yrs	1 - 9 yrs	
Age of first breeding:				
Males (n = 200)	10.31 ± 1.98 yrs	10 yrs	5 - 19 yrs	t = 3.42; P = 0.001
Females (n = 178)	9.64 ± 1.75 yrs	9 yrs	6 - 19 yrs	

Survival of Wandering Albatross in relation to age of first breeding

I had a sample size of 819 aged, sexed Wandering Albatrosses. For the investigation of the effects of age of first breeding, male to female ratio was 1:1 (411 males and 408 females). The best MARK model had survival probability being constant and recapture probablility being time dependent for both sexes,. For the aged individual breeder data, the MARK model produced adult survival rates of 92.5 ± 0.006 % for males, and 90.5 ± 0.007 % for females. Older males (>11 years) were 10% more likely to survive their first breeding attempt than those aged < 8 years (Figure 3.4). The males recruiting at ages younger than 8 years had the highest disappearance rates in the male category.. Female disappearance decreased with increasing age of first reproduction until 10 - 11 years but showed highest rates at ages older than 11 years. The timing of disappearance during breeding attempts proved that the first breeding year is the costliest in terms of survival. The lowest disappearance rate was in the second breeding year. This was due to only failed breeders from the first breeding year being present in year 2.

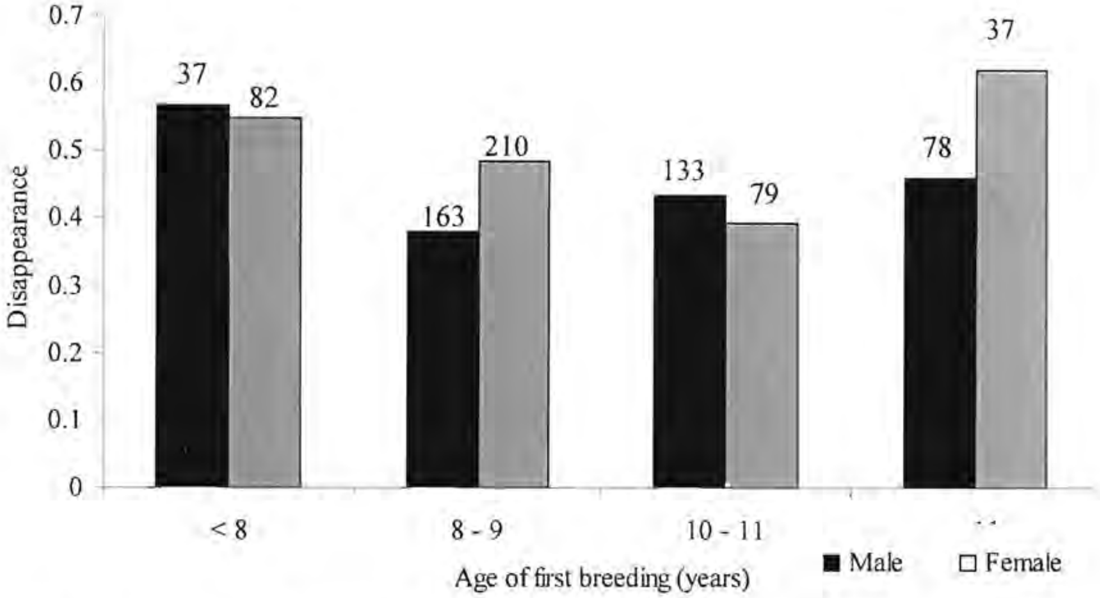

Figure 3.4. Disappearance within 5 y of the start of breeding as a function of age of first breeding for Wandering Albatross on Marion Island fledged (1980-1988).

Effect of age of first breeding on breeding success

The lowest breeding success, measured as average number of chicks produced in 5/10 year periods, occurred in the youngest age group (< 8 years old) for males and in the oldest age group for females (> 11 years).. The female success rate for the first breeding attempt increased with age of first breeding , peaking at ages older than 11 years (Figure 3.5). Males had their highest first time breeding success rates at ages older than 11 years. Highest first-time breeding success was recorded for the oldest recruits. The male sample of 411 birds produced a total of 1082 fledglings, failed 352 times and the 408 females produced 1021 fledglings and 330 failures. Thus, both sexes succeeded 75% of the time. For both sexes the number of chicks produced in the first 5 breeding years increased with increasing age of first breeding peaking at 11 years before dropping again (Figure 3.6). For the ten year breeding analysis of number of chicks produced according to age of first breeding these patterns were similar (Figure 3.7).

