Individual variation in reproductive success in the Wandering Albatross

M Genevieve W Jones

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Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence
Zoology Department, Faculty of Science,
University of Cape Town

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Declaration

This thesis is the result of original research I conducted under the auspices of the Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence at the University of Cape Town. Assistance I received has been acknowledged. This work has not been submitted for a degree previously.

With great gratitude to the folk who, 3 decades ago, started the ball rolling for this thesis:

Mike and Mandy Jones
nurtured the brain that wrote it
and took me bird watching at a very young age.

John Cooper
nurtured the nature
and initiated long-term seabird monitoring at Marion Island.

Table of Content

Abstract

Long-term breeding monitoring of uniquely ringed Wandering Albatrosses *Diomedea exulans* at sub-Antarctic Marion Island shows that some individuals and pairs are highly productive whereas others seldom rear young. To conserve threatened species it is important to protect the productive individuals, and so I aimed to identify factors accounting for individual-level variation in long-term reproductive success. I examined current breeding characteristics that might explain past reproductive performance amongst experienced breeders.

Despite Marion Island being more than 1000 km farther north than South Georgia, breeding started 6 days later, possibly to limit the exposure of small chicks to severe weather conditions in autumn at the more southerly location. Molecular sexing found that more female (56%) than male chicks were raised over four years. Amongst experienced mothers, better condition (derived from mass-size indices) enabled production of male chicks, the more energetically demanding sex, in agreement with Trivers-Williard hypotheses. However, parents with good reproductive histories tended to produce females, the less costly sex.

Microsatellite paternity testing revealed that both male forced copulations and consensual female infidelity resulted in 14% - 24% of males being cuckolded. Despite a tendency for specific pairs to engage in either repeated extra-pair paternity (EPP) or repeated within-pair paternity, EPP was not used by females with poor reproductive pasts to increase their productivity. There were no clear genetic benefits from EPP; it may counter mate incompatibility due to low genetic diversity in the population and/or be an adaptive alternative to mate swapping, facilitated by the lack of discrimination against extra-pair young by cuckolded fathers.

Amongst all adults, age and experience had the greatest impact on breeding behaviours. Experienced parents, although in better condition, spent less time in the colony and with their partners prior to laying, indicating that experience enables greater efficiency in breeding. Egg size increased with maternal age and experience. Mature parents also provided greater chick protection and their chicks grew faster, confirming that breeding competency is an acquired skill. Birds arriving earlier and staying longer in the colony prior to laying were more likely to go on to breed. Birds in better condition arrived earlier and stayed longer than those in poor condition. Amongst experienced birds, males with successful histories spent more time ashore and successful females spent more time with their mates, suggesting a relationship between pre-laying behaviour and long-term reproductive success. Most characteristics investigated failed to distinguish experienced parents with productive and impoverished pasts, suggesting that there is little variation in breeding behaviours, possibly due to selection for successful breeding characteristics. However, variation between individuals in reproductive characteristics (e.g. egg size and parental care) supports the idea that individual variation drives differences in reproductive success. A cross-fostering experiment suggested that both parental behaviour and inherent characteristics control breeding success.

Acknowledgements

Peter Ryan's great enthusiasm is motivation even in the most exhausting field conditions. Thanks to him I started a thesis on a topic that I found all-absorbing and, thanks also to him, I have ended up wishing for more. Besides supervising the project, he provided funding for the research and my own income. His detailed comments and contributions on all chapters are evident. He liberally allowed me to manage the Marion Island project, giving me the opportunity to gain experience over and above that of writing a thesis. I have been repeatedly grateful for his prompt responses to emails and manuscripts. He has so often done far more than might be reasonably expected: to the point of popping over early in the morning and checking last minute alterations to a conference presentation or to meeting and discussing manuscripts when he really should have been enjoying a day off. I was lucky enough spend time at Marion Island with him and so must also say thanks for the added benefit of a supervisor 'on tap'. It has been wonderful to have the chance to learn from his unflagging dedication in the field and from his discerning management of island logistics.

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Quentin Hagens worked with me for a year at Marion Island (Marion 63 team). He is probably the most dedicated field worker I will ever meet. A master of many trades, he was a sounding board when methods were being developed. We had a tough schedule, but Quentin managed to fit in extra and carry all tasks through to completion without trading quality for the quantity. For this thesis I have used less than half the data we collected: a mark of his readiness to expend more energy and collect more data. The additional observation schedules he initiated made large sections of this thesis possible (and exciting).

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When located on a remote islands some small tasks may literally be impossible to do for oneself. Kith and kin, back in civilization literally did the impossible for me and also sent surprise boxes when I was working in the south. Paddy Kuun sent me pertinent literature (and other exciting goodies), Erika sent me tools (and treats), the Falkland folk sent me more literature (and woolly things) and Peter packed parcels of surprises too.

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Chapter 1

Introduction: Individual variation in reproductive success

1. The genesis of this thesis

I have been lucky enough to spend three years at Marion Island; South Africa's sub-Antarctic research station. During those three marvellous years I met many individuals: albatrosses, not people (only 15 or so humans have the privilege of overwintering there each year). I unthinkingly refer to albatrosses as 'people', a Freudian slip I ascribe to my familiarity with albatrosses' distinct personalities and very human antics. My fleeting feathered friendships were illuminating: I met personalities from the curious comics to the tetchy or awkwardly amiable. Identifying with the subject is frowned upon in many scientific circles yet appraisal of their individuality in disposition leads to the observation that even in the bird world, all are not equal. In my thesis I explore just one aspect of their individuality: reproduction. In the early 1980s, John Cooper (as the Antarctic Research Officer at the Percy FitzPatrick Institute) initiated monitoring of individually marked seabirds breeding at Marion Island. The studies on Wandering Albatrosses (*Diomedea exulans*) have continued unbroken and individuals' breeding histories reveal that some birds are particularly prolific breeders, while others are singularly unproductive.

Wandering Albatross tales: The prolific parents

Wandering Albatrosses are known to be long-lived and thought to be faithfully monogamous, taking several years to select a mate after an extended juvenile period spent at sea. Due to a protracted chick rearing period they are biennial breeders and biparental care is required to hatch their single-egg clutch and raise the chick (Tickell 1968, Croxall 1990, Weimerskirch 1992, Croxall *et al*. 1998, Tickell 2000, Nel *et al.* 2003). One female (I called Rhona) with an impressive breeding history produced 10 chicks in 18 years with the same mate. She even managed to rear two chicks in consecutive years at the start of her breeding career (remarkable, as they usually cannot produce more than one in two years; Croxall *et al*. 1998). She remained with the same mate until 2004, but after that he failed to return and has not been seen since. She did not breed for three breeding seasons and then she paired with a new male (Charlie; of moderate reproductive ability; successfully rearing 5 chicks from 7 breeding attempts in 12 years with a previous partner). Their egg was probably inviable as it was incubated well beyond the expected hatching period. They attempted to breed again the following year but Charlie failed to return after she laid the egg and has not been seen since. Rhona incubated that egg continuously for 43 days (more than half the incubation period) before abandoning the breeding attempt. She was back in the colony during the following year's pre-laying period and she laid an egg but abandoned it after 7 days. I had seen her copulate with a male from a neighbouring nest but as he remained within a pre-existing partnership she lacked a social mate to assist with the breeding attempt. After abandoning the egg she was subsequently seen consorting with single males. Rhona illustrates an individual with remarkable breeding persistence and ability and, despite the loss of her mate and possibly age driven lowered reproductive success (Lecomte *et al*. 2010) she continued to attempt to breed.

The good and the bad or merely the consistent and the persistent?

Another top performing pair bred together for 25 years (1984-2009), fledging 15 chicks (an exceptional 0.6 chicks per year). Another three chicks died prior to fledging. Remarkably for 'obligate' biennual breeders, the pair successfully reared two chicks in consecutive years and then, a few years later, successfully reared three fledglings in three years running, resulting in the high chick production rate despite the three losses. In contrast to these exceptional producers are those pairs that never or seldom rear chicks, such as one below par pair who attempted to breed every year since 1987 (21 times in 21 years) and managed to fledge only one chick, losing three others and 17 eggs. Daily observations of the pair in one season revealed that the male took an extended foraging trip and left the female to incubate for 49 consecutive days. When he finally returned he lost the egg within 10 days. The following season they lost their egg within three days of laying. Hopeless. Nevertheless, despite the energetic costs of such persistent behaviour the pair bond survives and they continue to attempt breeding.

Aim of the thesis

Long-term breeding data on Wandering Albatrosses makes them ideal organisms for investigating characteristics driving individual differences in their long-term reproductive success. Investigating reproductive success in this single-egg clutch species removes complications associated with multi-egg clutches (e.g. sibling interactions and differential parental investment in the offspring). Parent investment and reproductive success also may be compared in terms of characteristics of their single chick, rather than number of offspring, produced during a breeding season. Using individuals' historic breeding records and their current breeding behaviour, I seek to identify characteristics responsible for variations in reproductive success of individual Wandering Albatrosses at Marion Island. In chapter 2 I provide baseline information on breeding characteristics of Marion Island's population of Wandering Albatrosses. Chapter 3 deals with the influences that breeding phenology and body condition have on long-term reproductive success. In chapter 4 I look for genetic and behavioural characteristics that influence the occurrence of extra-pair paternity and determine whether females with poor reproductive histories use extra-pair behaviour to improve their reproductive output. I discuss the relationship between reproductive success and parental investment in terms of egg size in chapter 5. Chapter 6 describes offspring sex ratios and in chapter 7 I examine attributes that may drive the female-biased offspring sex ratio. Using a cross-fostering experiment between parents with successful and impoverished breeding histories I examine differences in chick care, development and fledging success (chapter 8) and finally in chapter 9 I conclude the thesis.

2. Individual variation and reproductive success

Fitness, defined as an individual's genotypic contribution to subsequent generations relative to that of other individuals (Newton 1989), may be measured in terms of lifetime reproductive success (LRS). LRS is the number of offspring reared or, more germanely in terms of gene pool contribution, the number of offspring produced that survive to breed (Newton 1989). LRS is an approximation of biological fitness yet its evolutionary consequences should be related to its influence on increases of specific genotypes or phenotypes in future populations (Murray 1992). Within species, individual LRS varies considerably, even amongst socially monogamous, long-lived species, such as seabirds (Clutton-Brock 1988, Newton 1989, Moreno 2003). Relatively few breeding individuals produce a 'disproportionate number of the next generation' in many bird species (Cobley *et al.* 1998, Moreno 2003). For example, the 'top' 10% of breeding Barnacle Geese (*Branta leucopsis*) produce 34% - 39% of the young and 15% of breeders produce half of the next generation's recruits (Owen and Black 1989). In Short-tailed Shearwaters (*Puffinus tenuirostris*) the number of young produced increases with lifespan. However, only 14% of fledged young produced returned to breed (Serventy and Curry 1984, Bradley *et al.* 1991). Furthermore, of individuals that produce young, fully 71% had no offspring recruit to the breeding population (Wooller *et al.* 1989). Exploring factors linked to differences in LRS comes with difficulties since individuals must die before LRS can be estimated. One could obtain behavioural information during the study organism's lifetime, but waiting until they die may be impractical, particularly in long-lived species. Using individuals' averaged production prior to current breeding as a proxy for LRS is often the more pragmatic approach.

Life history characteristics should be taken into account when considering an organism's long-term reproductive success. Insects produce vast numbers of offspring in very short lives whereas long-lived species may produce few young that often require extensive parental care (Clutton-Brock 1988, Stearns 1992). Most males in polygynous species never get the chance to mate, but the few that do breed sire many more young than the females they mate (Krebs and Davies 1993). In monogamous birds the lifetime reproductive success of paired birds are more equal (Clutton-Brock 1988), although extra-pair fertilisations and sex-biased mortality may skew reproductive success of the two sexes.

High adult survival and longevity are often associated with increased reproductive success (e.g. Bérubé *et al*. 1999). Breeding competence increases with experience and so reproductive success may increase with experience and age until senescence reduces reproductive productivity (Nol and Smith 1987, Newton 1989, Lunn *et al*. 1994). Individuals beginning to breed at a very young age have potential to differentially increase reproductive success as a result of increased reproductive lifetime (Wooller *et al*. 1989). However, early breeding or high reproductive effort in initial breeding attempts may reduce adult survival resulting in reduced productivity later in life and potentially lower their long-term reproductive success (Nol and Smith 1987, Stearns 1992, Møller *et al*. 2005).

Besides genetic (heterozygosity or immunocompetence) and phenotypic (morphology, body condition) characteristics, environmental factors should be considered when assessing individuals' reproductive success. Stochastic events may prevent good breeders from realising their reproductive potential and in years of plentiful food supply even poor breeders may do well (although the effect of annual variability on lifetime reproductive success is likely to be less marked in long-lived species; Newton 1989).

Newton (1989) distinguished three classes of individuals in terms of LRS: individuals that die before attempting to breed, those that attempt to breed, but fail to raise young and those which raise young. Within this final group, there is a continuum of individuals from those that produce very few young to those that are highly successful. Based on a 75% success rate (Nel *et al.* 2003) and the Marion Island annual average of 1850 breeding pairs (i.e. 1850 eggs per year; Ryan *et al.* 2009), approximately 1390 chicks fledge each year. Since only one third of the fledged young survive to breed (Nel *et al.* 2003), the LRS of the other 67% is zero. In this thesis I look at current breeding behaviour to explain historical breeding performance in the sexually mature sector of the population, including those breeding individuals that fail to rear any young, through to those that are highly productive.

As I collected data from individuals that had not completed their breeding careers I could not use LRS as a measure of fitness. Instead, following Cobley *et al.* (1998), fitness of experienced breeders was measured in terms of reproductive success (offspring fledged) prior to their current breeding attempts. However, this approach requires consideration of age and breeding experience biases. Individual characteristics affect each breeding event differently, for example, some inexperienced breeders are less successful than experienced breeders (Weimerskirch 1992). Within a species costs of reproduction may reduce survival of poorer breeders, leaving better breeders in the older age groups (Stearns 1992). Alternatively, older individuals may have survived merely because they invested less effort in their early breeding attempts than those that died younger (Møller *et al*. 2005). Should poorer breeders die early, one might expect an increase in average breeding success in older age classes. However, this is complicated by senescent effects in Wandering Albatrosses associated with a decline in breeding success in birds older than 30 years (Lecomte *et al*. 2010). Yet, individuals maintain their 'quality' (encompassing reproductive ability) throughout their lives (Croxall *et al.* 1992). Thus, if age and experience are taken in to account, their reproductive abilities should be comparable through their lives. A key step in the study is to demonstrate that success of current breeding events positively correlate with long-term reproductive success and thereby confirm that 'quality' is maintained. (The word 'quality' has been used to mean reproductive ability, likened to fitness and such characteristics as egg size or content, body condition and breeding behaviours (Moreno 2003, Lewis *et al*. 2006, Silva *et al*. 2007, Lescroël *et al*. 2009). As a means of describing individuals it is convenient but ambiguous (Moreno 2003) and, owing to its usage for an array of characteristics, is fraught with confusion. So, while one might expect it to appear in a thesis of this theme, I will tend to avoid it unless referring to texts in which it is used.)

It would be ideal to use number of offspring recruited into the breeding population rather than offspring fledged to determine fitness in terms of previous reproductive success. However, Wandering Albatrosses start breeding at an average of 9 to 10 years so most offspring of currently breeding pairs will not have had enough time to return and breed. Furthermore, this approach is impeded by low sample sizes of recruited offspring and uncertainty about fate of offspring as some recruited offspring may not be detected. Consequently using numbers of chicks fledged was deemed more appropriate.

3. Quantitative evidence that Wandering Albatrosses vary in reproductive success

Each chapter is written as a stand-alone paper, which results in some inevitable recurrence of data. Where reasonable, I cross reference between chapters to reduce the repetition. Because the thesis and most chapters hinge on an assessment of characteristics in terms of individuals breeding experience and reproductive productivity I describe the long-term data collection and methods used to determine individual productivity here.

History of research on albatrosses at Marion Island

The Prince Edward Islands support the largest Wandering Albatross population (44%; Ryan *et al*. 2009) of any island group (Brooke 2004). However, most of the species descriptions come from smaller and distant population making it important to describe breeding characteristics for the studied population (chapter 2). The first, anecdotal, information on Wandering Albatrosses at Marion Island (46º52'S, 37º41'E) may be gleaned from records of sealers and explorers prior to the annexation of the island in 1947. Thereafter members of meteorological teams published some observations (Cooper and Brown 1990), and dedicated research on seabirds started in 1951 (Rand 1954, Brown and Oatley 1982). The project is based upon breeding records of individually marked birds going back approximately 25 years at three Wandering Albatross colonies at Marion Island. Most albatrosses nest repeatedly at the same locality, which, together with bird ringing and ease of recording the survival of their offspring, makes following individual's breeding lifetime relatively simple. Long-term monitoring of individuals' breeding success gives their breeding experience and numbers of chicks that individuals fledged. It also provides data regarding pair fidelity and numbers of mates with whom individuals have previously bred, pedigree information and age for those individuals ringed as chicks.

Determining previous reproductive experience and success from historic monitoring data

To establish comparative long-term reproductive success for individuals I required a sample of birds that had been breeding for a number of years or had made numerous breeding attempts. For this reason I distinguished breeders with no or limited experience from those with extensive breeding experience (Lequette and Weimerskirch 1990, Weimerskirch 1992, Berrow *et al*. 2000). Birds breeding together for the first time were considered 'new pairs'. 'New pairs' include those in which both individuals have never bred before ('naïve' individuals) but also comprise combinations of first time breeders or birds with varying degrees of prior breeding experience from previous pair bonds (widowed or 'divorced' individuals). Birds with prior breeding experience were subdivided into those with limited experience and those with more extensive experience. Birds with at least four previous breeding attempts or eight years since first breeding were considered 'experienced' breeders and partnerships persisting for this time 'experienced' pairs. Individuals and pairs with one to three breeding attempts and less than eight years since their first breeding attempt were considered to have limited breeding experience. Some birds were breeding when long-term monitoring was initiated and might have higher productivity rates than individuals recruited later merely because their early breeding attempts, when success is lower, cannot be included in the analysis. Yet the majority (approximately 83% of females and 81% of males) were recruited three or more years after the study began. During the study, 62% of females and 60% of males were known age birds. Experienced female's average age was 20.4 years (n=199, range 13-32), and male's average age was 21.3 years (n=209, range 13-33). Average age may be biased against old birds, since some birds may have hatched before chick banding began. However, there was also no difference in historic reproductive success between known aged and unknown aged birds (generalised estimating equation for males: W=1.82, p=0.180; females: W=2.48 p=0.120).

The study ran over four breeding seasons so some birds bred two or three times during the study. Birds breeding for the first time would move to the limited experience category in their the following breeding attempt, and some birds with limited experience would graduate into the experienced category. Each bird's breeding event was analysed as a separate sample. Thus, birds' ages and experience during a specific breeding season were analysed in relation to behaviours specific to the breeding attempt of that attempts year. However, this meant that I had to account for repeat sampling of individuals in analyses. Thus a mixed model approach was necessary (usually a generalised estimating equation, GEE) in which birds or individuals were treated as a random effect (Zuur *et al.* 2009), thereby allowing for annual changes in parental characteristics.

Previous reproductive success, calculated for only experienced individuals and pairs, is the number of offspring fledged per number of years individuals had been breeding or for the duration of the relationship in the case of pairs' previous reproductive success. So that I could compare categories of previous reproductive success, each year's sample of experienced breeders was roughly divided into thirds. 'Good' pairs (33.5% of experienced pairs), the category with the highest average reproductive success produced chicks at a rate of ≥0.450 per annum (Figure 1.1). At the opposite end of the scale, the category of 'poor' pairs (32% of experienced pairs) produced ≤0.375 chicks per annum (Figure 1.1). 'Moderate' pairs (34.5% of experienced pairs) fell between these two groups (Figure 1.1). The same rates were then used to establish categories for male (good=19%, moderate=31%, poor=50%) and female (good=27%, moderate=35%, poor=37%) parents.

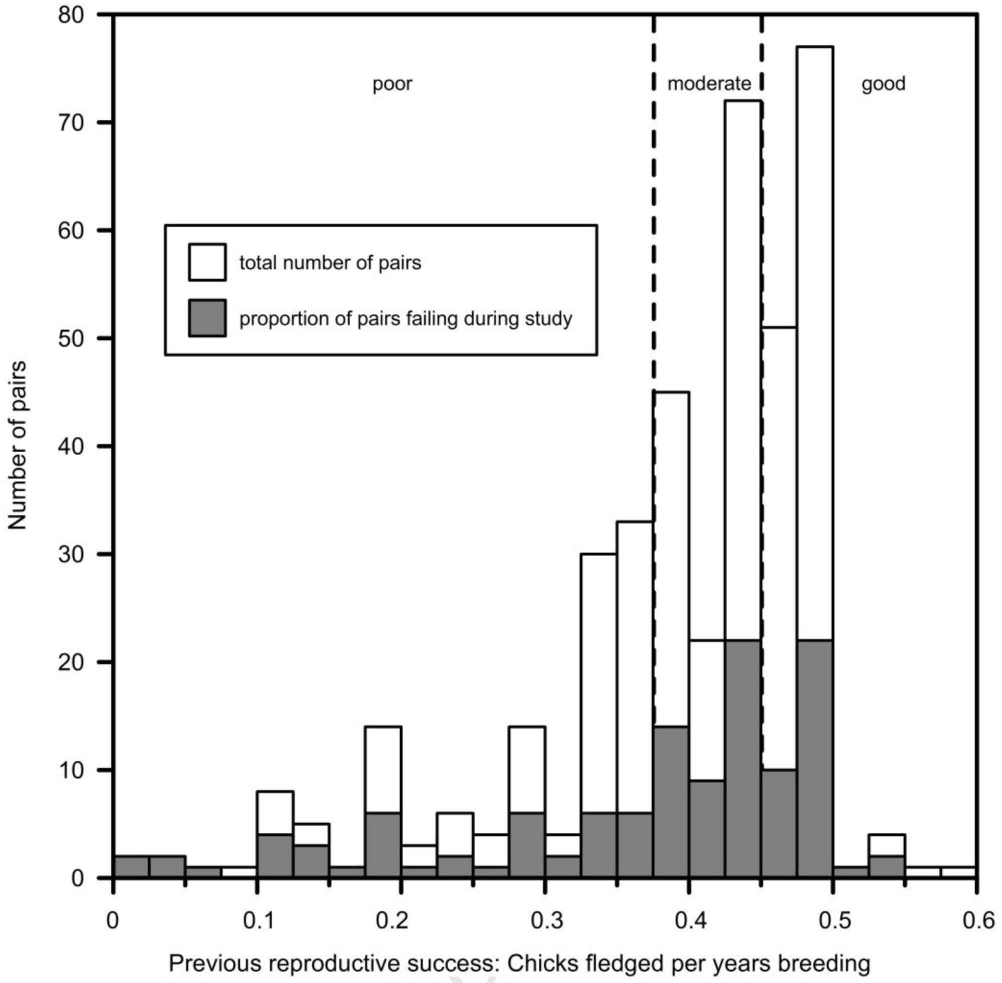

Figure 1.1 Good pairs produced ≥0.450 chicks per annum and only 26% of these pairs failed at breeding during the studied years (illustrated by shaded proportion). The third of pairs producing ≤0.375 chicks per annum are poor breeders and 34% of these pairs failed to fledge chicks during the study. Between these good and poor pairs, are those with moderate reproductive pasts of which 32% failed to fledge offspring when breeding during the study.

Success or failure of breeding attempts during the studied years significantly correlated with the previous reproductive success of pairs, males and females (GEE for pairs: W=11.4, p<0.001; males: W=6.4, p=0.011; females: W=5.35, p=0.021). Pairs with high previous reproductive success raised chicks from 74% of the 135 eggs laid whereas pairs of poor previous reproductive success reared chicks from 66% of the 128 eggs laid. Overall ‘Moderate’ pairs raised fewer chicks than ‘good’ pairs but more than ‘poor’ pairs but there was considerable variation between years (Table 1.1). There was no significant difference in the success rate of birds with different levels of breeding experience (chapter 3). Overall, new pairs fledged fewer chicks compared to pairs with prior breeding experience but these patterns varied from year to year (Table 1.1).

Table 1.1 Success of breeding attempts during studied years and number of eggs laid (n) by pairs with different levels of breeding experience and past reproductive success at three study colonies at Marion Island from 2006 to 2009.

	2006	2007	2008	2009	overall
all pairs	77%, n=199[a]	72%, n=258[a]	63%, n=253[a]	62%, n=271[a]	68%, n=981[a]
new pairs	81%, n=52	63%, n=56	52%, n=58	50%, n=44	61%, n=210
limited experience	82%, n=67	78%, n=88	76%, n=98	66%, n=105	72%, n=358
experienced pairs	73%, n=77	74%, n=112	67%, n=95[b]	64%, n=119	69%, n=403
good pairs	68%, n=28	81%, n=37	72%, n=32	74%, n=38	74%, n=135
moderate pairs	92%, n=26	68%, n=37	63%, n=38	55%, n=38	68%, n=139
poor pairs	57%, n=23	74%, n=38	71%, n=24	63%, n=43	66%, n=128

[a] Breeding experience of 3, 2, 2 and 3 pairs in the four respective years was unknown.

[b] Past reproductive success was not determined for one experienced pair because their breeding history was incomplete.

4. The importance of investigating variation in reproductive success in albatrosses

How understanding factors driving differential reproductive ability will benefit albatrosses

Models used for developing conservation protocols that are based on factors driving population trends could produce inaccurate predictions if those factors are incompletely understood (Connor and White 1999, Goss-Custard and Stillman 2008). For example, using an average estimate for LRS does not take into account that some individuals produce the majority of the next generation. These, in turn, may result in inadequate conservation protocols. In species characterised by low productivity, small reductions in survival and reproductive rates may have proportionally greater affects on demography than species of the other extreme (Connor and White 1999, Wendeln and Becker 1999). Understanding individual variation in reproductive success and the degree to which environmental, genetic and behavioural factors drive reproductive success will ensure that typically limited conservation resources are directed towards individuals responsible for a species' continued existence and evolution (*e.g.* through selective breeding programmes or conserving resources used by more successful individuals; Festa-Bianchet and Apollonio 2003, Lewis *et al.* 2006).

Although a fair amount is known about albatross behaviour, demography and ecology, little information is available about the factors influencing individual variation in characteristics such as survival and LRS (e.g. Tickell 1968, Croxall 1990, Croxall *et al*. 1990, Nel *et al*. 2003, Burg and Croxall 2006). Albatrosses are prime examples of species in which small increases in mortality affecting those individuals producing the greater proportion of the next generation, would greatly impact the species continued existence (Wendeln and Becker 1999, Tickell 2000). Most albatrosses are listed as threatened (BirdLife International 2011) owing to their small numbers, localised breeding areas and population decreases (Croxall and Gales 1998, Wanless *et al*. 2009). They are faced with a variety of threats, including exploitation, direct and indirect fishery-induced mortality (Weimerskirch *et al.* 1997, Nel *et al.* 2002a and b, Nel *et al.* 2003), breeding site disturbance, alien mammal predation (e.g. mice, rats and cats), loss of breeding sites (Higham 1999, Waugh *et al.* 2000, Wanless *et al.* 2007, 2009) and pollution (Cooper and Brown 1990). Despite receiving much publicity, resources for albatross conservation are limited and knowing which individuals contribute most to future generations will assist in channelling resources towards conserving productive individuals. Overall reproductive success will be influenced by a blend of individuals' innate, genetic, phenotypic and learnt characteristics. These characteristics might include foraging patterns (and then body condition), breeding phenology, pair synergistic effects (complementary behaviour between partners such as incubation and chick brooding shifts), parental ability (e.g. investment in incubation and provisioning rates) and mating strategies (e.g. extra-pair paternity skews males' reproductive success; Newton 1989; Perrins and Birkhead 1983).

5. Overview of the thesis

Body condition influences the decision to breed, breeding behaviours and also breeding success in Procellariiformes (Weimerskirch 1992, Chastel *et al.* 1995). Long-term studies show impacts of individual body mass on LRS (Mills 1989) making it an important factor to examine in relation to individual variation in reproductive success in Wandering Albatrosses. Some seabird studies indicate that more productive birds arrive at the breeding colonies earlier, lay earlier and share shorter incubation shifts (e.g. Cobley *et al.* 1998, Lewis *et al.* 2006). Breeding timing varies with experience and age in Wandering Albatrosses (Weimerskirch 1992). Breeding phenology (arrival date at the breeding colony, laying and hatching dates and incubation shifts) may also correlate with Wandering Albatross breeding success. In chapter 2 I describe average breeding phenology for the Marion Island Wandering Albatrosses. In chapter 3 I assess the influences of pre-breeding arrival, presence and body condition on the decision to breed and test whether differences in historic reproductive success of Wandering Albatrosses are related to individual differences in breeding phenology, body condition and pair co-ordination.

The potential of individual mating strategies to affect variation in LRS may be higher than current philosophy of albatross monogamy leads us to expect. Selecting a good quality mate is of particular relevance in albatrosses because rearing young demands the co-ordinated effort of both parents and divorce is reproductively costly (Jouventin *et al*. 1999, Mills and Ryan 2005). The long period over which mates are selected may be a reflection on evolutionary adaptive behaviour that ensures future reproductive success through current mate selection. Yet monogamous strategies may also bind individuals in barren partnerships or reduce the genetic diversity of their young. Recent genetic studies have shown varying levels of cuckoldry in some albatrosses (Huyvaert *et al*. 2000, Abbott *et al.* 2006, Burg and Croxall 2006, Huyvaert *et al.* 2006, Jouventin *et al*. 2007). Wrongly assigned parentage could inflate estimates of males' LRS. In chapter 4 I establish rates of extra-pair paternity amongst Marion Island's Wandering Albatrosses. I then determine whether females trapped in pairs with a history of poor reproductive success attempt to improve their fitness through extra-pair behaviour and whether producing extra-pair offspring has genetic benefits.

Parental investment may be evaluated at the egg stage. Studies show that investment in the egg influences survival and development of chicks (Williams 1994). Wandering Albatross egg size is influenced by environmental conditions but largely varies with maternal age and varied more between individuals than within individuals (Croxall *et al*. 1992). While egg size is often assumed to be a measure of parental ‘quality’ it has seldom been tested if egg size relates to fitness in terms of long-term reproductive success (e.g. Croxall *et el*. 1992, González-Solis *et al*. 2004, Silva *et al*. 2007 but see Cobley *et al*. 1998). Chapter 5 evaluates the relationship between long-term reproductive success and investment in terms of egg size, considering impacts of incubation length and parental characteristics (e.g. body condition, age and experience).

Trivers and Willard (1973) predicted that parents should adjust production of sons and daughters to benefit their fitness when conditions (both environmental and of the parents) differentially benefit one sex. In sexually dimorphic species, offspring of the larger sex may require greater provisioning effort (Weimerskirch *et al*. 2000) and parents in poorer condition may only succeed in rearing the smaller, less energetically costly offspring. Producing females may be beneficial in Wandering Albatrosses in which there is an apparent male bias in the breeding population (possibly as a result of female biased fishery mortality; Weimerskirch and Jouventin 1987, Croxall and Prince 1990, Weimerskirch *et al.* 2005). In chapter 6 I establish adult and offspring sex ratios for the Marion Island Wandering Albatross population. This provides baseline data for chapter 7, in which I discuss affects of parental reproductive ability and phenotypic characteristics, particularly body condition, on sex allocation.

Developmental conditions affect juvenile survival beyond the fledging stage and have repercussions on individuals’ physical condition and behavioural traits during their adult life (Newton 1989, Gebhardt-Henrich and Richner 1998). Developmental conditions are influenced by environmental conditions interacting with offspring genetic composition and parental investment behaviours, such as offspring protection and provisioning. Parents differ in their ability to provision their young. Amongst Wandering Albatrosses, parenting skills (affecting chick development) vary with experience and age (Lequette and Weimerskirch 1990, Croxall *et al*. 1992) but are also likely to vary between good and poor breeders (Cobley *et al*. 1998). Chapter 8 deals with chick development (growth rates) and parent investment behaviours in terms of chick protection in relation to parent reproductive ability. I made use of a cross fostering manipulation to tease out differences between parent behaviours and offspring genotypes on reproductive success. The cross fostering experiment complicated analyses because the manipulation had potential to influence reproductive success and offspring-parent interactions. I tested for an affect of the experiment and removed samples that might influence results in the relevant chapters. Chapter 9 concludes the thesis with a synopsis of the key findings.

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Chapter 2

Wandering Albatross breeding phenology at Marion Island

Abstract

The Prince Edward Islands support a large proportion (44%) of the Wandering Albatross (*Diomedea exulans*) breeding population yet most baseline breeding phenology data are derived from smaller and geographically distant populations. Although there was great overlap in breeding timing, male arrival at the colony, laying and hatching dates were, on average, later at Marion Island compared to the South Georgian birds. Earlier hatching chicks were more likely to survive, but timing of egg laying and incubation periods did not influence fledging success. Earlier breeding at South Georgia may ensure that chicks have time to grow sufficiently to survive the winter conditions that set in earlier at the more southerly South Georgian population. Parents' pre-laying arrival and presence at the colony did not affect the outcome of breeding attempts, suggesting that timing of breeding, rather than pre-laying timing and behaviour, influences breeding success.

Key words

hatching date, incubation, laying date, pre-laying presence

Introduction

The great albatrosses or gonys, *Diomedea*, are the largest Procellariiformes and comprise the wandering albatross complex and two royal albatrosses. The taxonomy of wandering albatrosses has been revised a number of times (e.g. Robertson and Nunn 1998, Burg and Croxall 2004) and currently four species are recognised: Wandering Albatross, *Diomedea exulans*; Antipodean Albatross, *D. antipodensis*; Amsterdam Albatross, *D. amsterdamensis* and Tristan Albatross, *D. dabbenena* (Brooke 2004). Wandering Albatrosses breed at the Prince Edward Islands, South Georgia, Crozet Islands, Kerguelen Islands and Macquarie Island amounting to some 8200 breeding pairs per year (Brooke 2004). The Prince Edward Islands, support roughly 44% (3650 breeding pairs) of the global breeding population (Ryan *et al*. 2009) and the data for this thesis were collected on the larger of the two islands, Marion.

Albatrosses are generally long-lived, have delayed maturity (spending their juvenile years at sea), are socially monogamous and have low reproductive rates (Croxall 1990, Tickell 2000). Wandering Albatrosses return to the breeding colonies at an average of five to seven years, and may take several years to select a mate, exhibiting extreme social fidelity (at Marion Island, some pair bonds have lasted at least 30 years; Percy FitzPatrick Institute unpublished data). Males and females first breed at an average of 10.4 and 10.7 years, respectively (Croxall *et al*. 1998), although Nel *et al*. (2003) report that those at Marion Island breed for the first time at an average of 10.2 and 9.6 years respectively. The oldest Wandering Albatross resighted at the Prince Edward Islands was a male, ringed (as an adult) 41 years previously and estimated to be at least 46-51 years old (Cooper *et al.* 2003). Weimerskirch and Wilson (2000) report an individual of more than 50 years old from the Crozet Islands and a closely related Northern Royal Albatross (*D. epomophora*) has been recorded breeding when at least 61 years (Robertson 1993). As with all Procellariiformes, Wandering Albatrosses lay single-egg clutches and chick rearing requires biparental care. Including the pre-laying courtship or pair bond reformation, nest building and copulation period (from mid-November to mid-December), the Wandering Albatross breeding season lasts for more than 1 year and the majority of young fledge in the following December (Tickell 1968). Wandering Albatrosses usually breed biennially, although many pairs breed in years following early breeding failures (Tickell 1968, Croxall 1990).

Although breeding biology averages are available for Wandering Albatrosses much of the data comes from the South Georgian population (e.g. Tickell 1968, Croxall 1990, Tickell 2000, Brooke 2004 but see Paulian 1953, Fressanges du Bost and Segonzac 1976, Weimerskirch 1992, Weimerskirch and Jouventin 1998, Nel *et al*. 2003). The species is philopatric and since some populations are located at different latitudes and are known to forage in different areas (Inchausti and Weimerskirch 2002, Charmantier *et al*. 2011), the Marion Island population may show differences in breeding phenology (the timing of life-cycle events; Visser *et al*. 2010) and demography. Breeding timing, which influences reproductive success (Perrins and Birkhead 1983, Visser *et al*. 2010), may vary as a result of genetic characteristics allowing for plasticity in expression of phenotypic characteristics (Stearns 1989). It is also influenced by individual's interactions with external factors, particularly environmental conditions such as climate or food availability (e.g. Charmantier *et al*. 2008, Moe *et al*. 2009). In this chapter I present breeding phenology of the Wandering Albatrosses at Marion Island and then discuss differences between the Marion Island and other populations.

Methods

Routine monitoring of Wandering Albatrosses at colonies at Marion Island

The fieldwork component of this thesis was conducted at three study colonies (Macaroni Bay, Sealer's Beach and Goney Plain; Figure 2.1) at Marion Island over five years (2006-2010), covering four successive cohorts of Wandering Albatrosses. However the project is founded on data that have been collected annually since 1984 at Sealer's Beach and Macaroni Bay and since 1987 at Goney Plain study colonies (Gartshore *et al.* 1988). During laying (mid-December to mid-January) nests are checked approximately every 5 days to detect all breeding attempts. Nests with incubating parents are numbered and frequent checks continue until both partners at each nest are identified. Nests are then checked every 10 to 15 days until the grey-brown chicks fledge or until the breeding attempt fails. When checking nests, field observers walk up to the nest and, when necessary, the adult bird is gently lifted with a crook so that the nest content (egg or chick) and adult's ring may be seen. Males change colour faster and attain whiter plumage than females and breeding birds are sexed by comparing plumage of mates, scored using the Gibson (1967) method or via the birds pre-laying behaviour. The accuracy of these methods was confirmed via genetic sexing of a subsample of birds (chapter 4). Prior to fledging, chicks are ringed with individually numbered metal rings. Parents breeding for the first time are also ringed with field readable darvic rings, which are recorded in all subsequent breeding attempts. These data provide approximately 25 years of Wandering Albatross wild pedigree data, breeding success of individuals and the population, age and experience of breeding individuals and their number of breeding partners. Whole island censuses of incubating pairs (January) and fledglings (November) are also conducted annually. Including the pre-laying copulation and nest building period, the Wandering Albatross breeding season spans two Gregorian years (November of year A to November/December of year B). Years I refer to are those in which chicks fledge (or, in the case of failures, the year in which fledging would have occurred had the breeding attempt been successful).

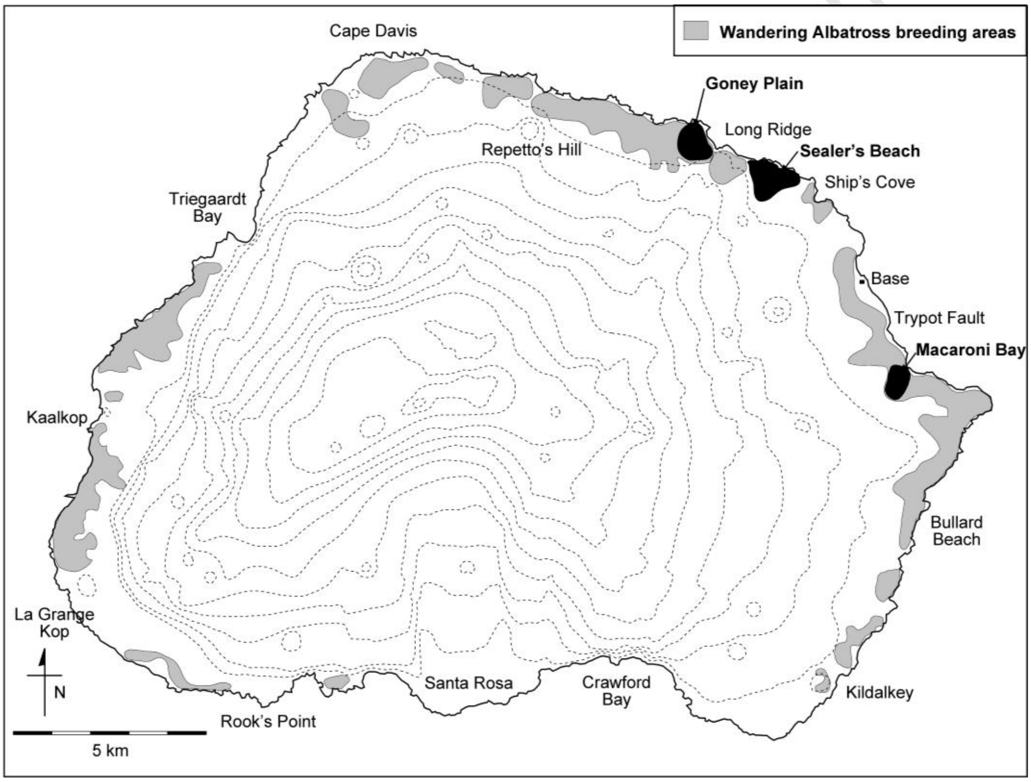

Figure 2.1 Wandering Albatrosses breed on the vegetated coastal plains at Marion Island. Greatest densities are found along the western and northern coasts whereas few birds breed on the southern coast. Study colonies, Goney Plain, Sealer's Beach and Macaroni Bay are located in the northeast within easy walking distance of the research station.