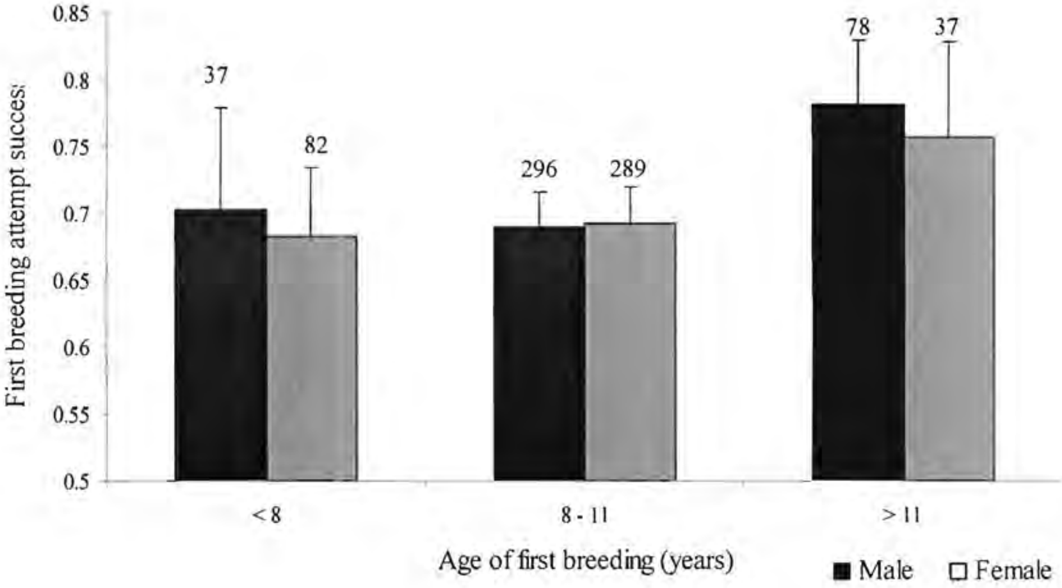

Figure 3.5. The effect of age of first breeding on the first time breeding success of Wandering Albatrosses.

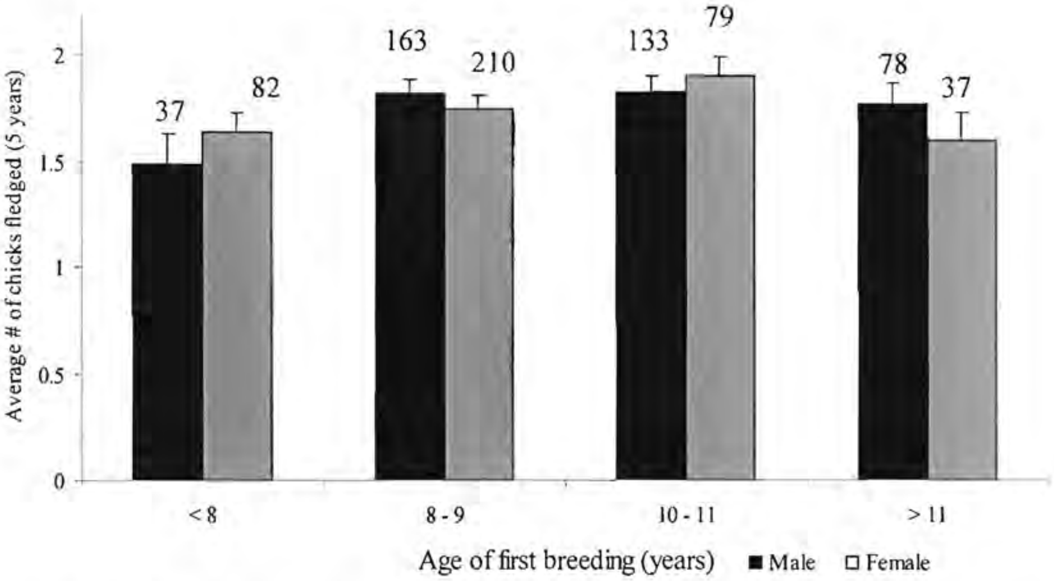

Figure 3.6. Chick production of Wandering Albatross during first 5 years of breeding in relation to age of first breeding.

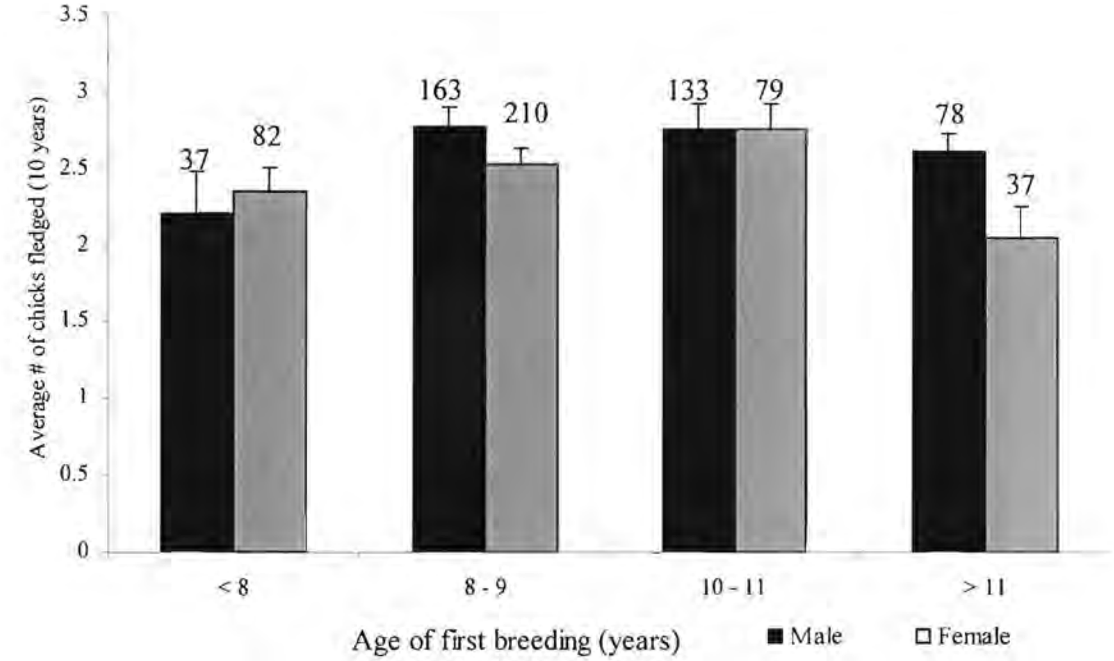

Figure 3.7. Number of chicks fledged by Wandering Albatross during first 10 years of breeding according to age of first breeding.

Effect of experience on breeding success

Contrary to expectations, breeding success showed little increase with initial experience (Figure 3.8). However, success decreased after 6 attempts, presumably as a result of an aging population. Breeding success was particularly low for the small sample of males surviving to make > 12 attempts.