Marion Island

Marion Island (46°52'S, 37°41'E) is the southern and larger (290 km^2) of two sub-Antarctic Prince Edward Islands situated in the southern Indian Ocean. The islands are of volcanic origin but shaped by glacial activity in some areas. They lie between the Subtropical Convergence and the Antarctic

Polar Front which, together with the Polar Frontal Zone cause variation in the islands' nutrient dynamics and create foraging zones utilised by biota feeding beyond the ambient conditions of the islands (Lutjeharms and Ansorge 2008). The central areas of the island are dominated by barren volcanic lava and scoria (Boelhouwers *et al.* 2008), whereas the coastal plains are characterised by vegetated mires and grasslands (Gremmen and Smith 2008). Politically, the islands form part of South Africa and fall within the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR; Cooper and Ryan 2001). They were declared Special Nature Reserves in 1995 (Hänel and Chown 1998, de Villiers 1995) and a Ramsar site in 2007 (http://ramsar.org).

Observations of pre-laying and breeding behaviour from 2007 to 2009

From 2007 to 2009, Goney Plain study colony (approximately 12 ha) at Marion Island was checked daily, starting from the 9-11 November until an adult Wandering Albatross of the new breeding season was sighted (deemed the start of the pre-laying period). Thereafter, birds wearing unique field readable rings were censused twice daily until the beginning of egg laying. Censuses were then continued daily until chick brooding was complete (in March or April). Birds rings were read by eye if observers were within 5 m of the bird or by using binoculars when rings could be read from a greater distance. In most cases approached birds did not appear to notice the observer or would look at the observer until the observer left and then it would resume its previous activity. In a few cases birds started to walk away from the observer in which case the observer would retreat. If a bird was present in one of two daily checks it was deemed present that day. If a bird was present during consecutive censuses it was deemed to have been continuously present. These data were used to identify adults first date of arrival at the colony. For those birds that went on to breed I totalled their number of days spent ashore prior to egg laying, maximum number of consecutive days they were present prior to egg laying, number of days individuals were paired with their social partner and mates' arrival date synchrony (number of days between mates' arrival dates). I also obtained laying dates of each pair, their incubation period, hatching date and breeding success. ANOVA showed no difference in incubation period (F=1.057, p=0.306) and hatching date (F=2.068, p=0.153) between non-fostered, control fostered and experimentally cross-fostered eggs (chapter 8). The results did not differ when cross-fostered samples were included or excluded in analyses of this chapter. Cross-fostered samples were thus included in the presented data. From March to December, I conducted colony checks every 10 to 15 days to establish whether chicks survived to fledge. Time of and, when possible, reasons for egg failures or chick deaths were recorded. Egg failures were recorded within 24 hours of failure since the colony was checked daily during incubation. Dates of chick death were less accurately estimated (to the date of the colony check on which the chick was recorded missing) because the colony was checked every 10 to 15 days once chick brooding was complete.

Statistical analyses

Generalised linear models (GLMs) were used to identify whether synchrony in pair arrival and overlapping presence at the colony was influenced by differences between, rather than within pairs (Crawley 2008). Generalised estimating equations (GEE) were used to determine the influence of breeding timing on breeding success and to determine relationships between pre-laying timing variables. Over the three year study some pairs, or individuals were sampled two or three times. A mixed model approach (rather than GLMs and simple t-tests) was required to account for the repeated measures on the same parents. GEEs (rather than generalised linear mixed models, for instance) were deemed appropriate because there were many pairs with few repeated measures per pair. GEEs were run with individuals or pairs included as a random term in R (R Development Core Team 2010) using geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2010). Unless I state that I used the binomial family, the default Guassian family was used throughout the thesis with an independent correlation structure.

Results

On average males arrived 5 days earlier than females and all males arrived before the end of December whereas some females were seen for the first time in January (Table 2.1). From year to year, both average and extreme arrival dates of males and females were highly consistent (Table 2.1).

Table 2.1 Arrival dates of adult Wandering Albatross males and females at the start of the pre-laying period.

	males		females	
	$\bar{x}$ ±SD (n)	first and last arrival	$\bar{x}$ ±SD (n)	first and last arrival
2006/7	3 Dec ±6.9 days (222)	17 Nov, 26 Dec	8 Dec ±7.7 days (191)	21 Nov, 3 Jan
2007/8	5 Dec ±7.6 days (213)	18 Nov, 30 Dec	10 Dec ±9.7 days (176)	18 Nov, 7 Jan
2008/9	4 Dec ±7.3 days (199)	17 Nov, 27 Dec	10 Dec ±8.9 days (168)	19 Nov, 10 Jan
total	4 Dec ±7.3 days (634)	17 Nov, 30 Dec	9 Dec ±8.9 days (535)	18 Nov, 10 Jan

Over the three-year period the maximum number of days that any breeding male was recorded ashore was 33 days (Table 2.2), although in 2007 a non-breeding male spent 36 days ashore prior to the mean laying date. The maximum number of consecutive days any male was recorded ashore was 29 days (Table 2.3). Presence in the colony was highly variable and 3 males in 2008 and 1 in 2009 were recorded ashore for only 1 day prior to laying. Females spent less time ashore than males (Table 2.2). The longest any breeding female was recorded ashore was 11 days and the maximum consecutive days any breeding females spent ashore was 5 days (Table 2.3). In 2007 a non-breeding female spent 17 days ashore prior to the mean laying date. Some females were not observed during the pre-laying period indicating that any length of time they spent in the colony was less than a day. Although observers were present in the colony for the whole day prior to laying, no single vantage point allows simultaneous observation of the entire colony at Goney plain. As censuses were done in the morning and the evening, it is possible that these females visited the colony, unobserved, between the twice daily censuses.

Table 2.2 Breeding adults number of days ashore in the breeding colony prior to laying.

	males ($\bar{x}$ ±SD (n), range)	females ($\bar{x}$ ±SD (n), range)
2007	17.4 ±5.7 days (126), 2-33	5.5 ±1.7 days (127), 0-11
2008	13.4 ±6.3 days (130), 1-31	3.9 ±1.8 days (129), 1-11
2009	17.4 ±6.5 days (133), 1-32	5.2 ±2.2 days (134), 1-11
total	16.0 ±6.5 days (389), 1-33	4.9 ±2.0 days (390), 0-11

Table 2.3 Breeding adults maximum number of consecutive days present in the breeding colony prior to laying.

	males ($\bar{x}$ ±SD (n), range)	females ($\bar{x}$ ±SD (n), range)
2007	9.7 ±5.4 days (126), 1-26	2.7 ±0.9 days (127), 0-4
2008	6.3 ±4.6 days (130), 1-29	1.9 ±0.9 days (129), 1-5
2009	9.2 ±5.4 days (133), 1-27	2.4 ±1.0 days (134), 1-5
total	8.4 ±5.3 days (389), 1-29	2.3 ±1.0 days (390), 0-5

On average, females arrived 6.3 ±8.5 days (n=381) later than their social mates. The range in differences in mates arrival was considerable; one female was recorded in the colony 25 days before her mate arrived and another female arrived 41 days after her male. Mates in social pairs were seen together for an average of 2.4 ±1.4 days (n=392) during the pre-laying period (ranging from 0-7 days over the three year study). Shore presence was positively correlated with arrival, with early arrival resulting in significantly more days ashore (GEE males: W=287.0, p<0.001; females: W=129.8, p<0.001) and significantly more maximum continuous days present (GEE males: W=166.0, p<0.001; females: W=32.8, p<0.001). Maximum number of consecutive days present was significantly positively correlated with total days ashore (GEE males: W=729.0, p<0.001; females: W=571.4, p<0.001). GLMs shows a significant improvement on the null model when the pair is included as the dependant variable on both the difference in mates arrival date (ΔAIC=97) and number of days partners spent together (ΔAIC=20). This indicates that variation in arrival date synchrony and mates days overlapping at the colony is driven by variation between pairs.

Date of first eggs laid and mean laying dates were highly consistent across years (Table 2.4) as were mean hatching dates (Table 2.5). Laying date (Table 2.4) did not correlate with incubation period (GEE W=0.3, p=0.570; Table 2.5), but longer incubation periods were associated with later hatching (GEE W=26.1, p<0.001; Table 2.5). In 2009, one young female (a first time breeder) laid much later than all other birds (10 February, this date is excluded from the mean laying date). On the day she laid a male attempted to copulate with her while she was incubating. Soon after that she was observed getting off her nest, leaving the egg exposed, and joining a courtship dance with her mate and another bird. The other bird moved away and she and her mate continued to dance until she returned to incubate. Her mate went and sat next to her at the nest and was seen either sitting next to the incubating female or incubating himself in the subsequent three days. Their behaviour was unusual and suggested the pair were not ready to breed. They failed four days later. Although egg failures generally occurred during late incubation, failure timing varied from December (on the day of laying) to mid April, at which stage eggs were usually addled (Table 2.6). The majority of chick failures occur at the young chick stage (April and May) but some large chicks also died, with the latest death occurring in August (Table 2.6).

Table 2.4 Laying dates and period of laying of Wandering Albatrosses at Marion Island.

	$\overline{x}$ ±SD (n)	first egg laid	last egg laid (laying period)
2007	29 Dec ±5.8 days (128)	16 Dec	13 Jan (28 days)
2008	30 Dec ±5.6 days (130)	14 Dec	15 Jan (32 days)
2009	30 Dec ±5.9 days (136)	15 Dec	18 Jan (34 days)
total	30 Dec ±5.8 days (394)	14 Dec	18 Jan (36 days)

Table 2.5 Hatching dates and incubation period (mean ± standard deviation (n), range) of Wandering Albatrosses at Marion Island.

	egg incubation period	hatching date
2007	78.8 ±1.4 days (99), 76-84	18 Mar ±5.9 days (100), 4 Mar - 31 Mar
2008	78.6 ±1.9 days (108), 72-85	18 Mar ±5.9 days (109), 6 Mar - 9 Apr
2009	79.2 ±1.4 days (110), 75-83	19 Mar ±5.9 days (110), 6 Mar - 3 Apr
total	78.9 ±1.6 days (317), 72-85	19 Mar ±5.9 days (319), 4 Mar - 9 Apr

Table 2.6 Mean egg and chick failure dates of Wandering Albatrosses at Marion Island (mean (n), range).

	egg failure dates	chick failure dates
2007	14 Mar (29), 9 Jan - 12 Apr	4 May (12), 25 Mar - 20 Jun
2008	20 Feb (22), 26 Dec -17 Apr	26 Apr (23), 12 Mar - 14 May
2009	9 Mar (26), 22 Dec - 14 Apr	16 May (26), 18 Mar - 16 Aug
total	6 Mar (77), 22 Dec -18 Apr	7 May (61), 12 Mar - 16 Aug

Breeding success

From 2006 to 2009, breeding success at Goney Plain averaged 68% and was within the range of the whole islands breeding success and similar to that of other study colonies (Table 2.7). Breeding attempts failing at the egg stage (18%) were similar to the proportion of chicks failing (14%; Table 2.7). Of 91 egg failures, 46 (50.5%) were inviable eggs (mostly addled and incubated beyond possible hatching dates, but one was deformed). Another 35 (38.5%) were lost due to inadequate nests, parents abandoning egg (mostly when mates did not return after extended periods) or Sub-Antarctic

Skua (*Catharacta antarctica*) predation and 10 failed for unknown reasons. Of the 71 chick deaths, 14 (20%) succumbed during severe weather conditions and 12 (17%) were lost by parents (due to predation, crushed in their nests (by parents) or starved). Two chicks died due to mouse predation, another two due to nest collapse caused by mouse burrowing (Jones and Ryan 2010), two died during hatching and 39 died for unknown reasons. An ability to construct nests affects breeding success and some Wandering Albatrosses with shallow, water logged, poorly constructed nests lost eggs. Some with poorly positioned nests (e.g. on sea cliffs within range of waves) also lost chicks due to exposure to environmental conditions.

Table 2.7 Wandering Albatross breeding success at Marion Island, at Macaroni Bay (MB) and Sealer's Beach (SB) study colonies (combined) and at Goney Plain (n=eggs laid) from 2006 to 2009. Numbers of egg or chick failures are from Goney Plain only.

	Marion Island	MB and SB	Goney Plain	egg failures	chick failures
2006	75% (n=1613)	76% (n=99)	78% (n=100)	12	10
2007	58% (n=1735)	77% (n=128)	68% (n=130)	30	12
2008	73% (n=1824)	61% (n=122)	65% (n=131)	23	23
2009	66% (n=1765)	61% (n=133)	62% (n=138)	26	26
total	68% (n=6937)	68% (n=330)	68% (n=499)	91	71

Factors affecting success of current breeding attempts

Males' and females' dates of arrival in the colony, the total number of days they spent ashore prior to laying and their maximum consecutive days ashore were not significantly related to the success of their breeding attempts. The success of a given breeding attempt was also not correlated with the number of days partners spent together prior to laying or synchrony in partners' arrival at the colony. Breeding success also did not correlate with parent age and number of partners in their breeding lifetime (including current partners). Chicks that fledged hatched significantly earlier (by an average of two days) than those that failed (GEE W=5.0, p=0.025) but there was considerable overlap in hatching date of fledged and failed chicks (Figure 2.2). Date of laying and incubation period did not differ for breeding attempts that succeeded or failed.

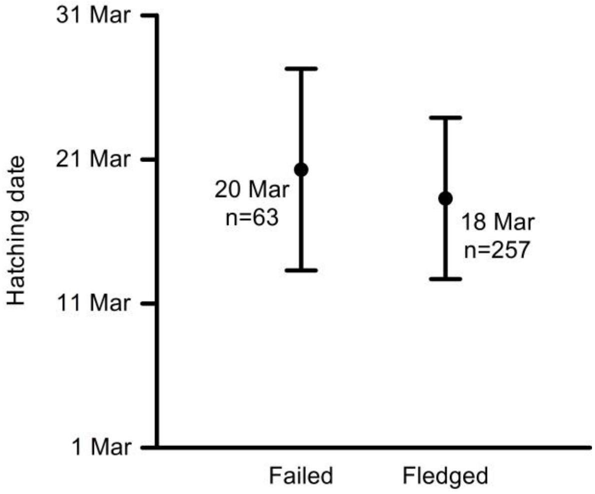

Figure 2.2 Wandering Albatross chicks at Marion Island that survive to fledge tend to hatch earlier (mean ± standard deviation) than those that fail (GEE W=5.0, p=0.026).

Discussion

Limited dispersal between Wandering Albatross populations (Inchausti and Weimerskirch 2002, Cooper and Weimerskirch 2003, Charmantier *et al*. 2011) apparently provides sufficient gene flow to maintain genetic homogeneity between populations (Burg and Croxall 2004). However, local adaptations can occur despite gene flow. Timing of breeding is plastic in bird species, allowing them to respond to environmental changes (e.g. Nager and Ruedi 1995, Charmantier et al. 2008). Mechanisms enabling breeding timing plasticity are not completely understood (Visser et al. 2010) however different expressions of plastic characteristics are likely to result in differentiation of populations rather than speciation. Latitudinal and temporal within species variation in phenology in response to regional differences in climate have been illustrated in numerous climate change studies (Walther *et al*. 2002, Both *et al*. 2004, Crick 2004, Barbraud and Weimerskirch 2006, Wanless *et al*. 2008). However, species vary in their response to environmental condition, some advancing and others delaying breeding (Wanless *et al*. 2008).

At South Georgia, the earliest male arrived at the colony five days earlier than the earliest arriving Marion Island male, whereas South Georgia's earliest arriving female landed six days later than the earliest arriving Marion Island female (Table 2.8; Tickell 1968). Mean pre-laying arrival date for Marion Island males was five days later than the South Georgian males' mean arrival date. Mean arrival of females of the Marion Island population was similar (only one day earlier) to those at South Georgia (Table 2.8; Tickell 1968). Mean laying date for the South Georgian population was six days earlier, and mean hatching date eight earlier than at the Marion Island population (Table 2.8; Tickell 1968). Although the first egg laid at South Georgia was 11 days earlier than at Marion Island, the last eggs were laid at a similar time to the last eggs at Marion Island suggesting that the laying period at South Georgia is longer than at Marion Island. Laying at Crozet (from 17 December until 25 January; Fressanges du Bost and Segonzac 1976) and Kerguelen (from 10 December to 15 January; Paulian

1953) Islands also started later than at South Georgia. The hatching period at Crozet Islands (4 March to 11 April; Fressanges du Bost and Segonzac 1976) was similar to Marion Island's. Mean incubation for the South Georgia, Crozet (79 days; Fressanges du Bost and Segonzac 1976) and Marion Island populations differed by less than a day, with the range being slightly greater at Marion Island (Table 2.8). While it might be expected that breeding phenology would be later in populations at more extreme latitudes (e.g. L'Hyver and Miller 1991), overall the more northern Marion, Crozet and Kerguelen Island birds tended to breed later than the South Georgian Wandering Albatrosses. South Georgia dates were recorded from 1958 to 1964 (Tickell 1968) and the 45 years gap between assembling of the two data sets may account for some of the differences between the South Georgia and Marion populations. However data collected at Crozet Island from 1966 to 1972 and at Kerguelen Islands in 1951, suggest that northern Wandering Albatross populations breed later due to latitudinal differences rather than temporal changes. Winter conditions start earlier and may be more extreme at South Georgia than at Marion Island due to the islands differences in latitude. Earlier breeding at South Georgia may be a local adaptation enabling chicks to grow sufficiently before the earlier starting winter conditions set in.

Table 2.8 Date of male and female arrival, egg laying, hatching and incubation period (mean ± standard deviation (n), range) at the South Georgian and Marion Island Wandering Albatross populations.

	South Georgia[a]	Marion Island
male arrival	29 Nov ±2.2 days (*ca* 60), 12 Nov - na	4 Dec ±7.3 days (634), 17 Nov - 30 Dec
female arrival	10 Dec ±9.4 days (*ca* 60), 24 Nov - na	9 Dec ±8.9 days (535), 18 Nov - 10 Jan
laying	24 Dec ±5.6 days (261), 5 Dec - 17 Jan	30 Dec ±5.8 days (394), 14 Dec - 18 Jan
hatching	11 Mar ±5.4 days (336), 27 Feb - 29 Mar	19 Mar ±5.9 days (319), 4 Mar - 9 Apr
incubation	78.4 ±1.2 days, (163), 75-82	78.9 ±1.6 days (317), 72-85

[a] South Georgian data was extracted from Tickell (1968) and unavailable information is marked as 'na'.

More than half of the failures occurring at the egg stage resulted from addled eggs, which may be indicative of genetic inadequacies driving some egg failures but also of ill-formed eggs (e.g. eggs negatively influenced by oceanic pollutants; Ludwig *et al.* 1998) or inadequate incubation techniques resulting in the death of the embryo. Chicks hatch at the onset of winter and chicks hatching earlier are more likely to have grown to a sufficient size that enables them to survive the commencing harsh weather conditions, potentially accounting for the influence of hatching timing on the success of breeding. Since weather conditions vary annually, the influence of hatching timing on chick survival may vary annually and may be of greater importance for breeding success in specific years than on parents' reproductive success over many years.

At Marion Island, regular standardised island counts began in the mid 1980s showing an increase in Wandering Albatross breeding pairs until 1986, followed by a slight decrease until 2005, but, subsequently, an increase in numbers (Cooper and Brown 1990, Nel *et al*. 2003, Ryan *et al*. 2009). Counts during the course of the study were slightly lower than the best estimated annual breeding population number (1850; Ryan *et al*. 2009) but remained stable. Population numbers at the Crozet and Kerguelen Islands decreased from 1970 to 1985, but have since also increased (Weimerskirch and Jouventin 1998). In contrast to Marion, Crozet and Kerguelen Islands, the South Georgian population continues to decrease in numbers (Croxall *et al*. 1998). Wandering Albatross population decreases are frequently ascribed to fishery mortality, which may influence the populations differentially according to their different foraging localities (Weimerskirch and Jouventin 1987, Weimerskirch *et al*. 1997, Croxall *et al*. 1998, Gales 1998, Weimerskirch and Jouventin 1998, Nel *et al*. 2002, 2003). Breeding success during the study was lower than the population average of 74.6% reported by Nel *et al*. (2003), but over the four study years breeding success in the colonies was similar to that of the whole island. Despite fairly intense investigations, breeding success at Goney Plain was higher than at other, less disturbed, study colonies in three of the four studied years and similar to that of the whole island indicating that intense investigation during this project did not negatively influence breeding success.