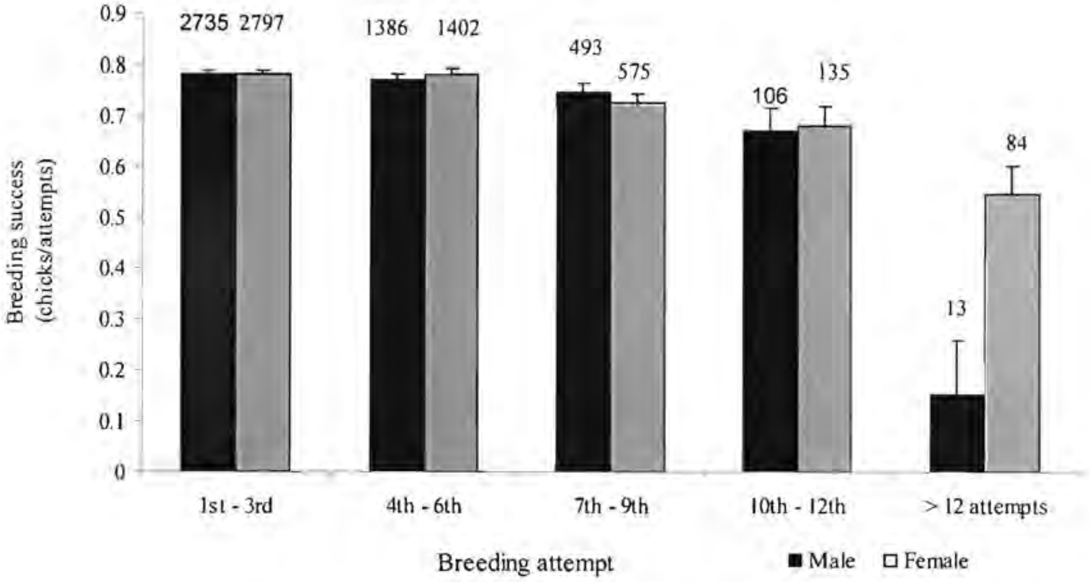

Figure 3.8. The effect of experience on the average breeding success of sexed Wandering Albatrosses on Marion Island.

Alternative tests for selection and experience hypotheses

Birds that disappeared within 5 years of breeding were compared to those that survived ten years of breeding. Among males, breeding success (fledglings/attempts) of birds that survived the first 5 years after recruiting (79.3%, n = 236) was appreciably greater that that of those that disappeared during this period (70.3%, n = 178). However, there was no difference between females (77.3%, n = 210 and 78.1%, n = 205, respectively). In both sexes there was a slight increase in breeding success in the last 5 years of breeding (females: 3.1%, males: 2.33%) either attributed to age or experience. It seems that there may be some selection pressure on males and greater effects of experience on females.

Discussion

The Wandering Albatross population at Marion Island has an average age of first breeding that was lower than that measured for populations at Crozet and South Georgia (Weimerskirch & Jouventin 1987, Weimerskirch et al. 1987, Croxall et al. 1990). On all three islands, females return to colonies at younger ages and breed significantly earlier than males, which could be a direct consequence of a male-biased population, but this remains to be demonstrated (Mills & Ryan 2005, Weimerskirch et al. 2005). On Possession Island, in the Crozéts, males outnumbered females 2.5:1 within the non-breeding population (Weimerskirch & Jouventin 1987). Females may attempt to breed earlier than males if they gain more from experience. Weimerskirch and Jouventin (1987) stated that the age of first breeding on Possession Island has decreased since 1973. The data for Marion also suggest a decrease in this parameter for both males and females since 1983, but the pattern is weak. Population trends on Marion Island suggest a population decrease during the 1980s and an increase in the 1990s. The drop in population size during the 1980s (see chapter 1) may explain why both sexes from the 1980-1990 cohorts bred earlier as this would allow immature birds into the effective population earlier through a decrease in intraspecific competition (Weimerskirch & Jouventin 1997). Males are less affected by long-lines, but competition during displaying, where males aggressively compete for females, should reduce the number of males breeding at younger ages (Tickell 2000, Nel et al. 2003). However, when choosing partners, females tend to select birds of similar age (Jouventin et al. 1999). It has been suggested that current Wandering Albatross populations are younger than those prior to 1960, but that no decrease in breeding success has occurred (Weimerskirch 1992). This would mean that there are more resources available for less-skilled birds to capture.

The 'selection' hypothesis states that as a cohort ages, lower quality individuals die off, resulting in a higher average quality of older cohorts (Cam and Monnat 2000). However, in our test of selection, the females that disappeared within five years of recruitment had similar breeding success in their first five years to birds that survived the same period. It seems the selection hypothesis does not explain the variation in female Wandering Albatrosses. Whether this is too crude a comparison and quality should be measured in terms of life-time reproductive success is debatable. Bradley et al. (1989) suggested that increased production at younger ages results in increased mortality at older ages. Perhaps these females that died increased their effort to reproduce. For many bird species, it has been suggested that success of females is affected more by experience than by age (Lequette and Weimerskirch 1990, Pyle et al. 1991). It has been shown that females lose weight at ages older than 20 y (Weimerskirch 1992). When I compared the breeding success of the first and second five years of breeding for females, there was an improvement, suggesting experience does improve breeding success. Thus, it seems that experience gained by females could prevent these losses in weight from affecting the outcomes of breeding attempts at older ages. The experience hypothesis also could explain why females are most successful at older ages. It may be that these high success rates are linked to increased experience rather than increased effort. To test for increased effort would likely require some form of foraging study and many scientists have outright dropped it as a potential explanation for increased success at older ages (Nur 1984).

As predicted, male Wandering Albatrosses exhibit different demographic responses to those of females. The breeding success of male birds that disappeared was almost 10% lower than birds that survived the first five years as adults, suggesting a 'selection' effect. The survivors performed better with time, also suggesting an 'experience' effect on breeding success. Males that bred at ages older than the mean (10 years) had survival and initial success rates as high as those that bred at 10 years. Although males may be limited by a shortage of suitable mates if the population is male-biased, the older first-time breeders may be constrained by the 'experience' hypothesis and required a longer time to achieve a threshold body condition to breed successfully (Weimerskirch 1992). The experience effect must even out within a few years of the initial breeding attempt, because success was similar for all ages over the ten year period.

Males that commenced breeding either very young (< 8 years) or very old (>11 years) were the least successful recruits on Marion Island. This is likely the effect of lack of experience and poor quality birds, respectively. Female mortality due to long-line fishing is higher than that of males due to their foraging habitat clashing with the waters used by long-line fishing vessels (Nel et al. 2002). In these accidental drowning and capture events, males can lose their female breeding partners and this has a severe impact on breeding success (Nel et al. 2003). Without bi-parental, care the chick typically dies, thus if the lost female was a breeder, her male partner will suffer from the failure in terms of current and future breeding success. Older, widowed males (>20 y) remained unmated for longer periods than older females (Jouventin et al. 1999) and this compounds the problem of mate loss for older, adult males. Even though older, widowed males have experience, they may not be seen as good mates as their life expectancy is lower, and young females tend to choose young males (Jouventin et al. 1999). Older females, however, would benefit from the sex skew with a greater number of older males to select.

In the first years of life an albatross must develop its foraging skills, and learn to fend for itself and achieve a threshold body condition capable of withstanding the costs of reproduction. Mortality is greatest in the first 4 years of life (Croxall et al. 1990). Once Wandering Albatrosses return to their colonies they must select a partner. On average, females display to 30% more potential mates than males, selecting the most favourable (Tickell 2000). The breeding behaviour of Wanderers shows that it is optimal to first breed at the age where success and survival are maximised, which is the mean age of first breeding for both sexes. For such long-lived birds, the rate of reproduction is slow, and survival high. Survival is the key factor in driving population growth for long-lived, slow reproducing organisms (Heppel et al. 2000). My research shows that delaying the onset of breeding to 10-11 years is the best strategy for maximising fitness. There is a cost in term of disappearance for those that breed at younger ages than the mean, and a cost in terms of less chick output for those that start later than the mean.

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SYNTHESIS

The Wandering Albatross is the largest pelagic seabirds on earth and has the longest wingspan of any bird (Weimerskirch et al. 1993, Weimerskirch et al. 1987, Tickell 2000). Its large size confers benefits including increased defence against predation and in predation success, a greater range of acceptable foods, increased success in mating and intra- and interspecific competition, extended longevity, increased intelligence (with increased brain size), survival through lean times and resistance to climatic variation and extremes (Hone and Benton 2005). However, large size also is associated with increased development time (both pre- and post-natal), increased requirement of food, lower fecundity (fewer offspring with a high parental investment in each offspring over many 'poorer' offspring), and, consequently, a reduced ability to adapt to sudden change (a longer generation time gives a slower rate of evolution) and thus increased susceptibility to extinction.

The actions of humans add a new element of mortality for seabirds, most commonly in the form of long-line fishing (Brothers 1991). Before the impact of man, populations of Wandering Albatross were larger (de la Mare and Kerry 1993). Wreck survivors, sealers and whalers would harvest eggs and cache albatrosses for food. The accidental drowning and capture of albatrosses by the long-line fishing industry has been linked to sharp drops in survival and is considered the biggest threat to long-term persistence of these birds (Mills and Ryan 2005, Brothers et al. 1998; Gales 1998; BirdLife International 2004). For instance, Wandering Albatrosses are accidentally drowned by long-line fishing because they forage in the same zones the boats and are attracted to the fishing vessels (Weimerskirch et al 1986, Weimerskirch et al 1993). This may well only have started in the last century but these inquisitive birds have been 'ship-followers' for centuries (Tickell 2000). Direct consequences of mortality by human action include decrease in population size and survival rates (Croxall & Gales 1998). If the victim is a breeder there is the additional loss of a breeding attempt (two mortalities!) and a disruption of the pair bond (Mills & Ryan 2005).