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Chapter 3

To breed, or not to breed: Is that the question? Effects of phenology and condition on long-term reproductive success in Wandering Albatrosses

Abstract

To conserve threatened species it is important to protect the productive individuals, yet there is little information identifying such individuals. I used Wandering Albatross (*Diomedea exulans*) historic breeding data to distinguish birds with poor or productive reproductive pasts and examined whether I could differentiate good from poor breeders based on body condition on return to their colony and breeding phenology. Individuals that arrive early and stay at the colony for longer prior to egg laying had greater body condition indices. Pre-laying arrival and presence appears to drive the ability to breed, or not. Males breeding for the first time had lower body condition indices than experienced males. Females and males with breeding experience arrived later and spent less time with their partners at the colony prior to laying compared to first time breeders and eggs of experienced males were laid earlier suggesting that experience enables economy in reproductive effort. However, amongst experienced breeders, males in pairs with good reproductive histories were present in the colony for longer prior to laying compared to those with poor reproductive histories. Females with good reproductive histories spent more days with their mates prior to laying than those with poor breeding histories suggesting that pre-laying pair interactions may distinguish productive and unsuccessful breeders. Timing of egg laying and hatching did not relate to long-term reproductive success, but more productive pairs and females tended to incubate for shorter periods.

Keywords

arrival date, body condition, deferring breeding, hatching date, incubation, lay date, pair synchrony, pre-laying presence

Introduction

A primary stage that separates productive from unproductive individuals is whether they breed, or not (Mills 1989, Newton 1989, Owen and Black 1989, Saurola 1989, Wooller *et al*. 1989). Of individuals that go on to breed, some have greater competency because of prior breeding experience (Lequette and Weimerskirch 1990, Weimerskirch 1990, Weimerskirch 1992, Moreno 2003). In time, experienced breeders may be subdivided into those with successful reproductive pasts and others that reared very few young (Clutton-Brock 1988, Cobley *et al*. 1998, Newton 1989, Moreno 2003). Phenotypic traits (such as body condition, breeding phenology, offspring care and pair fidelity) may influence variation in reproductive success (Clutton-Brock 1988, Newton 1989). Identifying the characteristics causing variation in productivity is important to understand demographic patterns; knowledge of both the characteristics and their influence on species demography is necessary for conservation-oriented decisions (Newton 1989, Lewis *et al*. 2006). I use data from a long-term study at Marion Island to examine the relationship between long-term reproductive success and condition, pre-laying timing and breeding phenology in Wandering Albatrosses (*Diomedea exulans*).

In monogamous birds, arrival date and presence at the colony prior to laying may be indicative of individuals' breeding abilities because pair bond reaffirmation, copulation, breeding site selection and nest building occur during this time (e.g. Mills 1989, Huyvaert *et al.* 2006). Earlier arriving males who are present for longer have more mating opportunities (both within and extra-pair) and can guard their mate when she arrives, which may assist in mate retention and fidelity (e.g. Huyvaert *et al.* 2006). In some birds (e.g. migratory birds) carrying weight has energetic costs (e.g. Chandler and Mulvihill 1992, Burns and Ydenberg 2002), but in seabirds greater weight frequently correlates with improved reproduction (Mills 1989, Weimerskirch 1992, Chastel *et al.* 1995, Chaurand and Weimerskirch 1995, Wendeln and Becker 1999). Better condition enables earlier arrival, longer presence at the nest site and affects investment in the breeding attempt, ultimately influencing breeding success (Drent and Daan 1980, Mills 1989, Weimerskirch 1992, Chastel *et al*. 1995, Møller *et al*. 2003). Timing of breeding and chick rearing also vary amongst individuals depending on genetic, behavioural and condition differences (Mills 1989). Earlier laying, earlier hatching and shorter incubation periods have been associated with better breeders (Kim and Monaghan 2006, Lewis *et al*. 2006, Olson *et al*. 2006) and ultimately correlate with lifetime reproductive success (Saurola 1989).

Do pre-laying arrival, presence and body condition influence the ability to breed?

The ability to breed in a given year may be affected by mate availability and/or body condition (Weimerskirch 1992). Body condition, in turn, influences arrival date and pre-laying presence in the colony and consequently pre-laying behaviour differs between breeders and non-breeders (e.g. Mills 1989, Chastel *et al.* 1995). Due to physiological reproductive costs, life history theory predicts trade-offs between breeding in the current season and survival (influencing future reproductive potential; Stearns 1992, Møller *et al*. 2005). Survival may be jeopardised in birds attempting to breed below a threshold body condition (Drent and Daan 1980). I predict that lowered body condition influences the deferment of breeding for a given season and that non-breeders arrive at the colony later and spend less time ashore than breeders.

Does breeding experience increase breeding efficiency and performance?

Because learnt behaviours increase competency, breeding performance increases with breeding experience although senescence reduces reproductive success in very old birds (Newton 1989, Lequette and Weimerskirch 1990, Croxall *et al*. 1992, Weimerskirch 1992, Chastel *et al.* 1995, Lecomte *et al*. 2010). Wandering Albatrosses reaching sexual maturity do not breed unless they attain a threshold body mass and body mass increases during their lifetime potentially reflecting increased foraging efficiency due to increased experience or skill (Weimerskirch 1992). Thus I predict that more experienced breeders arrive at the colony in better condition than naïve breeders. If experienced birds manage to attain better body condition, they could arrive earlier, spend more time ashore and as a result mates may spend more time together than first time breeders. As learnt behaviours increase efficiency (Pickering 1989, Lequette and Weimerskirch 1990, Weimerskirch 1990), I predict that experienced breeders lay earlier, hatch chicks earlier and incubate for shorter than new breeders.

Do breeding phenology and body condition correlate with long-term reproductive success?

Body condition may vary with environmental conditions (Chastel *et al*. 1995) but some individuals may be better at foraging or metabolising food, thereby buffering the effects of environmental variability. An individual's ability to maintain good condition would augment offspring production regardless of each season's environmental conditions, and ultimately differentially increase that individual's lifetime reproductive success. This leads to the prediction that birds with impoverished breeding histories display poorer body condition than productive birds. Pre-laying presence and arrival were not found to relate to reproductive success in some albatrosses (e.g. Cobley *et al*. 1998), but positively correlate with breeding success in other seabirds (Mills 1989, Lewis *et al.* 2006). One may intuitively expect better Wandering Albatross males to arrive earlier and stay in the colony for longer because experienced breeders arrive earlier than pre-breeders (Pickering 1989). This leads to predictions that more productive birds arrive at the colony earlier and spend more time ashore prior to laying than those with poor reproductive pasts. More productive males, arriving earlier would have more opportunity to mate guard and copulate, and also enable greater simultaneous presence between mates which should reduce females need to swap partners. Amongst seabirds of several species, breeding success correlates with earlier laying, shorter incubation and earlier hatching (e.g. Mills 1989, Cobley *et al*. 1998, Lewis *et al*. 2006) so I predict that more productive Wandering Albatrosses lay eggs and hatch chicks earlier and have shorter incubation periods.

Albatrosses return to the same nest site, which may facilitate mates reuniting (Tickell 1968, 2000, Brooke 2004). Most males return before females and stay on land for extended periods (Tickell 1968, 2000, Brooke 2004, chapter 2). Females return to their nest site for shorter periods when the pair may copulate. The female takes the first incubation shift after the single-egg clutch is laid and thereafter parents share incubation and chick rearing responsibilities (Tickell 2000). Wandering Albatrosses produce only one chick every two years but their breeding career can span a few decades (Tickell 1968, 2000, Weimerskirch and Wilson 2000). While reproductive effort during early breeding attempts may reduce survival in some species (Stearns 1992, Møller *et al*. 2005), in others (e.g. long-lived birds), individuals that were highly productive in early breeding attempts lived longer (e.g. Wooller *et al*. 1989). However, even in long-lived birds some individuals may burn out after breeding only once or twice. These breeders would not realise the levels of long-term reproductive success that more persistent breeders achieve (Wooller *et al*. 1989). Thus Wandering Albatrosses that continually attempt breeding over a few decades are biased towards more productive individuals. Nevertheless, even birds managing to breed for many years show disparity in reproductive performance (e.g. Cobley *et al*. 1998, chapter 1).

Methods

Ringed adults were censused twice daily at Goney Plain during the pre-laying period until laying began (chapter 2). Adults who had bred before, but who did not breed in the studied year were considered non-breeders for that season (but parents who had just completed chick rearing were excluded). Census data were used to identify each birds arrival dates at the colony, number of days spent in the colony prior to egg laying (or prior to mean lay date for non-breeders) and maximum number of consecutive days they were present during the pre-laying period (details are provided in chapter 2). Observers were present in the colony for approximately nine hours per day during the pre-laying period during which time pairings (including couples sitting together and engaging in allopreening or other pair reaffirmation behaviours, courtship displays or copulations; Tickell 2000) were recorded. Pair synergy of birds that bred was assessed from the number of days birds were paired with their social partner, and also pair arrival date synchrony (as explained in chapter 2) and number of extra-pair partners that they consorted with during the pre-laying period.

Censuses were continued daily throughout incubation to the end of the brood phase (from mid-December to the end of April), providing dates of birds arriving post the start of laying, but also laying dates of each pair, their incubation period and hatching date. After the end of the chick brood phase, chicks were checked approximately every 10 days between May to July and every 15 days from July to December to establish fledging success.

Breeding adults were sexed based on behaviour and comparative plumages between mates (males are larger and whiter than their mates; Gibson 1967, Tickell 1968). Sex was confirmed for a subset of birds indicating that behaviour and plumage sexing was 100% accurate (chapter 4). Sexes of non-breeders were ascertained from historic breeding records (and had also been inferred by comparison of plumages between mates). Historic breeding data of individually ringed birds was used to identify parent age, breeding experience and minimum number of previous breeding partners (see chapter 1 for details). Amongst the experienced breeders, I distinguished less successful Wandering Albatrosses from those with more productive breeding histories using methods described in chapter 1.

Adult body condition indices

Methods used to measure body condition were constrained by the need for a non-destructive approach, using no more than the most basic, weather resistant equipment and minimal bird handling time. Mass controlled for size was used to determine body condition (Brown 1996) on each bird’s first day back at the Goney Plain study colony during the pre-laying periods of the 2007, 2008 and 2009 seasons. Upon arrival at the study colony each Wandering Albatross adult was weighed using a 20 kg Salter macro-line spring balance (accuracy 200 g). Measurements of each bird’s culmen length, maximum bill depth at the gonys, minimum depth behind the gonys (Figure 3.1) and tarsus length were taken to 0.1 mm using Vernier callipers (Appendix 1). Flattened right wing length was measured to the nearest millimetre using a 1 m wing rule (Appendix 1). The first principal component (PC1) of the five body measurements provided an index of body or structural size for each adult. Separate regression analyses were conducted each year to provide a body size index per year and to avoid repeated measures of the same individuals (PC1; accounting for 71%, 73% and 70% of the variance in the three respective seasons). Residuals of structural size indices regressed against body mass provided body condition indices for each individual in each year sampled (2007: n=304, F=524.9, $p<0.001$, $r^2=0.633$; 2008: n=304, F=561.1, $p<0.001$, $r^2=0.649$; 2009: n=294, F=470.5, $p<0.001$, $r^2=0.615$). I attempted to run analyses including mass and specific body size measures in mixed effects models rather than body condition indices since these methods are considered more reliable (García-Berthou 2001, Green 2001, Hayes and Shonkwiler 2001). However, this approach proved impractical due to the increased number of terms (which frequently caused model failures). Schulte-Hostedde *et al.* (2005) found ordinary least squares regression analysis to be adequate for small vertebrates provided measurement error and individual variation were not high. Using a principle component of body size measurements increased reliability of body condition indices by ensuring that the size index is a measure of size rather than shape (Green 2001). The relationship between mass and size was linear and condition indices were independent of structural size.

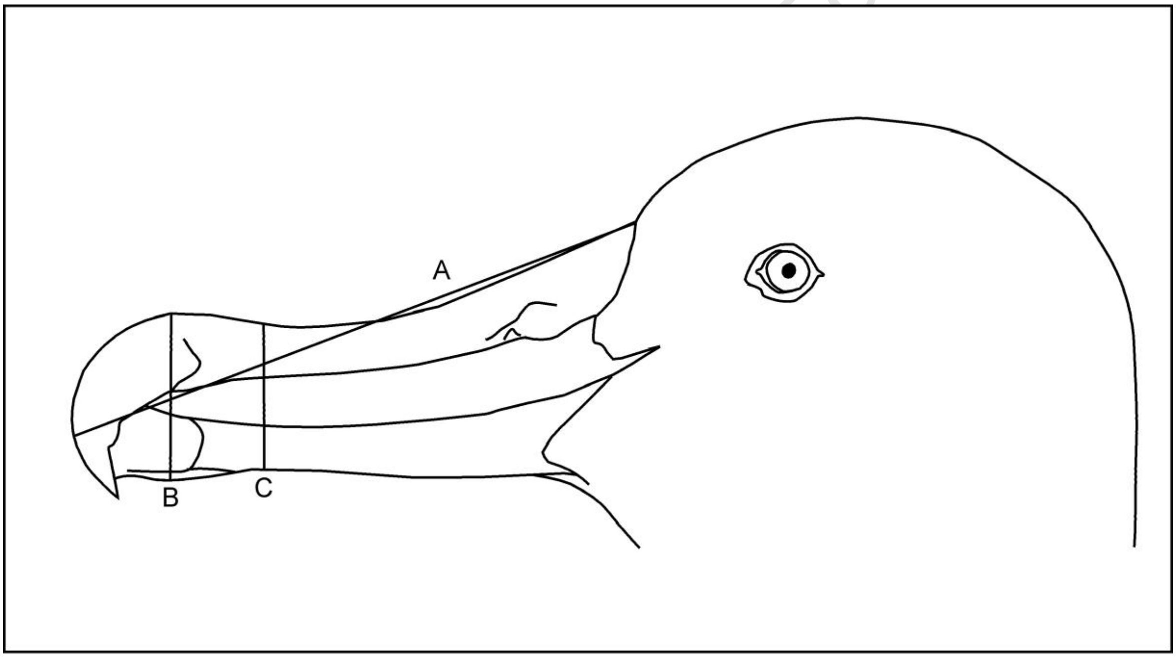

Figure 3.1 Wandering Albatross bill measurements include culmen length (A), maximum depth at the gonys (B) and minimum bill depth behind the gonys (C).

Statistical analyses

Differences between breeder and non-breeder condition indices, arrival date and pre-laying presences were analysed using generalised estimating equations (GEEs; using a binomial family with individuals included as a random effect). GEEs were then used to determine the relationship between long-term reproductive success and breeding phenology, condition indices and pair synergy and also to establish whether experience influences these characteristics. Eggs fostered between parents of different past reproductive success (chapter 8) were excluded from breeding success, incubation period and hatching date analyses (although their inclusion did not alter patterns of statistical significance). Analyses were run in R (R Development Core Team 2010) using geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2005) and models were compared using a stepwise removal of terms based on significance and ANOVA comparisons (Zuur *et al*. 2009). Although many models were run, in general only those yielding significant results are reported.

Results

Body condition influences pre-laying presence at the breeding colony

Breeding and non-breeding males with higher arrival body condition indices arrived significantly earlier (GEE W=16.50, p<0.001), spent more days ashore (GEE W=39.90, p<0.001) and a greater number of continuous days ashore (GEE W=28.59, p<0.001) than those with lower body condition indices. Total number of days ashore was the variable best associated with male condition indices (GEE W=39.8, p<0.001). Overall, females with higher body condition indices arrived earlier (GEE W=20.46, p<0.001), spent more continuous (GEE W=5.66, p=0.017) and total days ashore (GEE W=3.86, p=0.049) but analysis of all terms together showed arrival date to be the variable best associated with female body condition indices (GEE W=20.50, p<0.001).

Body condition of breeders and non-breeders

In all years, body condition indices of both females that bred and those that did not were lower than those of the males. Although the average arrival body condition indices of females and males that subsequently bred were greater than non-breeding males and females in all years, the differences were not significant (GEE males: W=0.13, p=0.720; females: W=0.21, p=0.650; Table 3.1).

Non-breeders and breeders arrival dates

The earliest breeding males arrived on 18, 18 and 17 November in 2007, 2008 and 2009 and first breeding females were seen on 23, 18 and 20 November in the three seasons. Although some females were not seen in the colony until January (towards the end of laying; 12, 7 and 10 January), all breeding males were seen in the colony prior to the mean laying dates in December (latest arrivals; 11, 29 and 22 December). Non-breeding males and females arrived throughout the pre-laying period but breeders tended to arrive earlier (Figure 3.2; Table 3.1).

Mean arrival dates of males that subsequently bred were 1, 3 and 2 December. The average arrival dates for non-breeding males were five days later in all three years (GEE for all years W=47.80, p<0.001; Table 3.1; Figure 3.2). The mean arrival dates in 2007, 2008 and 2009 for females that subsequently bred were 7, 9 and 9 December and on average non-breeding females arrived two to three days later. Although female breeder and non-breeders arrival dates did not differ significantly when analysed per year, the pattern over three years showed arrival day of female non-breeders was significantly later than that of breeders (GEE W=4.67 p=0.031; Table 3.1; Figure 3.2).

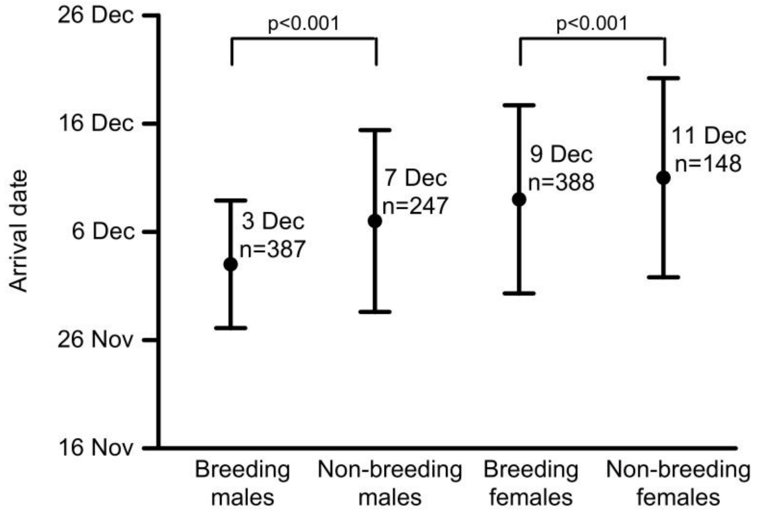

Figure 3.2 Males and females that subsequently bred arrived significantly earlier (mean ± standard deviation) than non-breeders.

Non-breeders and breeders presence at colonies prior to laying

In the three study years breeding males averaged 13-17 days ashore prior to laying while non-breeding male attendance was more variable and they averaged significantly fewer days ashore (6-11 days; GEE W=87.90, p<0.001; Figure 3.3). Breeding females averaged 4-6 days ashore, significantly more than non-breeding females (2 days; GEE W=33.20, p<0.001; Figures 3.3). Overall, breeding males and females spent a greater number of consecutive days ashore than non-breeding males and females (GEE males: W=38.10, p<0.001; females: W=26.10, p<0.001; Table 3.1).

Models in which arrival date, pre-laying presence and body condition indices were run interactively showed greater number of days ashore prior to laying to be the most important characteristic defining whether males breed in a given season (GEE W=88.70, p>0.001). Both early arrival (GEE W=12.50, p>0.001) and greater number of days present (GEE W=35.00, p>0.001) explain differences between breeding and non-breeding females when terms were run interactively in a multivariate GEE.

The influence of breeding experience on reproductive success

Although newly formed pairs had a slightly greater failure rate (39% n=103) than pairs with breeding experience (30% n=342) there was no significant difference in breeding success between them. Similarly, failure rate of naïve males (35% n=57) and females (42% n=60) did not differ from those with breeding experience (males: 32% n=386; females: 31% n=387).