Wandering Albatrosses have evolved a breeding strategy that ensures their own survival is protected and that their chances of long-term reproductive output are increased. The reproductive strategies of delayed first breeding, higher investment in fewer offspring and post success 'sabbaticals' are characteristics of being at the slow extreme of the 'fast-slow' continuum (Read and Harvey 1989). Complex breeding cycles present great challenges to population analysis. This thesis tackled the problem of biennial mark-recapture modelling by using a new multi-state approach to the biennial breeding cycle thereby reducing bias in survival and encounter estimates (Kendall et al. 1997, Fujiwara and Caswell 2002). This is definitely a step in the right direction for modern analyses of complex breeding cycles.

This study took two different approaches to demographically analyse a long-lived bird population. Wandering Albatrosses should have upwards of 94% adult survival rates (Tickell 2000). My MSMR model for Marion Island presents a new challenge to other population studies as they show low survival estimates for the world's largest population of Wandering Albatrosses (Woehler et al. 2001). It is important to base other studies on a multi-state approach so that biases are eliminated and we can then compare populations from other islands. The MSMR model is highly demanding of data and this is a significant limitation if data are not great. I could not run the model with sex effects or with breeders that do not take sabbaticals after successful attempts. Also, the best fit model indicated constant survival, yet population trends show distinct trends at Marion Island (but less so in the colonies). The MSMR model was quite simple in the fact it does not take age or experience into account. At this stage this would complicate the model and increase the number of parameters to estimate, thereby increasing the deviance. The addition of covariates such as age, sex, experience, partnership duration, environmental change, stochastic disasters and fisheries effort would increase the power of MSMR modelling.

The results of the MSMR model are promising as transition projections of theoretical statistics such as recruitment rate and per capita chick production were similar to those calculated using the real data in chapter 1. The fact that both my work, and the multi-state model used on Marion Island Grey-headed Albatross *Thalassarche chrysostoma (Converse et al. in press),* both show significant bias in conventionally-estimated parameters, is reason to encourage further analyses.

Never before have we been able to estimate the Marion Island Wandering Albatross population breeding state distribution. This is quite an achievement only made possible by creating a model that estimates survival for unobservable states. The population on Marion Island is the largest, single island breeding Wandering Albatross colony but has suffered 20% reductions in size in the last three generations and its breeding population interacts with the fishing industry at several locations (Nel et al. 2003). My research estimates that a breeding population of around 3000 birds use the island for nesting grounds, which would mean that before the decrease the population would have been around 3750 breeding birds.

Descriptive analyses, such as chapter 3, can contribute further to increased complexity of models. There clearly is age, sex and experience related effects with regard to reproductive success. There are other factors such as mate loss, mate selection and pair experience which also affect individual performance. These should be addressed using the Marion Island data and further test hypotheses concerning evolutionary theory. The 5/10 breeding years rule of comparison may be useful in such studies and in others concerning long-lived birds as a proxy to life-time reproductive success.

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"I know the meaning of plagiarism and declare that all the work in this document, save for that which is properly acknowledged, is my own."

Appendices (from Chapter 2)

Appendix 1 A. Results for 4-state Wandering Albatross biennial adult life-cycle model fit. Models are ranked according to Δ AIC and their weights computed for M_A, the generalized average model. The Akaike weight represents the contribution of the model parameters to M_A parameter calculations. T = time variation, A = additive variation and C= constant constraints on parameters in order (σ β γ).