Table 3.1 Marion Island Wandering Albatross male and female pre-laying arrival date, presence ashore and body condition index from three breeding seasons. Birds are subdivided into breeders and non-breeders, pairs breeding for the first time and those with prior breeding experience and pairs of three different levels (good, poor and moderate) of historic reproductive success. Data presented are means over three years (2006-2008) ± standard deviation (n) and range.

	arrival date	days ashore	consecutive days ashore	body condition index
Males				
non breeders	7 Dec ±8.4 days (247), 18 Nov - 30 Dec	8.7 ±8.4 days (247), 1-36	4.6 ±5.0 days (247), 1-28	108 ±964 (145), -2267 to 2957
breeders	3 Dec ±5.9 days (387), 18 Nov - 29 Dec	16.0 ±6.5 days (389), 1-33	8.4 ±5.3 days (389), 1-29	141 ±966 (373), -2680 to 2618
new pairs	28 Nov ±6.6 days (71), 18 Nov - 29 Dec	16.9 ±7.0 days (72), 1-33	8.5 ±5.4 days (72), 1-25	-98 ±1019 (69), -2621 to 2318
experienced pairs	3 Dec ±5.4 days (316), 20 Nov - 24 Dec	15.8 ±6.4 days (317), 1-32	8.4 ±5.3 days (317), 1-29	195 ±947 (304), 2680 to 2618
good pairs	3 Dec ±5.6 days (53), 23 Nov - 23 Dec	16.1 ±6.4 days (53), 3-28	9.1 ±6.1 days (53), 1-26	308 ±987 (56), -2438 to 2366
moderate pairs	2 Dec ±4.3 days (55), 23 Nov - 11 Dec	16.2 ±6.5 days (55), 4-31	9.0 ±5.7 days (55), 1-29	213 ±963 (104), -2340 to 2348
poor pairs	4 Dec ±5.2 days (56), 25 Nov - 14 Dec	15.0 ±5.9 days (57), 1-27	7.2 ±4.0 days (57), 1-21	244 ±905 (158), -2356 to 2318
Females				
non breeders	11 Dec ±9.2 days (148), 18 Nov - 30 Dec	2.1 ±2.5 days (148), 1-17	1.2 ±0.9 days (148), 1-7	-280 ±875 (38), -1930 to 1727
breeders	9 Dec ±8.7 days (388), 18 Nov - 10 Jan	4.9 ±2.0 days (390), 0-11	2.3 ±1.0 days (389), 0-5	-168 ±665 (352), -2329 to 1702
new pairs	3 Dec ±8.4 days (70), 18 Nov - 7 Jan	5.7 ±2.5 days (71), 0-11	2.3 ±1.0 days (71), 0-4	-241 ±700 (64), -1781 to 1452
experienced pairs	10 Dec ±8.3 days (316), 22 Nov - 11 Jan	4.7 ±1.9 days (317), 0-10	2.3 ±1.0 days (316), 0-5	-153 ±659 (286), -2328 to 1702
good pairs	9 Dec ±8.6 days (53), 26 Nov - 2 Jan	4.8 ±1.6 days (53), 2-9	2.3 ±0.8 days (53), 1-4	-109 ±665 (84), -1996 to 1677
moderate pairs	9 Dec ±7.6 days (55), 25 Nov - 3 Jan	4.7 ±1.7 days (55), 1-8	2.3 ±0.9 days (55), 1-5	-205 ±634 (106), -2241 to 1526
poor pairs	10 Dec ±7.7 days (56), 24 Nov - 31 Dec	4.5 ±1.7 days (56), 1-9	2.4 ±1.0 days (56), 1-4	-54 ±706 (105), -1358 to 1702

Table 3.2 Marion Island Wandering Albatrosses pair synchrony in terms of gap between mates' arrival dates and the number of days mates were together in the colony prior to laying (mean ± standard deviation (n) and range, from 2006 to 2008). Pairs are grouped into first time breeders, pairs with prior breeding experience and pairs of different levels (good, poor and moderate) of historic reproductive success.

	difference in mates arrival date	number of days mates overlapped in colony prior to laying
new pairs	5.5 ±8.6 days (67), -14 to 41	2.86 ±1.6 days (73), 0-7
experienced pairs	6.5 ±8.4 days (314), -25 to 36	2.31 ±1.4 days (317), 0-7
good pairs	6.2 ±9.6 days (53), -25 to 34	2.36 ±1.4 days (53), 0-6
moderate pairs	6.7 ±7.6 days (55), -11 to 28	2.44 ±1.4 days (55), 0-6
poor pairs	5.9 ±7.9 days (55), -11 to 30	2.27 ±1.2 days (56), 0-5

Table 3.3 Breeding phenology of Wandering Albatrosses at Marion Island of pairs breeding for the first time, pairs with breeding experience and pairs of different levels of past reproductive success. Data are means from three seasons (from December 2006 ending in 2009) ± standard deviation (n) and range.

	lay date	hatching date	incubation period
new pairs	29 Dec ±7.4 days (75), 14 Dec - 15 Jan	18 Mar ±7.2 days (58), 6 Mar - 4 Apr	79.1 ±1.5 days (56), 77-83
experienced pairs	30 Dec ±5.4 days (317), 16 Dec - 18 Jan	19 Mar ±5.6 days (230), 4 Mar - 10 Apr	78.8 ±1.7 days (219), 72-85
good pairs	30 Dec ±5.7 days (53), 16 Dec - 18 Jan	18 Mar ±5.4 days (29), 4 Mar - 28 Mar	78.3 ±1.5 days (29), 75-82
moderate pairs	30 Dec ±4.5 days (55), 20 Dec - 6 Jan	19 Mar ±4.6 days (42), 9 Mar - 26 Mar	79.1 ±1.7 days (42), 76-84
poor pairs	30 Dec ±5.6 days (56), 18 Dec - 12 Jan	19 Mar ±6.5 days (25), 6 Mar - 30 Mar	79.3 ±1.8 days (24), 76-83

Table 3.4 The number of breeding partners experienced Wandering Albatross bred with during their breeding career and interactions parents had with non-social mates (extra-pair partners) during the pre-laying period of each season (mean ± standard deviation (n) and range from 2006 to 2008 at Marion Island).

	females breeding partners	females extra-pair partners	males breeding partners	males extra-pair partners
good breeders	1.2 ±0.44 partners (66), 1-3	0.26 ±0.74 interactions (53), 0-4	1.4 ±0.60 partners (66), 1-3	0.31 ±0.68 interactions (51), 0-3
moderate breeders	1.2 ±0.52 partners (70), 1-3	0.20 ±0.45 interactions (55), 0-2	1.3 ±0.63 partners (69), 1-3	0.43 ±0.79 interactions (54), 0-3
poor breeders	1.1 ±0.44 partners (68), 1-3	0.20 ±0.52 interactions (56), 0-3	1.2 ±0.44 partners (68), 1-3	0.34 ±0.58 interactions (56), 0-2

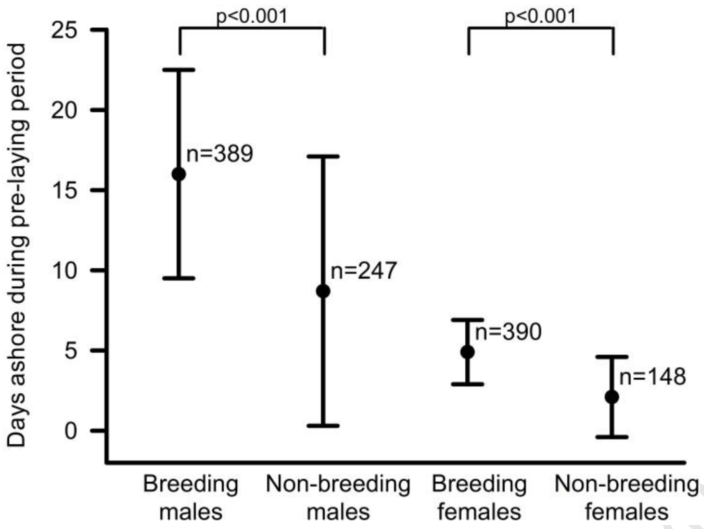

Figure 3.3 The number of days breeding males and females were present (mean ± standard deviation) in the colony prior to laying was significantly greater than the number of days non-breeding males and females were present in the colony prior to mean laying date.

Pre-laying body condition indices, presence and behaviour in relation to breeding experience

The body condition indices of males with breeding experience were greater than those that had not bred before (GEE W=16.44, p<0.001; Figure 3.4) but experience did not influence females' body condition indices. Males and females in pair bonds with prior breeding experience arrived at the colony on average five days later than individuals in new pairs (GEE males: W=4.30, p=0.038; females: W=8.90 p=0.003; Table 3.1; Figure 3.5). Days ashore and consecutive days present did not differ between males breeding in new pairs and those in pairs with prior experience (Table 3.1). Females in new pairs spent more consecutive days ashore (GEE W=4.25, p=0.039) and on average one more day ashore than those in experienced pairs, but the pre-laying presence of females in new pairs was more variable than those with breeding experience (GEE W=9.39, p=0.002; Table 3.1). There was no difference in mates' arrival (arrival synchrony) between newly formed pairs and those with prior breeding experience (Table 3.2). Partners in pairs with experience spent on average significantly less time together prior to laying than partners breeding together for the first time (GEE W=8.04, p=0.005) but time together varied greatly (Table 3.2; Figure 3.6).

Breeding phenology in relation to breeding experience

Breeding experience had no effect on incubation period or hatching date (Table 3.3). Female experience did not significantly influence laying date (GEE W=3.83, p=0.050) but eggs of experienced males were laid on average three days earlier (GEE W=6.21, p=0.013; Figure 3.7).

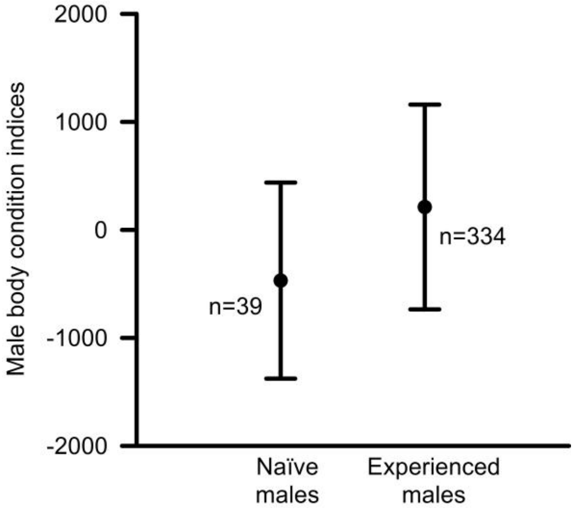

Figure 3.4 Body condition indices (mean ± standard deviation) of males with breeding experience were significantly greater than condition indices of males breeding for the first time (GEE W=16.44, p<0.001).

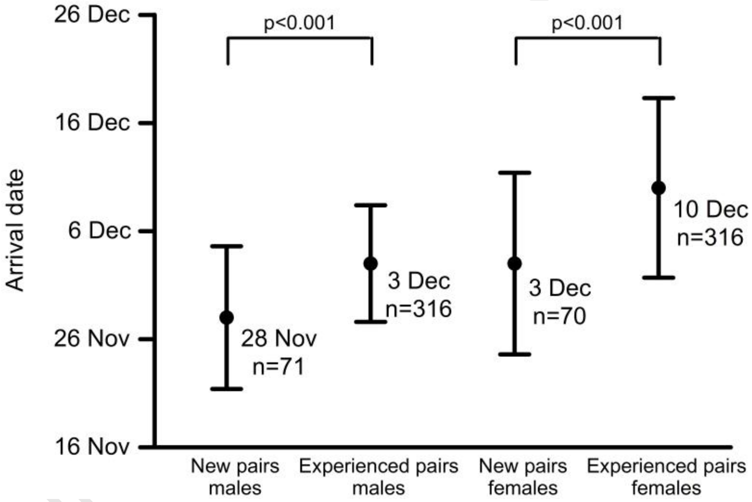

Figure 3.5 Males and females in pairs with prior breeding experience arrived significantly later (mean ± standard deviation) than those parents in new pair bonds.

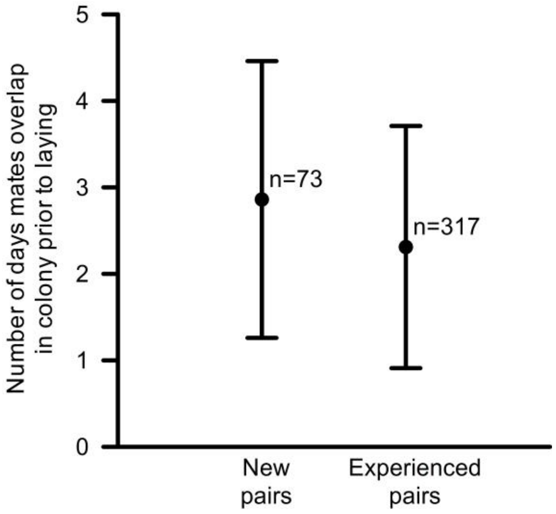

Figure 3.6 Mates in newly formed pairs spent more days together (mean ± standard deviation) prior to laying than mates in established pairs (GEE W=8.04, p=0.005).

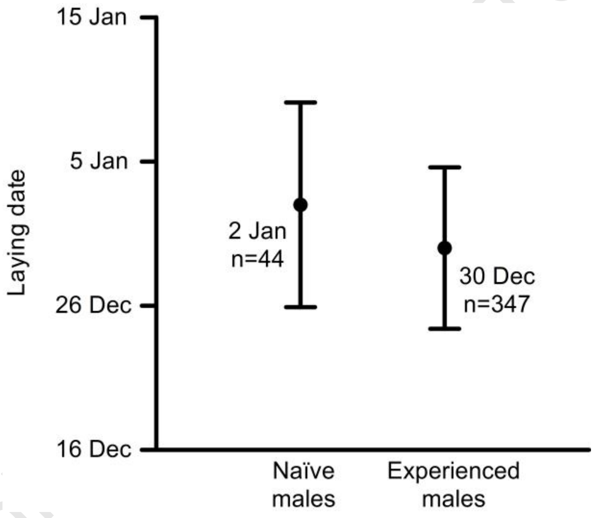

Figure 3.7 Eggs of males with prior breeding experienced were laid on average three days earlier (mean ± standard deviation) than eggs of naïve males (W=6.21, p=0.013).

Correlates of past reproductive success

There was no relationship between age and long-term reproductive success for either males (GEE W=0.03, p=0.85) or females (GEE W=0.18, p=0.668) and too few study birds were old enough to detect a decline in reproductive productivity due to senescence. Amongst experienced breeders, past reproductive success did not correlate with parents' body condition indices (GEE males: W=0.11, p=0.740; females: W=2.25, p=0.130). Nor was there a difference in arrival dates (GEE males W=2.23, p=0.135; females W=2.47, p=0.116), the total number of days ashore prior to laying (GEE males W=2.16, p=0.140; females W=3.58, p=0.059) or in maximum number of consecutive days ashore (GEE males W=0.54, p=0.460; W=0.53, females p=0.470). Long-term reproductive success of males and females did not correlate with body condition indices, pre-laying presence and arrival when tested using multivariate GEEs either. Multivariate GEEs including these variables showed that pair's historic reproductive success was negatively correlated with females' body condition indices (GEE W=4.58, p=0.032; Table 3.1) but positively correlated to the number of days the male spent ashore prior to laying (GEE W=5.48, p=0.019; Table 3.1).

Previous reproductive success in relation to pair synchrony and extra-pair interactions

There was no difference in arrival synchrony between pairs with low and high previous reproductive success (GEE W=0.34, p=0.560; Table 3.2). The of number days partners spent together prior to laying did not differ between pairs (Table 3.2) or males of high and low previous reproductive success. But female's previous reproductive success was positively correlated with the number of days mates spent together (GEE W=5.03, p=0.025), although when only good and poor categories of females were compared they did not differ significantly (GEE W=0.26, p=0.610). Female's previous reproductive success did not correlate with their number of pre-laying extra-pair encounters or the number of partners they had during their breeding career (Table 3.4). Males previous reproductive success did not correlated with their number of pre-laying encounters but males with lower previous reproductive success had more breeding partners during their breeding career (GEE W=18.50, p<0.001; Table 3.4). Multivariate GEEs investigating the importance of pair co-ordination (pair synchrony and extra-pair interactions) showed that these variables do not correlate with males and pairs previous reproductive success. However these analyses provided further indication that number of days mates spent with each other prior to laying is positively correlated with female's previous reproductive success.

Previous reproductive success and breeding phenology

Laying and hatching dates did not differ for pairs (Table 3.3), males or females of differing levels of reproductive success. Although previous reproductive success did not correlate with incubation period, birds in the category of good pairs incubated eggs slightly less time than poor pairs (GEE pairs: W=4.83, p=0.028; Table 3.3).

Discussion

Pre-laying condition, arrival and presence influence on reproductive success

During the pre-laying period, male Wandering Albatrosses stay at their nest areas for extended periods, consort with females and build nests (Tickell 1968, 2000). Location of the nest within the colony (Coulson 1968) and nest site quality (Potts *et al*. 1980) is known to significantly affect breeding success in some seabirds. Pre-breeding fighting by male nest holders occasionally occurs in Wandering Albatrosses (Tickell 2000, personal observation). This aggressive behaviour may be a form of resource defence (Krebs and Davies 1981) with better quality males or better condition males gaining access to their selected resources (e.g. their mate or nest site). Early arrival and longer presence means that they can establish ownership of their nest site, have sufficient time to construct a nest and be available to guard and copulate with their partner during her fertile phase. When male Waved Albatrosses (*Phoebastria irrorata*) were at the nest sites, pairing occurred immediately upon female arrival but pairing took hours to days if the male was not present when the female arrived (Huyvaert *et al.* 2006). However, in both Grey-headed Albatrosses (*Thalassarche chrysostoma;* Cobley *et al.* 1998) and Wandering Albatrosses (this chapter) there was no connection between early arrival and long-term reproductive success. Similarly, Huyvaert *et al.* (2006) concluded that while early arrival may increase opportunities for extra-pair copulation it was only weakly related to fitness in Waved Albatrosses.

Body condition drives arrival date and pre-laying presence of Wandering Albatrosses in Marion Island's colony, with better-condition birds arriving earlier and staying for longer. Arrival and presence in the colony prior to breeding, in turn, influence individuals' ability to breed in that season. In other Procellariiformes (e.g. Blue Petrels; *Halobaena caerulea*) male condition significantly affected their decision to breed and was positively correlated with breeding success (Chastel *et al.* 1995). Good condition Blue Petrel males tended to arrive earlier and stay longer than poorer condition males. On the other hand, female condition and arrival date were not correlated which is not unexpected because female Procellariiformes visit the colonies for shorter, contracted periods prior to their pre-laying exodus (Chastel *et al.* 1995). Since survival is high and reproductive rates low in Wandering Albatrosses, birds in poor body condition may opt to defer breeding to reduce the risk of mortality induced by breeding in poor condition (Lack 1968, Drent and Daan 1980). While this might ensure that individuals have the opportunity to breed in the future, the missed breeding years reduces their reproductive output in the long-term (Mills 1989, Newton 1989, Owen and Black 1989, Saurola 1989, Jouventin *et al*. 1999). This provides some evidence that body condition and pre-laying behaviours affect lifetime reproductive success in Wandering Albatrosses. Counter intuitively, Wandering Albatross females in more productive pairs had lower body condition than those in less productive pairs. Since females spend less time in the colony prior to laying they may not require extra body fat. Possibly females benefit from carrying less fat, since less weight lowers wing loading and is known to reduce costs of foraging in some birds (Shaffer *et al*. 2001). If a minimum threshold body condition is necessary to produce an egg there may be little difference in body condition between breeding birds, potentially explaining the lack of difference in body condition between experienced and less experienced females.

Earlier arrival and greater simultaneous presence at the breeding colony should expedite copulation during the female's short fertile period; yet males and females in established pair bonds arrived later and spent less time together than newly formed pairs. The later arrival and reduced presence of experienced pairs was not driven by lowered body condition, because experienced males had better body condition than naïve males. The greater presence of females in established pairs may reduce the need for earlier arrival. With breeding experience comes greater predictability of partners' behaviours, possibly allowing for greater accuracy in pair synchrony. Newly formed pairs, lacking the security of partner predictability, may allow for a greater margin of error when it comes to pair synchrony by arriving earlier and thereby providing more time for partners to meet. Wandering Albatrosses return to the same nest area and in many cases directly to the remains of their nest from their previous breeding attempt (Inchausti and Weimerskirch 2002). Repeatedly nesting at the same locality facilitates reuniting of partners in established pair bonds. Newly formed pairs may not have this advantage, explaining their greater pre-laying presence. This suggests that pair bond experience spares parents the extra effort of earlier arrival and greater presence required by birds in new pairs, giving experienced males more time to forage and enhance their body condition prior to breeding. Although experience may reduce the need for an extended shore presence, amongst experienced pairs, more productive males spent more time ashore than less productive males. Furthermore, females with greater productivity spent more overlapping days ashore with their partners. Overall behaviours improved by experience allow for later arrival and less time together. However, amongst the experienced parents, productivity is enhanced by males spending more time in the colony and greater within-pair synchrony during the pre-laying phase. Considering that time is required to establish pair bonds, partner swapping uses up time that could be better spent breeding (Jouventin *et al*. 1999). Males with numerous lifetime breeding partners had resultant lower historic reproductive success. Overall pair synergy during a breeding event and fidelity in the long-term appear to increase individuals' chances of more productive breeding careers.

Breeding phenology in relation to reproductive success

In Red-billed Gulls (*Chroicocephalus scopulinus*) more successful birds bred earlier in the season (Mills 1989) and Common Guillemots (*Uria aalge*) laying earlier had greater probability of raising a chick (Lewis *et al.* 2006) suggesting that seabirds breeding earlier may be better breeders. In line with this, eggs of males breeding for the first time were laid later than those of experienced males (contrary to Wandering Albatrosses at the Crozet Islands; Weimerskirch 1992). Yet, in both Grey-headed (Cobley *et al.* 1998) and Wandering Albatrosses (this chapter) there was no difference in laying and hatching dates between parents with different rates of previous reproductive success. Neither was there a difference in the duration of incubation between more and less productive Grey-headed Albatrosses (Cobley *et al.* 1998). Shorter incubation periods are indicative of smaller eggs (chapter 5) or more efficient incubation (rolling eggs and maintaining constant temperatures enhances embryo and chick growth; Kim and Monaghan 2006, Olson *et al*. 2006). While more productive females did not lay smaller eggs (chapter 5), more productive pairs incubated for shorter than other pairs, which suggest that incubation behaviour influences reproductive ability.

Since I compare long-term reproductive success of experienced breeders, this study excludes individuals that may have low productivity because they stopped breeding at a young age, after their first few breeding attempts (Møller *et al*. 2003). Pre-laying and breeding behaviour are influenced by experience, which suggests that learnt behaviours do enhance breeding. Pre-laying arrival and presence influence reproductive success at an elementary stage of the breeding season (whether individuals actually attempt to breed or not) and are indicative of individuals' reproductive ability. Arrival, shore presence, laying, incubation period and hatching affect reproductive success at different stages in the breeding cycle and different stages of the breeding career, presenting flexibility in the stage at which reproductively productive and impoverished individual can be distinguished. Amongst experienced birds there are differences in pre-breeding behaviours (male pre-laying presence, time spent with partner prior to laying and incubation) that distinguish individuals of differing reproductive ability. However, results did not show a strong influence of condition and breeding phenology on long-term reproductive success in Wandering Albatrosses.

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Appendix

Appendix 1 Body mass, wing, tarsus and bill size (mean ± standard deviation, range) of Wandering Albatross adults at Marion Island. All measurements were taken prior to laying on their first date of arrival at the Goney Plain study colony from December 2006 to December 2008.

	males (n=288)	females (n=237)
pre-laying body mass (g)	11646 ±967, 8550 to 14050	9579 ±752, 7950 to 13950
wing (mm)	674 ±14, 623 to 707	655 ±15, 595 to 694
tarsus length (mm)	128.6 ±3.0, 117.4 to 136.7	122.0 ±3.0, 112.6 to 132.9
culmen length (mm)	175.2 ±4.3, 165.0 to 187.9	168.0 ±4.6, 153.6 to 184.4
gonys maximum depth (mm)	46.3 ±1.2, 41.0 to 50.1	42.5 ±1.3, 39.4 to 47.0
minimum depth behind gonys (mm)	40.2 ±1.3, 36.4 to 45.4	36.9 ±1.4, 32.4 to 40.6

Chapter 4

Dalliances and doubtful dads: What determines extra-pair paternity in socially monogamous Wandering Albatrosses?

Abstract

Genetic techniques have revealed surprising rates of extra-pair paternity (EPP) in socially monogamous, long-lived albatrosses. Microsatellite loci were used to show that EPP rates in Wandering Albatross, *Diomedea exulans*, at Marion Island ranged from 14% to 24% in three seasons. Such levels will influence estimates of individuals' lifetime reproductive success. I sought to identify who benefits from extra-pair behaviour and to establish social and genetic influences on EPP, which probably resulted from both female solicited extra-pair behaviours and male forced copulations. EPP was not linked to breeding experience nor was it used by females in pairs with poor reproductive pasts despite a tendency for pairs to consistently produce either within or extra-pair chicks. Parental arrival and presence in the colony prior to laying, as well as pre-laying pair synchrony did not correlate with EPP providing little indication that mate guarding inhibited extra-pair behaviour. Contrary to hypotheses predicting that benefits of cuckoldry include increased offspring genetic variability, extra-pair offspring were not more genetically variable than within-pair offspring. Furthermore, parents of extra-pair young did not suffer lower genetic variability than those producing within-pair young. However, the population is characterised by low genetic variability, which may result in mate incompatibility. Mates failing and those producing extra-pair young showed a tendency for greater genetic similarities to each other than mates producing within-pair young which suggests that cuckoldry may be used to counter mate incompatibility. Extra-pair chicks survive and grow equally well compared to within-pair chicks, suggesting that cuckolded males do not reduce investment in extra-pair chicks. The lack of discriminatory behaviour by cuckolded males together with low genetic diversity in the population may influence EPP in this long-lived, monogamous species. In albatrosses pair bonds are typically long lasting and costs of forming new pairings may discourage mate swapping. Extra-pair copulations and EPP may be an adaptive alternative to mate swapping, supported evolutionarily since risks associated with extra-pair behaviour are small.

Keywords

extra-pair paternity, forced copulation, genetic variability, mate choice, monogamy, parental investment, pre-laying attendance

Introduction

Evolutionary processes occurring within social mating systems (monogamy, polygamy and promiscuity) are sculpted by gene flow. Long-lived species with long-term pair bonds are expected to exhibit genetically monogamous mating systems (Abbott *et al*. 2006, Huyvaert *et al*. 2006) because longevity is inversely related to extra-pair paternity (EPP, Wink and Dyrcz 1999). EPP rates also decrease as the probability of pair bond survival increases (Wink and Dyrcz 1999). Long-lived species have more time to find high quality, genetically compatible mates, resulting in less need to cuckold (Bried and Jouventin 2002, Burg and Croxall 2006). Møller (2000) found rates of EPP to be lower in species with high parental investment, a trait typical of monogamous species. Yet, molecular marker techniques provide quantitative evidence of genetically promiscuous individuals within apparently monogamous mating systems of different taxa (e.g. Wink and Dycrz 1999, Fietz *et al*. 2000, Griffith *et al*. 2002, Munshi-South 2007, Crawford *et al*. 2008, Cohas and Allainé 2009). Albatrosses are famous examples in which fidelity is expected (Tickell 2000) as they have a long pair bond formation period, display strong mate fidelity and obligatory biparental care is required to rear young (Burg and Croxall 2006). Nevertheless, moderate levels of cuckoldry occur in some albatrosses (Huyvaert *et al*. 2000, Abbott *et al*. 2006, Burg and Croxall 2006, Huyvaert *et al*. 2006, Jouventin *et al*. 2007). In this study I established levels of EPP in a single-egg-clutch species, Wandering Albatrosses (*Diomedea exulans*), over a three-year period at Marion Island.

Does variation in individual characteristics influence EPP?

Despite their strong social monogamy, divorce does occur amongst albatrosses (Jouventin *et al*. 1999, Ryan *et al*. 2007). Pair bond disruption is costly since re-pairing takes time. Re-mating reduces fecundity and lifetime reproductive success by increasing inter-breeding intervals (Jouventin *et al*. 1999, Bried and Jouventin 2002). Cuckoldry in monogamous relationships may provide benefits of divorce and re-mating without the costs of forming new pair bonds. Historic breeding success may influence fidelity and females with poor reproductive pasts may increase their chances of raising offspring by obtaining extra-pair fertilisations from better males (Dubois *et al*. 2004). Thus I predict that historically unproductive pairs should display higher rates of EPP. Extra-pair copulations may occur via female choice (Kempenaers *et al*. 1992, Petrie and Kempenaers 1998) or be forced. Females may learn to avoid forced copulations and experienced males may be more adept at mate guarding, so I predict that EPP will be more prevalent amongst inexperienced birds.

Do breeding behaviour and phenology influence EPP?

Extra-pair behaviour has been ascribed to lack of mate guarding, density of breeding colonies, synchronous breeding, male availability and sexual size dimorphism (Griffith *et al*. 2002, Burg and Croxall 2006, Cohas and Allainé 2009). An apparent male bias in the Wandering Albatross breeding population (Weimerskirch *et al*. 2005, chapter 6) and the greater size of males may expedite the occurrence of forced copulations and extra-pair fertilisation in this species (Burg and Croxall 2006). Synchronised breeding in many Procellariiformes also creates opportunities for extra-pair copulations (Burg and Croxall 2006). Early arrival at a colony, guarding of females and nest sites is energetically costly for male albatrosses who stay on land (fasting) for numerous consecutive days prior to laying (Tickell 1968, 2000, chapter 2). Albatrosses in better condition may return earlier and have greater ability to sustain lengthy fasts, enabling them to stay in the colony for longer (chapter 2). Greater pre-laying presence provides more opportunity for mate guarding (Chastel *et al*. 1995, Møller *et al*. 2003). It also provides more extra-pair copulation opportunities. Late arrival or absence of males facilitates infidelity in their mates (Huyvaert *et al*. 2006). I predict greater simultaneous presence of mates decreases EPP. I also predict that cuckolded males arrive later, in poorer body condition and stay in the colony for shorter periods prior to laying. However, cuckolded males might discriminate against extra-pair offspring, thereby selecting against EPP (Westneat *et al*. 1990, Møller and Birkhead 1993, Westneat and Sargent 1996, Burg and Croxall 2006). If discrimination occurs, extra-pair offspring are predicted to suffer slower growth and decreased survival compared to that of within-pair paternity (WPP) young.

Does genetic variability influence EPP?

Individuals may benefit from extra-pair copulations by reducing risks of infertility or incompatibility with their social mate and increasing their re-mating potential (Birkhead and Møller 1992, Petrie and Kempenaers 1998, Wink and Dyrcz 1999, Griffith *et al*. 2002, Zeh and Zeh 2003). Genetic variability in species with strong natal philopatry is often reduced (Abbott and Double 2003, Bried *et al*. 2007) and genetic similarities between mates may result in genetic incompatibility (Wink and Dyrcz 1999, Amos *et al*. 2001). If low genetic variability drives EPP in philopatric species, I hypothesise that EPP will be more prevalent in parents with low genetic variability and in mates that are more genetically similar (Petrie and Kempenaers 1998, Wink and Dyrcz 1999, Amos *et al*. 2001, Griffith *et al*. 2002). If EPP is a result of female mate choice, females producing extra-pair chicks should show lower heterozygosity and greater inbreeding than those producing within-pair chicks. Pairs producing extra-pair offspring should be more genetically similar to each other than mates producing within-pair chicks. Females may benefit by increasing the genetic diversity and quality of their offspring (Kempenaers *et al*. 1992, Petrie and Kempenaers 1998, Wink and Dycrz 1999, Griffith *et al*. 2002) suggesting that a female's EPP offspring should be more genetically variable than her within-pair offspring (Foerster *et al*. 2003).

I use Wandering Albatross historic breeding data, breeding behaviourial observations and genetic characteristics to investigate behavioural and genetic influences on EPP. Burg and Croxall (2006) found annual variation in EPP in related albatrosses. Their study illustrates the importance of investigating EPP variation within species. EPP in the large Marion Island Wandering Albatross population (Ryan *et al*. 2009) will be contrasted against the occurrence in smaller South Georgian, Kerguelen and Crozet Islands' populations.

Methods

Long-term monitoring data of uniquely banded individuals from Goney Plain study colony at Marion Island were used to determine parents' ages, breeding experience and historic reproductive success via methods described in chapter 1. From 2007 to 2009, uniquely ringed adults arriving at the Goney Plain colony were recorded daily, as described in chapter 2, and mass-size regression analyses were used to calculate parent arrival body condition as described in chapter 3. The two daily attendance checks (morning and evening) during the pre-laying period provided parents' arrival dates, number of days ashore, greatest number of consecutive days ashore and number of days simultaneously present with mates prior to laying (chapter 2). Differences in mates' arrival dates were used to calculate each pair's arrival synchrony (chapter 3). Observers were also present throughout the day and noted individuals present between the daily checks and recorded breeding behaviours; specifically, individuals interacting in pairs and copulatory behaviours (including extra-pair copulations and apparent forced copulations). The presence of observers in the colony did not appear to influence extra-pair or within-pair copulatory behaviour.

Although seemingly subjective, forced copulations were distinguishable from cooperative copulations. In consensual copulations mates usually spent time together at the nest before and after copulating, frequently copulating more than once. In most cases in which females consensually copulated outside their pair bond, it was only identified as extra-pair once she commenced breeding with another mate. In consensual copulations only a single male interacted with a female, but in forced copulations, usually more than one male competed for access to the female (up to five males were observed competing for access to a female). Copulation was considered forced if the female attempted to evade the male (usually by running and flying off) and snapped at the male while she was pinned down. As the male frequently chased the female or approached her at her nest or landing locality, forced copulations did not take place at the male's nest and the male usually walked away after copulating (back to his nest). If males did not manage to climb on top of the female or if the female, in copulation position, did not raise her tail and the male did not appear to make cloacal contact, the event was recorded as an attempted forced copulation.

Examples of forced copulation

A female returned to the colony at the peak of the pre-laying period and her long time mate of eleven years (who is blind in one eye) was not present at the nest site. She was aggressively approached by males and pinned down by one male who attempted to copulate with her but she was aggressive towards him, snapping at him, until he climbed off her. Another male attempted to copulate with her and two more males approached, fought with each other around the female who snapped at them. One of the males managed to mount the female, appeared to successfully forcibly copulate with her and then walked back to his nest area, approximately 50 m away. All other males had left the site by that time. She and her usual mate subsequently reared a within-pair chick.

In another case, a male attempted to copulate with a female and was joined by two more males. The female's usual partner was present, and rushed over, chasing the first male away, which resulted in the other two males leaving. The pair had limited breeding experience and subsequently failed on egg in their breeding attempt.

At another time a young female without prior breeding experience, landed in the colony and was chased by three males, one of whom mounted and attempted to copulate with her. The males then fought and the female left. She landed again and was approached by two of the males. A dispute between these males occurred during which they trampled the female. One of the males walked away while the remaining male copulated with the initially resisting female and subsequently stayed with her as if they were in a pair bond. The two subsequently successfully raised a within-pair chick.

Chick growth and survival

Laying and hatching dates of each family group were recorded and the fate of each breeding attempt monitored by daily checks from incubation to guarding hatchlings and, thereafter, 10-15 day checks until chicks fledged. Chicks were weighed every 10 to 15 days using 5 kg (accuracy: 50 g), 10 kg (accuracy: 100 g) and 20 kg (accuracy: 200 g) macro-line spring balances. Chick growth rate parameters and asymptotic mass were estimated using the Gompertz logisitic growth curve:

$$M = Ae^{-e^{-k(t-t_i)}},$$

where M is chick mass, *A* is the fledging mass, *k* is the growth rate, t_i is the time at which fledging mass is attained and *t* is age in days (Richards 1959, Ricklefs 1968, 1973, Ricketts and Prince 1981, chapter 8).

EPP and sex determination

Blood (100 µl) was collected from the tarsal vein of putative parents prior to laying and from immediately post brood phase chicks and stored in lysis buffer (Longmire's solution 100 mM Tris, 100 mM EDTA, 10 mM NaCl and 0.5% SDS). In a few cases chicks died before blood could be collected. If the carcasses were present, tissue samples were collected and stored in 96% ethanol and used instead of blood. Total genomic DNA was extracted using an extraction solution of 10% Chelex® 100 Resin (BioRad), 10 mM Tris, 0.2% SDS and 5 µl of Proteinase K (100 mg/mL). Approximately 20 µl of blood was added to 200 µl of the extraction solution and incubated at 65 ºC for at least 8 hours followed by boiling for 10 min.

Chicks were sexed by amplification of the CHD gene, using primers 2550F and 2718R following the protocol of Fridolfsson and Ellegren (1999). Breeding adult sex was determined via behaviour and comparison of plumage between mated individuals and confirmed genetically for a subset of birds. Males lose the dark grey-brown fledging colouration faster and more completely than females and attain a comparatively whiter plumage (Gibson 1967, Tickell 1968). Ideally the sex of cuckolded fathers should be confirmed genetically since female-female pairings have been recorded in another albatross species (Laysan Albatross, *Phoebastria immutabilis;* Young *et al*. 2008). However, the factors driving female-female pairing in Laysan Albatross (e.g. female-biased sex ratios; Young *et al*. 2008) are unlikely to be operating in the Wandering Albatross population at Marion. To confirm this I used genetic techniques to verify the sex of parents raising EPP young and parents failing to raise young.

Genotyping for paternity analysis was conducted using 12 microsatellite loci: 11H1, 12H8, 11H7, 12C8, 12E1, 10C5, 6A3, 11F3, 7D8 (Dubois *et al*. 2005), Dc20, De11 and De37 (Burg 1999, Burg and Croxall 2004). PCRs were multiplexed in 2 subsets of loci (6A3, 11F3, 12H8, 12C8, 10C5, 11H1, 11H7, Dc20, De11 and 7D8; 12E1 and De37) in a 10 µl final volume, including 0.2 µM of each primer and 1 µl genomic DNA, using the Qiagen multiplex PCR kit (Qiagen). PCRs were conducted using an ABI GeneAmp® PCR System 2700 under the following conditions: 15 min activation of the HotStart*Taq* DNA polymerase at 95 ºC, 30 cycles of 30 sec of initial denaturation at 94 ºC, 90 sec annealing (58 ºC for 6A3, 11F3, 12H8, 12C8, 10C5, 11H1, 11H7, Dc20, De11 and 7D8; 54 ºC for 12E1 and De37) and 60 sec extension at 72 ºC, and then a final extension of 30 min at 60 ºC. PCR products were combined and electrophoresed on an ABI3730xl using POP7 and a 50 cm capillary using Rox350 (Applied Biosystems) as the standard at the Central DNA Sequencing Facility of the University of Stellenbosch (www.sun.ac.za/saf). Profiles were analysed using GeneMapper Software version 3 (Applied Biosystems). To avoid genotyping errors that might confound paternity assignment, samples with ill-defined peaks were re-amplified and run again.

Paternity by the social father was rejected when more than one mismatch occurred between chick and social father and this mismatch could not be explained by a null allele. CERVUS v. 2.0 (Marshall *et al*. 1998) was used to estimate the combined probability of exclusion and to assign paternities where possible. In general extra-pair sires were not determined because the sample of potential sires was large (and could not be completely collected) and genotyping all potential sires was not feasible.

Determining parent and offspring genetic diversity

To increase the reliability of my data individual heterozygosity was estimated using three measures: Homozygosity by locus (HL), calculated using STORM v. 1.1 (Frasier 2008), is a microsatellite-derived measure that improves heterozygosity estimates in open populations by weighing the contributions of each locus to the homozygosity value depending on their allelic variability (Aparicio *et al*. 2006). Standardized d^2-values assess the length difference between alleles carried by an individual at a locus divided by the populations' maximum observed difference at this locus (Amos *et al*. 2001). Standardized individual heterozygosity is the number of heterozygous loci divided by the total number of typed loci in the individual (Foerster *et al*. 2003). A complementary measure to heterozygosity, Internal Relatedness (IR), is based on allele sharing where the frequency of every allele counts towards the final score thereby allowing the weighting of rare alleles (Queller and Goodnight 1989, Amos *et al*. 2001). When the measure is calculated over several loci, the resulting value has an approximately normal distribution and has similar properties to an r-value. The distribution is centered, more or less, on zero for individuals born to 'unrelated' parents, with negative values for 'outbred' individuals and high positive values indicating 'inbreeding'.

Genetic relatedness between mates

To test whether Wandering Albatrosses avoid selecting genetically similar partners, we compared the observed distribution of mated pair relatedness MP with a simulated distribution obtained if birds pair randomly. MP was calculated following Li *et al*. (1993) using STORM v. 1.1 (Van de Casteele *et al.* 2001, Frasier 2008). If observed mate relatedness values are less than expected from random mating simulations, birds are selecting genetically dissimilar partners. If mate relatedness is higher than expected, individuals are choosing to pair with genetically similar partners. Mated pair relatedness of EPP partners was compared to mated pair relatedness of WPP partners to determine whether pairs producing extra-pair offspring are more genetically related than those producing within-pair offspring.

Allelic inheritance (AI) was used to test whether mate incompatibility influences reproductive success in the colony. Allelic inheritance is calculated from the proportion of paternal alleles that differ from maternal alleles (which should be 50% under Mendelian inheritance), weighted by the average expected heterozygosity of the genotyped loci (Frasier 2008). Values higher than 0.5 (50%) indicate that paternal alleles differing from the maternal allele were inherited more often than expected (Frasier 2008). If mate incompatibility influences reproductive success, then surviving chicks will represent a biased sample of all fertilizations. In this situation observed AI values will be greater than expected (expected values were from simulated offspring of the same pairs if alleles were inherited solely in a Mendelian fashion).