	Model	*Number of Parameters*	*Deviance*	*AIC*	*Δ AIC*	W_i	*Akaike Weight*	*Cumulative weight*
1	M4CCC	26	21027.494	21079.494	0.00	1	0.354047423	0.354
2	M4CCT	74	20932.780	21080.780	1.29	0.5259	0.186201769	0.540
3	M12CCC	27	21027.482	21081.482	1.99	0.3702	0.131076466	0.671
4	M8CCC	27	21027.482	21081.482	1.99	0.3702	0.131076466	0.802
5	M12CCT	75	20932.768	21082.768	3.27	0.1946	0.068912037	0.871
6	M8CCT	75	20932.768	21082.768	3.27	0.1946	0.068912037	0.940
7	M12TCC	59	20967.066	21085.066	5.57	0.0617	0.02183864	0.962
8	M12ACT	91	20903.317	21085.317	5.82	0.0544	0.019258083	0.981
9	M8TCC	61	20965.130	21087.130	7.64	0.022	0.007779802	0.989
10	M12ACC	43	21002.117	21088.117	8.62	0.0134	0.004750885	0.994
11	M4TCC	43	21003.263	21089.263	9.77	0.0076	0.002678698	0.997
12	M4TCT	91	20911.094	21093.094	13.60	0.0011	0.000394487	1.000
13	M12CTC	75	20962.847	21112.847	33.35	6E-08	2.02558E-08	1.000
14	M8TCC	75	20968.794	21118.794	39.30	3E-09	1.03587E-09	1.000
15	M8CTC1	75	20970.470	21120.470	40.98	1E-09	4.48002E-10	1.000
16	M4CTC2	74	20975.160	21123.160	43.67	3E-10	1.16734E-10	1.000
17	M7CCC	26	21161.070	21213.067	133.57	1E-29	3.5004E-30	1.000
18	M10CCC	26	21161.480	21213.475	133.98	8E-30	2.85445E-30	1.000
19	M9CCC	25	21173.990	21223.990	144.50	4E-32	1.48668E-32	1.000

	Model	*Number of Parameters*	*Deviance*	*AIC*	*Δ AIC*	*W_i*	*Akaike Weight*	*Cumulative weight*
20	M2CCC	25	21174.050	21224.050	144.56	4E-32	1.44275E-32	1.000
21	M5CCC	25	21174.650	21224.645	145.15	3E-32	1.07149E-32	1.000
22	M3CCC	25	21174.880	21224.882	145.39	3E-32	9.51751E-33	1.000
23	M1CCC	24	21191.210	21239.209	159.71	2E-35	7.36979E-36	1.000
24	M8ACC	44	21860.229	21948.229	868.73	2E-189	8.0498E-190	1.000
25	M8ACT	92	21765.671	21949.671	870.18	1E-189	3.9133E-190	1.000
26	M6CCC	26	23990.902	24042.902	2963.41	0	0	1.000

Appendix 1.B. Wandering Albatross survival probability estimates for weighted Average Model (M_A) for time period 1987-2005.

Year	σ_1	± (95% Confidence limit)	SE	σ_2	± (95% Confidence limit)	SE	σ_3	± (95% Confidence limit)	SE	σ_4	± (95% Confidence limit)	SE
1988	0.9266	0.0073	0.0037	0.9274	0.0075	0.0038	0.9275	0.0076	0.0039	0.9282	0.0078	0.004
1989	0.9271	0.0072	0.0037	0.9268	0.0076	0.0039	0.9279	0.0075	0.0038	0.9276	0.0079	0.004
1990	0.9287	0.0073	0.0037	0.9298	0.0076	0.0039	0.9274	0.0077	0.0039	0.9285	0.008	0.0041
1991	0.93	0.0072	0.0037	0.9299	0.0075	0.0038	0.9284	0.0079	0.004	0.9283	0.0081	0.0041
1992	0.9256	0.0079	0.004	0.9261	0.0081	0.0041	0.9267	0.0076	0.0039	0.9272	0.0079	0.004
1993	0.9308	0.0077	0.0039	0.9312	0.0081	0.0041	0.9295	0.0079	0.004	0.93	0.0083	0.0042
1994	0.9263	0.0076	0.0039	0.926	0.008	0.0041	0.9273	0.0076	0.0039	0.927	0.008	0.0041
1995	0.9264	0.0076	0.0039	0.9258	0.0082	0.0042	0.9299	0.0081	0.0041	0.9292	0.0084	0.0043
1996	0.9274	0.0071	0.0036	0.9276	0.0074	0.0038	0.9297	0.0081	0.0041	0.9299	0.0084	0.0043
1997	0.9289	0.0069	0.0035	0.9291	0.0072	0.0037	0.9289	0.0077	0.0039	0.9292	0.008	0.0041
1998	0.9298	0.0073	0.0037	0.93	0.0076	0.0039	0.9296	0.0079	0.004	0.9299	0.0082	0.0042
1999	0.9279	0.0071	0.0036	0.9285	0.0074	0.0038	0.9272	0.0077	0.0039	0.9278	0.0079	0.004
2000	0.9257	0.0081	0.0041	0.9257	0.0084	0.0043	0.9268	0.0079	0.004	0.9267	0.0082	0.0042
2001	0.9285	0.0071	0.0036	0.929	0.0074	0.0038	0.9299	0.0084	0.0043	0.9303	0.0088	0.0045
2002	0.9284	0.0071	0.0036	0.9283	0.0074	0.0038	0.9286	0.0077	0.0039	0.9285	0.008	0.0041
2003	0.9251	0.0087	0.0045	0.9254	0.0089	0.0046	0.9272	0.0077	0.0039	0.9275	0.008	0.0041
2004	0.9306	0.0081	0.0042	0.932	0.0087	0.0044	0.9267	0.0088	0.0045	0.9281	0.0089	0.0046
2005	0.932	0.0085	0.0043	0.9323	0.0088	0.0045	0.9279	0.0088	0.0045	0.9282	0.009	0.0046