Statistical analyses

Goodness of fit (χ^2 or G) was used to compare rates of EPP between parental categories of breeding experience and previous reproductive success. ANOVA and t-tests were used to compare genetic characteristics of WPP and EPP offspring and parents (Crawley 2008). Binomial generalised estimating equations (GEE) were used to examine the influence of parents' ages, breeding experience, past reproductive success, their arrival body condition indices, pair synergy and breeding timing on the occurrence of EPP. To determine whether parents invest less in extra-pair chicks these statistics were also used to investigate differences between within and extra-pair chicks in brooding periods, offspring sex, growth and survival. Families involves in the cross-fostering analysis were excluded in parental investment analyses because egg provenance was experimentally altered (chapter 8). Analyses were run in R (R Development Core Team 2010) using geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2005). Models were reduced using a stepwise removal of terms based on significance (with individuals or pairs included as a random effect and chick sex as a fixed term when comparing growth parameters) and compared using ANOVA (Zuur *et al*. 2009).

Results

Over three breeding seasons 399 eggs were laid by 270 pairs. Blood samples could not be collected from all social fathers and some offspring samples were not available due to failures at the egg or hatchling stage. Consequently, paternity analyses were run on 247 chicks from 194 pairs (53 pairs produced two siblings that could both be tested for paternity). The rate of EPP varied, from 14% to 24% between 2007 and 2009, averaging 18% over three seasons (Table 4.1). Genetic sexing of 91 adults confirmed that based on phenotype sexing was 100% accurate. All pairs that failed or produced EPP chicks consisted of male and female parents.

Table 4.1 EPP occurrence at Goney Plain, Marion Island.

	eggs laid	chicks fledged	paternity samples	EPP	WPP
2007	130	88 (68%)	82 (63%)	14 (17%)	68 (83%)
2008	131	85 (65%)	85 (65%)	12 (14%)	73 (86%)
2009	138	86 (62%)	80 (58%)	19 (24%)	61 (76%)
total	399	259 (65%)	247 (62%)	45 (18.2%)	202 (81.8%)

Amongst pairs producing two chicks during the study there was a tendency for pairs to have either two extra-pair chicks (n=6, 2.00 times the expected ratio) or two within-pair chicks (n=32, 1.10 times the expected ratio) rather than one extra-pair and one within-pair chick (n=15, 0.75 times the expected ratio). However, sample sizes were too small to produce a significant result (χ^2=2.442 p=0.295). Of the 12 EPP chicks, 11 fledged successfully. None of the six pairs that produced two successive extra-pair chicks were new pair bonds and all parents had bred at least twice previously. Parents of both poor and good reproductive histories were represented in the sample. Four of 12 parents (in two pairs) had had only one mate in their lifetime while others had bred with two partners. In the six pairs, females' ages ranged from 15 to 26 (n=3) and the males' ages from 12 to 24 (n=4), but parents' ages were within ranges of parents producing within-pair chicks.

Forced copulations

Twenty-four attempted or successful forced copulations were detailed but many more were missed, and information of individuals involved is limited due to the rapid dispersal of birds. Forced copulation attempts were also speedily rebuffed, either because the female escaped directly or during an ensuing dispute when other males arrived. Coercion may play a role in mate acquisition; one female harassed by two males, finally mated with one of them and reared a within-pair chick. Genotyping confirmed that one experienced male successfully sired an extra-pair chick via forced copulation. Forcing copulations may be an indiscriminate behaviour: One male was observed attempting to copulate with a fledgling chick still in the colony from the previous season.

Seven of the non-consensual females did not breed and five were not ringed so were not monitored. Of the other 15 females that subsequently bred, eight were in experienced pair bonds, five were moderately experienced and two had never bred before, similar to sampled proportions of experienced, limited experienced and new pairs (G=0.668, p=0.716). Six females produced within-pair chicks but one pair breeding for the first time and three experienced pairs produced extra-pair chicks. Females subjected to forced copulations produced EPP offspring at double (40%) the population EPP rate (18%). Forced copulations were not limited to inexperienced females but targeted females were usually unguarded and alone. Interestingly, of the 32 males involved in the forced copulation attempts (3 making repeated attempts on different females), 17 bred with a social mate. This sample of males was skewed towards experienced breeders (n=16, the other was a first time breeder) and two were cuckolded themselves.

Female solicited extra-pair behaviours

Eleven females were seen consensually copulating with a non-social mate and two of these females produced extra-pair chicks. One of the females successfully rearing an EPP chick was a first time breeder (the other female had limited experience). In her next breeding season she swapped partners and bred with one of the extra-pair males she had copulated with in the previous season. The other nine females were seen with only one extra-pair mate, but the two that produced extra-pair chicks were associated with two or three non-social mates prior to laying. All levels of breeding experience were represented in similar proportions to the total number of females sampled (G=1.462, p=0.481; naïve females n=2, intermediate experienced females n=4 and experienced females n=5). The sample included females of different reproductive pasts (good females n=1, moderate females n=3 and poor females n=1), also at similar ratios to the population (G=1.323, p=0.516).

Thirty-eight other females were recorded amicably paired, but not observed copulating, with non-social mates (five females associated with two or three extra-pair males). Two of the 38 females produced extra-pair offspring. Although more of these females were experienced (n=22) than naïve (n=7) or intermediate experienced (n=9), the occurrence is similar in proportion to numbers of females sampled (G=1.323, p=0.516) .The females also ranged from good (n=7), to moderate (n=6) and poor (n=9), also in similar ratios to the sampled population (G=0.600, p=0.741). Although females may obtain extra-pair copulations from neighbouring males while their partners are absent from their nest site, females also may actively seek extra-pair interactions elsewhere. For example, a specific female was frequently observed in the study colony paired (courting) with a male at a neighbouring nest site. Breeding records show that she had actually bred once with that male but after that season resumed breeding with her original long-term partner. She was also seen paired and courting with a third unringed male outside the study colony, on Long Ridge (Figure 2.1; chapter 2) during the pre-laying period. However, she did not go on to breed in that season.

Do naïve females produce more extra-pair offspring than experienced females?

Despite fairly large sample sizes, power to detect factors driving EPP amongst subsets of birds was limited given only 45 EPP chicks. However there was no evidence of an effect of pair bond experience or lack thereof (G=0.048, p=0.877). Rates of EPP in newly formed pair bonds between two naïve breeders did not differ from those comprised of experienced individuals (Table 4.2).

Do females with poor reproductive histories use EPP to increase their productivity?

Amongst experienced breeders, historic reproductive success was not significantly related to EPP (GEE pairs: W=0.180, p=0.670; females: W=0.740, p=0.390; males: W=0.010, p=0.940). The occurrence of EPP also did not differ between categories of good and poor pairs (G=0.121, p=0.727; Table 4.2).

Table 4.2 Occurrence of EPP and WPP in pairs with different levels of experience and previous reproductive success.

	EPP	WPP	total
new pair bonds	6 (13%)	39 (87%)	45[a]
new pairs: both parents naïve breeders	2 (11%)	17 (89%)	19[a]
new pairs: both parents had bred before	2 (10%)	18 (90%)	20[a]
intermediate experience pairs	23 (25%)	70 (75%)	93
experienced pairs	16 (15%)	93 (85%)	109
good breeders	5 (13%)	33 (87%)	38
moderate breeders	6 (15%)	34 (85%)	40
poor breeders	5 (16%)	26 (84%)	31

[a] Six new pair bonds were comprised of a combination of naïve and experienced breeders and are excluded from the table.

Parents' dates of return to the breeding colony, their body condition indices on arrival, ages, number of days spent with their social partner, partner arrival synchrony as well as number of days ashore and greatest number of consecutive days ashore prior to laying were not found to differ between pairs producing EPP or WPP chicks (Table 4.3). Further, laying dates, hatching dates and incubation periods did not differ between pairs producing extra-pair and within-pair chicks. However, the time spent brooding chicks post hatching was two days shorter for extra-pair chicks (GEE W=9.200, p=0.002; Table 4.3). Females producing extra-pair chicks tended to interact (couple, court or copulate) with more extra-pair individuals than those producing within-pair chicks. However, the result was non-significant due to the very large variances in numbers of female extra-pair interactions (GEE W=3.240, p=0.072; Table 4.3).

Genetic variation of parents producing extra-pair chicks and within-pair chicks?

Overall differences in heterozygosity were minimal and non-significant, providing no indication that females producing extra-pair chicks are more heterozygous than those producing within-pair chicks (Table 4.4; Figure 4.1). Males rearing extra-pair chicks also had similar levels of heterozygosity when compared with those producing within-pair chicks (Table 4.4; Figure 4.1). Females (but not males) rearing extra-pair chicks tended to be more inbred (averaged greater internal relatedness value) than those producing within-pair chicks (Table 4.4; Figure 4.2). Internal relatedness also tended to be higher in females failing to rear chicks (F=1.424, p=0.244; Table 4.4).

Table 4.3 Mean, standard deviation and sample size (n) of characteristics associated with parents' pre-laying and pair behaviour (significant differences shown in bold).

	parents of EPP chicks	parents of WPP chicks
females		
arrival date	9 Dec ±8 days n=43	9 Dec ±9 days n=198
days present	5.1 ±2.2 days n=44	4.8 ±2.0 days n=200
consecutive days present	2.3 ±1.1 days n=44	2.3 ±1.0 days n=199
interactions with other birds	0.39 ±0.9 interactions n=44	0.21 ±0.5 interactions n=202
condition index	-202 ±738 n=37	-182 ±682 n=183
age	18 ±6 years n=19	16 ±5 years n=85
number of previous partners	1.4 ±0.6 partners n=45	1.3 ±0.7 partners n=202
males		
arrival date	2 Dec ±5 days n=44	2 Dec ±6 days n=202
days present	15.4 ±6.8 days n=45	16.6 ±6.3 days n=202
consecutive days present	8.8 ±5.3 days n=45	8.7 ±5.6 days n=202
interactions with other birds	0.27 ±0.8 n=45	0.39 ±0.7 n=200
condition index	293 ±1023 n=44	131 ±916 n=195
age	17 ±5 years n=23	17 ±6 years n=108
number of previous partners	1.5 ±0.6 n=45	1.5 ±0.7 n=202
pairs		
days mates simultaneously present	2.6 ±1.7 days n=44	2.4 ±1.3 days n=202
difference in mates arrival day	6.8 ±8.2 days n=42	7.0 ±8.6 days n=200
mean lay day	29 Dec ±6 days n=45	30 Dec ±5 days n=201
mean hatching day	19 Mar ±6 days n=37	18 Mar ±6 days n=173
incubation period	79 ±1.2 days n=37	79 ±1.6 days n=172
brood period	**31 ±5 days n=37**	**33 ±4 days n=160**

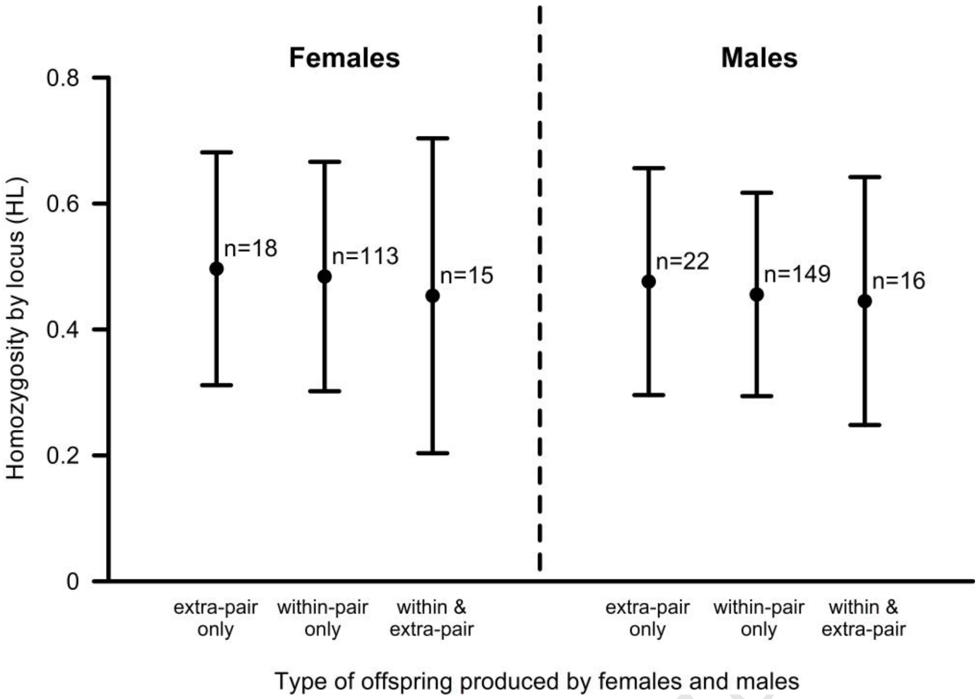

Figure 4.1 Means (± standard deviation) of homozygosity by locus (HL) show that both males and females rearing WPP, EPP or one of each chick had similar levels of heterozygosity.

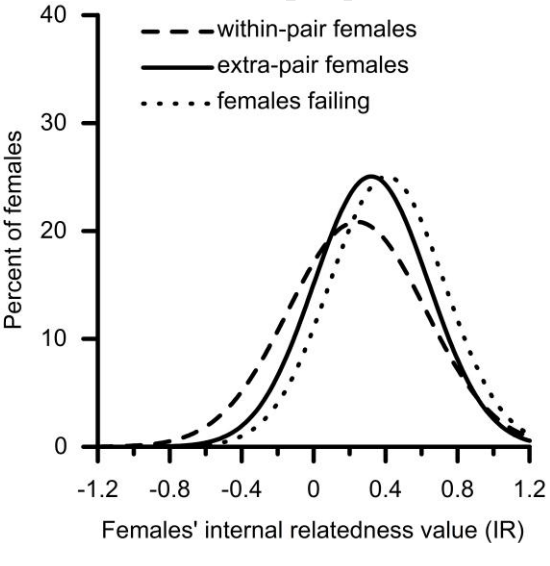

Figure 4.2 Gaussian fits of internal relatedness values (IR) showed females raising extra-pair chicks tended to be slightly more inbred than those rearing within pair chicks. Those failing to produce offspring (paternity could not be tested) were more inbred than those producing offspring.

Table 4.4 Genetic characteristics of parents failing to rear a chick, rearing only within-pair chicks, rearing only extra-pair chicks, rearing one within-pair and one extra-pair chick and overall average. Data presented are the mean ± standard deviation (sample size).

	homozygosity by locus	standard d^2	standard heterozygosity	internal relatedness
females	0.482 ±0.191 (187)	0.306 ±0.110 (186)	1.578 ±0.110 (186)[b]	0.438 ±2.066 (183)
failed	0.527 ±0.183 (16)	0.283 ±0.087 (16)	1.615 ±0.087 (16)	0.423 ±0.237 (15)
rearing WPP chicks	0.484 ±0.182 (113)	0.298 ±0.095 (112)	1.585 ±0.095 (112)	0.287 ±0.621 (112)
rearing EPP chicks	0.496 ±0.185 (18)	0.298 ±0.116 (18)	1.582 ±0.116 (18)	0.321 ±0.328 (18)
rearing WPP and EPP chicks	0.454 ±0.250 (15)	0.397 ±0.043 (15)	1.480 ±0.197 (15)	0.232 ±0.399 (15)
males	0.470 ±0.170 (240)	0.294 ±0.086 (241)	1.598 ±0.098 (241)[b]	0.234 ±0.432 (238)
failed	0.488 ±0.180 (23)	0.263 ±0.046 (23)	1.609 ±0.046 (23)	0.198 ±0.455 (22)
rearing WPP chicks	0.456 ±0.161 (149)	0.280 ±0.051 (150)	1.615 ±0.051 (150)	0.197 ±0.386 (148)
rearing EPP chicks	0.476 ±0.180 (22)	0.288 ±0.059 (22)	1.610 ±0.059 (22)	0.197 ±0.397 (22)
rearing WPP and EPP chicks	0.445 ±0.220 (16)	0.240 ±0.159 (16)	1.564 ±0.043 (16)	0.148 ±0.458 (16)
population[a]	0.476 ±0.180 (427)	0.299 ±0.098 (427)	1.589 ±0.098 (427)[b]	0.324 ±1.402 (421)
failed	0.504 ±0.180 (39)	0.271 ±0.066 (39)	1.612 ±0.066 (39)	0.289 ±0.394 (37)
rearing WPP chicks	0.468 ±0.171 (262)	0.288 ±0.073 (262)	1.602 ±0.073 (262)	0.236 ±0.502 (260)
rearing EPP chicks	0.485 ±0.180 (40)	0.292 ±0.088 (40)	1.597 ±0.088 (40)	0.253 ±0.368 (40)
rearing WPP and EPP chicks	0.449 ±0.220 (31)	0.316 ±0.197 (31)	1.523 ±0.159 (31)	0.189 ±0.425 (31)

[a] The population sample includes some families in which paternity testing failed. Sample sizes vary because some genetic analyses failed for some individuals.

[b] Expected standard heterozygosity from simulation is 1.421 for the population, 1.410 for females and 1.430 for males.

Genetic similarity between mates

The observed mean mated pair relatedness (MP=0.029 ±0.414, n=179) was greater than expected from random mating (simulated range -0.075 to -0.280) suggesting selection for genetically similar mates in the population. Chicks showed a mean AI of 0.935, which was marginally higher than the simulated range of 0.630 to 0.930, giving some evidence that reproductive success is influenced by mate incompatibility.

Females and males raising extra-pair chicks tended to show greater genetic similarity to each other (MP=0.190 ±0.384, n=18) than those raising within-pair chicks (MP=0.062 ±0.380, n=111; t=1.895, p=0.064). Females and males in pairs producing one extra-pair and one within-pair chick tended to be even more genetically dissimilar to each other. However, the average of these pairs is strongly influenced by an outlying pair; excluding this outlier shows pairs producing one extra-pair and one within-pair chick to be typical of the population (MP=-0.162 ±0.605, n=15; Figure 4.3). Parents in pairs that failed during the egg or young chick stage tended to be more genetically similar to each other (MP=-0.034 ±0.397, n=15) than parents that successfully reared offspring (regardless of paternity), albeit also non significantly (t=0.825, p=0.421).

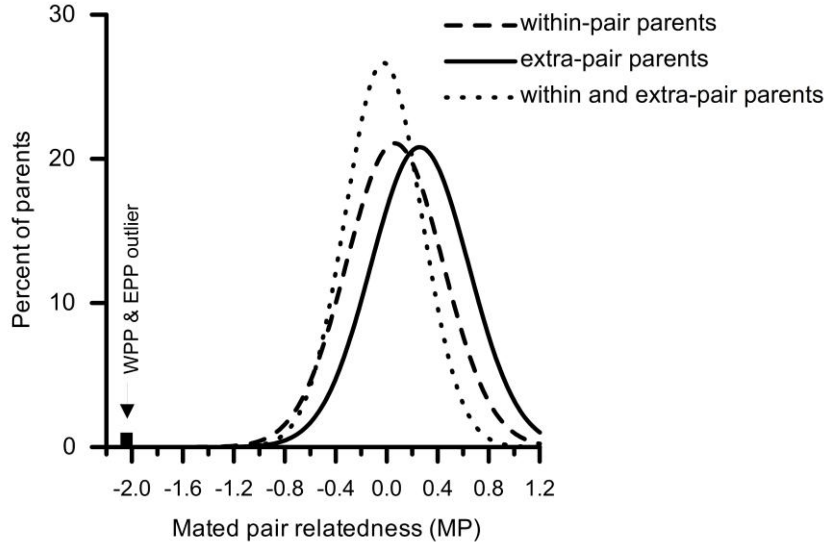

Figure 4.3 Gaussian fit of mated pair relatedness (MP) of pairs raising extra-pair chicks was slightly greater than pairs producing within-pair chicks. The distribution of mates producing one EPP chick and one WPP chick falls within the population’s distribution when an outlying pair is removed.

Are extra-pair chicks more genetically variable than within-pair chicks?

Regardless of the measure used, heterozygosity of within-pair chicks (e.g. HL=0.523 ±0.179, n=201) was similar to that of extra-pair chicks (e.g. HL=0.551 ±0.154, n=45; t=1.080, p=0.284; Figure 4.4). Internal relatedness for all chicks (IR=0.294 ±0.358, n=273) did not differ from values created by simulations (p=0.860; IR range 6.990 to -3.600). Outlying internal relatedness values of two within pair chicks were removed from analyses. Internal relatedness of within-pair chicks (IR=0.327 ±0.315, n=198) and extra-pair chicks (IR=0.284 ±0.433, n=45) were not significantly different (t=0.628, p=0.533) indicating that extra-pair chicks are not more outbred than within-pair chicks. Siblings from pairs producing one WPP and one EPP (i.e siblings sharing maternal but not paternal genes) showed no difference in heterozygosity (t=1.055, p=0.309, n=15) or internal relatedness (t=0.007, p=0.995, n=14), indicating that females did not increase their offspring's genetic diversity through EPP.