Appendix 1.C. Breeding success probability for Marion Island Wandering Albatrosses from 1987-2005 data.

Year	γ_2	± (95% Confidence limit)	SE	γ_3	± (95% Confidence limit)	SE	γ_4	± (95% Confidence limit)	SE
1988	0.5785	0.0342	0.0175	0.6735	0.0489	0.025	0.7963	0.1433	0.0731
1989	0.5785	0.0342	0.0175	0.6735	0.0489	0.025	0.7963	0.1433	0.0731
1990	0.5846	0.035	0.0179	0.6878	0.0394	0.0201	0.7963	0.1433	0.0731
1991	0.5865	0.0359	0.0183	0.7168	0.038	0.0194	0.7963	0.1433	0.0731
1992	0.5504	0.045	0.0229	0.6886	0.0388	0.0198	0.7963	0.1433	0.0731
1993	0.5915	0.0368	0.0188	0.724	0.0415	0.0212	0.7963	0.1433	0.0731
1994	0.5946	0.0396	0.0202	0.6959	0.036	0.0184	0.7419	0.1603	0.0818
1995	0.5464	0.0483	0.0247	0.7047	0.0343	0.0175	0.6605	0.166	0.0847
1996	0.5883	0.0357	0.0182	0.6903	0.0379	0.0193	0.7089	0.1532	0.0782
1997	0.5631	0.0375	0.0191	0.7057	0.0345	0.0176	0.651	0.6418	0.3275
1998	0.5946	0.0384	0.0196	0.7224	0.0402	0.0205	0.5977	0.2474	0.1262
1999	0.5761	0.0329	0.0168	0.7243	0.0412	0.021	0.5312	0.2554	0.1303
2000	0.5706	0.0342	0.0174	0.6844	0.0407	0.0208	0.7174	0.1693	0.0864
2001	0.5996	0.0416	0.0212	0.7304	0.0453	0.0231	0.6516	0.1577	0.0805
2002	0.5356	0.0562	0.0287	0.6938	0.0363	0.0185	0.7963	0.1433	0.0731
2003	0.5779	0.033	0.0168	0.714	0.0361	0.0184	0.5456	0.1985	0.1013
2004	0.5551	0.0409	0.0209	0.6986	0.0358	0.0183	0.5731	0.2655	0.1355
2005	0.603	0.0462	0.0236	0.6887	0.0384	0.0196	0.6751	0.2408	0.1229

Appendix 1.D. Survival estimates from CJS MARK model with time-varying survival and recapture probability (1987-2005). The first and last two years have been removed due to biased estimation (Rothery and Prince 1990).

Year	Survival Estimate	Standard error	95% Confidence lower	95% Confidence upper
1989	0.888	0.023	0.834	0.926
1990	0.937	0.021	0.883	0.967
1990	0.968	0.022	0.882	0.992
1991	0.880	0.021	0.832	0.916
1992	0.971	0.020	0.895	0.992
1993	0.932	0.021	0.877	0.963
1994	0.914	0.021	0.863	0.947
1995	0.910	0.019	0.866	0.941
1996	0.956	0.018	0.903	0.980
1997	0.952	0.019	0.897	0.979
1998	0.919	0.020	0.870	0.950
1999	0.909	0.020	0.860	0.942
2000	0.936	0.020	0.884	0.966
2001	0.979	0.024	0.827	0.998
2002	0.998	0.033	0.000	1.000
2003	1.000	0.000	1.000	1.000
Average	0.941	0.036		