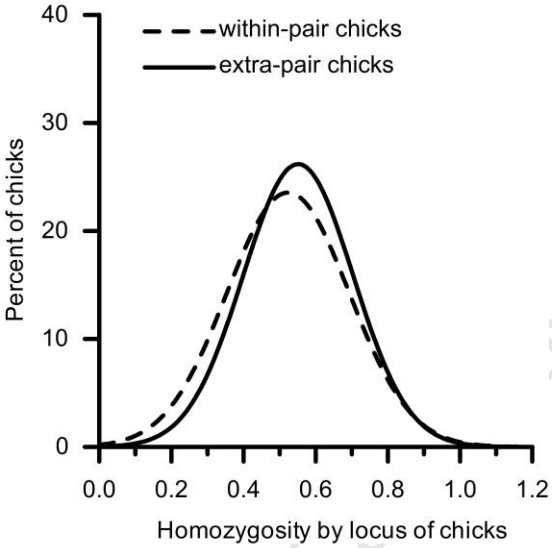

Figure 4.4 Gaussian fit of EPP chicks' heterozygosity (measured as homozygosity by locus, HL) follows a similar distribution to that of WPP chicks.

Is there lowered parental investment in extra-pair chicks?

Although greater, failure rate of EPP chicks (21%) was not significantly different from that of within-pair chicks (10%; χ^2=2.305, p=0.130; Table 4.5). The sex ratio of EPP chicks was female biased (χ^2=5.688, p=0.017), but was similar to the female-biased ratio of within-pair chicks (χ^2=2.546, p=0.111; Table 4.5). Chick growth rates and projected fledging masses did not differ between extra-pair and within-pair chicks (Table 4.5).

Table 4.5 Mean chick survival, sex and growth parameters (± standard deviation) of within-pair and extra-pair chicks.

	extra-pair chicks	within-pair chicks
percent fledged	79% n=34	91% n=147
percent female offspring	69% n=45	54% n=200
female chick fledging mass	12.4 ±1.4 kg n=19	12.3 ±1.4 kg n=72
male chick fledging mass	13.2 ±1.1 kg n=8	14.1 ±1.3 kg n=58
female chick growth rate	0.023 ±0.006 g/day n=19	0.023 ±0.006 g/day n=72
male chick growth rate	0.026 ±0.007 g/day n=8	0.024 ±0.006 g/day n=58

Discussion

Rates of EPP in Wandering Albatross at four different colonies (Table 4.6) were fairly consistent ranging from 6% to 24%, levels typical of socially monogamous species (Griffith *et al*. 2002). Jouventin *et al*. (2007) suggest that there may be little annual variation in EPP in Wandering Albatrosses because factors leading to changes in extra-pair copulation rates should not vary from year to year. However, there is some indication of inter-year variability at both South Georgia and Marion Island, but samples are too small to confirm a pattern. Rates exceed levels predicted to effect estimates of lifetime reproductive success (Burg and Croxall 2006). For demographic modelling purposes, it is arguably necessary to continue paternity testing in studies monitoring pedigrees and individual breeding success so that accurate estimates of individual lifetime reproductive success are available (Newton 1989).

Table 4.6 Global (χ^2=2.762, p=0.251) and annual (χ^2=8.954, p=0.111) variation in EPP of Wandering Albatrosses.

location	year	EPP
South Georgia[a]	1998	21% (n=53)
	1999	6% (n=51)
Crozet and Kerguelen Islands[b]	2002-2003	11% (n=75)
Marion Island	2007	17% (n=82)
	2008	14% (n=85)
	2009	24% (n=80)

[a] Burg and Croxall (2006)

[b] Jouventin *et al*. (2007)

Individual characteristics and breeding behaviour have little influence on EPP

While there was a tendency for pairs to produce either extra-pair or within-pair sired chicks rather than to switch between the two strategies, EPP was not employed to counteract low rates of past reproductive success. Since multiple past breeding partners did not correlate with EPP, there is also little evidence to suggest that extra-pair mothers are those shopping around for potentially better mates. EPP was not linked to inexperience and youth (as at Crozet and Kerguelen Islands' Wandering Albatrosses; Jouventin *et al*. 2007). This suggests that experience does not enable females to evade forced copulations and EPP is not driven by youthful or inexperienced female extra-pair liaisons. A male-biased operational sex ratio (Jouventin *et al*. 1999, Weimerskirch *et al*. 2005, chapter 6) may increase opportunities for extra-pair copulations (Burg and Croxall 2006). In addition to paired males, the presence of divorced and widowed males, males who bred in the previous season and socially immature but physiologically reproductive males amplifies the male-biased sex ratio in the population (Burg and Croxall 2006). Wandering Albatross males' greater sizes may enable them to force copulations and my genotyping results indicate forced copulations can result in EPP. Yet, there is evidence that females solicit or respond consensually to extra-pair behaviour which also results in EPP. In Waved Albatrosses (*Phoebastria irrorata*), females that arrived before their mates (and would have been unguarded) had more extra-pair copulations (Huyvaert *et al*. 2006). Yet neither synchrony in partner arrival nor partners' pre-laying time together was correlated with EPP in the Marion Island Wandering Albatross population. Pre-laying body condition, arrival and presence at the breeding colony of both females and males did not influence the occurrence of extra-pair sired chicks. This indicates that mate guarding and mate availability do not entirely prevent EPP in Wandering Albatrosses.

Parental investment and tolerance of EPP

Females risk desertion by cuckolded partners (Westneat *et al*. 1990, Westneat and Sargent 1996, Burg and Croxall 2006). Although there are a few notable cases of single females successfully rearing Wandering Albatross chicks, lone parenting results in lowered chick growth rate or chick death (Brown and Adams 1984, Tickell 1968). While other costs of extra-pair behaviour may occur (e.g. exposure to disease or predation; Westneat *et al*. 1990, Westneat and Sargent 1996, Burg and Croxall 2006), the similar growth and survival of extra-pair and within-pair chicks suggests that social fathers do not discriminate against extra-pair chicks. Jouventin *et al*. (2007) also found that cuckolded Wandering Albatross males at Crozet and Kerguelen did not decrease parental investment and suggested that reduced breeding effort would decrease their future parental attractiveness. Males might tolerate cuckoldry for future reproductive success rather than desert the female, because divorce is costly (in terms of missing breeding years; Bried and Jouventin 2002). Individuals with reduced future reproductive opportunities might be more tolerant of cuckoldry (Mauck *et al*. 1999). A male-bias in the population means that divorced males are less likely to re-pair than females and would have fewer future reproductive opportunities than females (Jouventin *et al*. 1999). A further difference between the sexes is that males restore body fat more rapidly than females (Weimerskirch 1995). Thus, the cost of rearing young may be slightly lower for males than females, resulting in males tolerating cuckoldry (Jouventin *et al*. 2007). It is also possible that males do not abandon extra-pair young merely because they lack cues to identify whether the chick is their own, or not (e.g. Møller and Birkhead 1993, Fietz *et al*. 2000, Rios-Cardenas and Webster 2005). Cross fostering experiments provide indirect support for the notion that albatrosses fail to discriminate against EPP chicks, given neither abandonment nor reduced parental care occurred (Prince and Ricketts 1981, chapter 8).

Genetic influence on EPP

Similarities in genetic heterozygosity and inbreeding between mothers of within-pair and extra-pair young or between cuckolded and non-cuckolded males rule out lowered genetic diversity as a reason for infidelity in the studied population. This was also observed in the Crozet and Kerguelen Islands populations (Jouventin *et al*. 2007). Genetic diversity in the Marion Island population was low, consistent with predictions that natal philopatry (Inchausti and Weimerskirch 2002) results in low genetic variability. It is possible that selection against EPP is reduced in such species because costs to the cuckolded parent are reduced when sires are close relatives (Fietz *et al*. 2000, Huyvaert *et al*. 2000). In the population, paired individuals were more genetically similar to each other than was expected under random mating circumstances. Breeders failing at the egg and young chick stage tended to show an even greater degree of genetic similarity between paired individuals. This may be indicative of low genetic diversity and inbreeding causing mate incompatibility or inbreeding depression in the population. At Crozet and Kerguelen Islands genetically similar birds were more likely to have EPP chicks (Jouventin *et al*. 2007). There was a similar tendency at Marion Island, but the effect remained weak despite a much larger sample. However, the tendency for parents of EPP chicks to be more genetically similar than those producing WPP chicks gives some support for the notion that extra-pair behaviour counters potential incompatibility (Zeh and Zeh 2003). These results suggest that lowered genetic diversity may influence EPP in natally philopatric populations. Yet, similar levels of heterozygosity and inbreeding between within-pair and extra-pair chicks provides little evidence that females produce genetically more variable offspring by cuckoldry. In a population with low genetic diversity, even extra-pair sires are genetically similar, limiting the genetic diversity of all young.

EPP may be a means to counter mate incompatibility (causing egg or early chick failure), with its occurrence facilitated by low costs (e.g. the failure of cuckolded males to discriminate against EPP offspring). Nevertheless, which individuals take part in extra-pair behaviour and the reasons for their behaviour remain unclear, even after intensive study with large sample sizes. With little cost involved, cuckolding males derive clear benefit from forced copulations (Petrie and Kempenaers 1998), but some females interacted consensually with extra-pair mates. Extra-pair behaviour may be dependant on many different factors acting variably according to the circumstances of pairs and females. Since females make choices according to their differing individual circumstances, the ability to distinguish behavioural and genetic effects driving EPP is limited. Our results suggest that EPP provides little genetic advantage to females. However, a female may derive social benefits from extra-pair behaviour. In the event of mate loss, she would have recourse to an alternative mate from an established relationship.

Long-term monitoring of Wandering Albatrosses at Marion Island does not usually include paternity testing and so my estimates of long-term reproductive success cannot account for skewed reproductive success of cuckolded and cuckolding males. I have not attempted to exclude extra-pair paternity when examining parental investment behaviours in following chapters. Removing the EPP samples reduced already limited sample sizes to impractically low samples. However, the fact that parents do not appear to discriminate against extra-pair young should alleviate some concerns about the impact that EPP has on the relationship between parental investment and reproductive success. Few studies can account for EPP when examining long-term reproductive success in long-lived species, and so the information I present should remain comparable to currently published studies. Continued paternity testing as part of long-term monitoring would be ideal. Besides allowing for more accurate calculations of lifetime reproductive success, a greater sample of extra-pair families might confirm trends hinted at by smaller sample sizes.

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Chapter 5

Differences in egg size do not reflect differences in long-term reproductive success in Wandering Albatrosses

Abstract

Large egg size has been related to chick survival and development, and used as a measure of egg and maternal quality, however the pattern may not be universal across bird species. Egg size of Wandering Albatrosses (*Diomedea exulans*) at Marion Island did not influence hatching or fledging success. Eggs that did not hatch and the subset that were addled were similar in size to successful eggs. Eggs size was not influenced by chick sex, year or parental condition, but larger eggs were incubated for longer suggesting that larger eggs require greater breeding investment. Experienced breeders produced significantly larger eggs than first time breeders. Female age was positively correlated with egg size until 30 years, after which egg size decreased. The principal factor explaining egg size was individual variation, suggesting that egg size is driven by genetic parental characteristics. However, long-term reproductive success did not correlate with egg size, suggesting that differences in egg size do not correlate with fitness.

Keywords

age, body condition, egg size, incubation, offspring sex, parental experience, reproductive success

Introduction

Investment in eggs is one means of investing in a breeding attempt (Congdon 1989, Whittow 2002). If egg attributes influence the outcome of breeding attempts and offspring fitness, eggs are potential indicators of individual reproductive ability. Investment in eggs may be measured in terms of number, volume and weight or from egg material such as shell thickness and, destructively, by internal content such as yolk proteins (Williams 1994, Christians 2002, Whittow 2002). Procellariiformes produce one egg clutches (Brooke 2004) and differential investment in eggs is in size and constituents rather than number. An ability to produce large eggs may be limited by metabolic costs involved, the additional nutrients that would be required and has also been related to female mass and size (Congdon and Gibbons 1985, Nager and Zandt 1994, Chastel *et al*. 1995, Perrins 1996, Monoghan and Nager 1997, Christians 2002). Egg size in some species is related to timing of laying (Christians 2002) however, larger eggs generally require longer incubation (Wilson 1991, Bollinger 1994, Whittow 2002). Incubation is energetically taxing (Croxall and Ricketts 1983, Whittow 2002) and so laying a larger egg pre-requires greater parental investment in terms of incubation. As producing and subsequently incubating larger eggs is costly (Perrins 1996, Whittow 2002), parents in poor body condition may be unable to produce eggs or may produce smaller eggs (Chastel *et al*. 1995).

More than one third of studies (36%) showed supplementary diets increased egg size (to a maximum of 13%; Christians 2002). As birds age they may learn to forage more effectively and/or develop the ability to convert their food into egg content more efficiently. As a result, in some species, egg size changes with maternal age and experience (Lequette and Weimerskirch 1990, Croxall *et al.* 1992, Christians 2002, Michel *et al.* 2003). Yet, age and experience usually explain only a small proportion of variation in egg size (Christians 2002), with most variation resulting from variation amongst individuals (e.g. Williams 1990, Czapulak 2001, Christians 2002, González-Solis *et al*. 2004). As individuals lay successive eggs that are more similar in size than those laid by different birds, egg size is thought to be a heritable trait (van Noordwijk 1981, Moss and Watson 1982, Bacon and Mountford 1990, Christians 2002).

Numerous studies have shown a positive relationship between egg size and hatching success, hatchling survival, growth and ultimately fledging (e.g. Amundsen and Stokland 1990, Croxall *et al.* 1992, Williams 1994, Czapulak 2001, Michel *et al*. 2003, Cabezas-Díaz and Virgós 2007, Silva *et al*. 2007). Consequently, larger eggs have become synonymous with good quality eggs, and by extension with good quality parents (e.g. Bolton 1991, Silva *et al*. 2007) although hatching success and parental characteristics are independent of egg size in some species (e.g. Meathrel *et al*. 1993). Fewer data are able to relate egg size to individuals' long-term reproductive productivity as a measure of parental quality. Using long-term breeding data, for Wandering Albatrosses (*Diomedea exulans*) at Marion Island, I test whether better parents lay larger eggs (i.e. birds with successful reproductive histories).

At South Georgia, eggs laid by the same individual in separate breeding seasons were more similar in size than eggs laid by different birds suggesting that Wandering Albatross egg size is also a genetically controlled maternal characteristic (Croxall *et al.* 1992). If egg size is a genetic trait, a female will lay similar sized eggs throughout her breeding career (allowing for variability due to age and experience). Given that larger eggs have higher hatching success (Croxall *et al.* 1992), I predict that females tending to lay larger eggs will sustain high levels of breeding success throughout their lifetime. As Wandering Albatrosses produce single-egg clutches, complexities associated with investigating parental investment in terms of number of eggs per season are eliminated.

Initially I establish baseline information by determining average egg size and whether it correlates with timing of breeding and influences breeding success in the Marion Island population. Egg size may vary according to environmental conditions (Croxall *et al.* 1992) so I check whether egg sizes differ in the years studied. Wandering Albatrosses are sexually dimorphic and so I also test whether eggs of male chicks are larger than those of female chicks. Maternal age, experience and body condition are known to influence egg size in Wandering Albatrosses (Lequette and Weimerskirch 1990, Croxall *et al.* 1992). Thus these characteristics are included in the analyses with the expectation that older parents, with more breeding experience and better body condition produce larger eggs.

Methods

From 2007 to 2009, at Goney Plain study colony at Marion Island (46°52'S, 37°41'E) the length and breadth of 173 Wandering Albatross eggs (43% of eggs laid) were measured in the first half of the incubation period using Vernier callipers accurate to the nearest 0.1 mm. Besides content changes, eggs are porous and water loss during incubation alters egg mass, yet the volume of eggs remains stable and may be calculated using the equation:

$$V = k_v LB^2$$

where V is egg volume, L is egg length (mm), B is maximum egg breadth (mm) and k_v is the volume constant (Hoyt 1979). I use an associated measure of egg size, fresh egg mass, which is the weight directly after laying, and may be obtained by substituting a weight constant (k_w) for the volume constant (k_v) in the equation:☐

$$M = k_w LB^2$$

where M is fresh egg mass. k_w is species specific and may also vary between populations at different localities (Hoyt 1979). In the absence of the specific value for K_w for Marion Island's Wandering Albatrosses, I used the value for Wandering Albatrosses at Bird Island, South Georgia (0.0005722 g mm^{-3}; Croxall *et al.* 1992). ☐

Monitoring the fate of the egg

Nests at Goney Plain were checked daily from before laying commenced until chick brooding finished. Thereafter chicks were checked every 10 to 15 days until fledging to determine chick survival. Stage of failure (egg or chick) was recorded and eggs failing as a result of parental behaviour (inadequate nests, abandonment, predation) were distinguished from eggs failing because they were deformed or addled (chapter 2). Addled eggs were either rotten when lost by the parents or were incubated beyond the hatching date. Chicks from 134 of the measured eggs were sexed following molecular methods described by Fridolfsson and Ellegren (1999; chapter 6).

Age, breeding experience, reproductive potential and body condition

Historic breeding records were used to determine parents' breeding experience, past reproductive success and ages at Goney Plain study colony as described in chapter 1. Parents were sexed by behaviour and mates comparative plumage (Weimerskirch 1989) and these methods verified as 100% accurate from a subsample of genetically tested adults (chapter 4). Pairs with extensive breeding experience (n=155) were specifically targeted so that I could examine the relationship between their breeding history and egg size, but eggs from some pairs with limited (n=12) or no prior breeding experience (n=5) were also measured. Chicks have been ringed at Goney Plain since 1983 and a subset of the females (42%) and males (48%) were known age birds. Females were grouped into age categories (5-9, 10-14, 15-19, 20-24, 25-29, 30-35) for comparison of mean egg size per age group. The first principal component (PC1) of culmen length, bill depth at the gonys, minimum depth behind the gonys, tarsus length and flattened wing length provided an index of body size for each adult (chapter 3). Pre-laying mass-size indices were used as a measure of parent body condition using methods described in chapter 3.

Statistical analyses

Egg sizes (overall, per year and per categories) were tested for normality using the Shapiro test and by eye. As all samples were parametric, single factor analysis of variance (ANOVA) was used to test for egg size differences between breeding seasons and categories of previous reproductive success. All statistics were run in R (R Development Core Team 2010).

The relationships between egg size and hatching success, chick sex, parents' attributes and breeding phenology were assessed via generalised estimating equations (GEE) in geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2005) of the R programme. A generalised additive mixed model (GAMM) was used to examine the non-linear relationship between female age and egg weight (from the mgcv library in R; Zuur *et al*. 2009). Eggs cross fostered between pairs of different categories of previous reproductive success (chapter 8) were excluded from laying date, hatching date and breeding success statistics. ANOVA was used to detect the most appropriate models (Zuur *et al*. 2009). Although 173 eggs were measured over the three years, some females laid two or three of these eggs. In order to account for an effect of individuals or pairs, they were introduced as a random effect in the GEE. Hierarchical partitioning (Chevan and Sutherland 1991) using the R package hier.part (Walsh and MacNally 2008) was used to investigate the proportion of the variance explained by each dependent variable in the best fitting models. Together with hierarchical partitioning, generalised linear models (GLMs) were used to assess the influence of individuals on variation in egg size (Crawley 2008).

Results

Egg length and breadth averaged 132 mm (range: 118 mm to 147 mm) and 82 mm (range: 76 mm to 87 mm; Table 5.1). Average estimated fresh egg mass over three seasons was 505 g (standard deviation ±34 g) and the largest egg was 32% larger than the smallest egg. Egg size did not differ from year to year (F=0501, p=0.823; Table 5.1). Eggs from Marion were larger in estimated fresh mass and breadth than those sampled in South Georgia (estimated fresh mass: t=4.751, p<0.001; breadth: t=3.245, p<0.001; length: t=1.200, p=0.116; Table 5.1).

Does egg size correlate with breeding success and offspring sex?

Eggs hatching averaged larger (508 ±31 g n=101) than failed eggs (500 ±39 g n=22), but non-significantly (GEE W=0.836, p=0.360), possibly due to large variance in egg size. A subset of the failed eggs that were addled (497 ±43 g n=11) averaged smaller than others that failed during incubation (500 ±39 g n=10; GEE W=0.17, p=0.865) and than eggs that hatched (GEE W=1.09, p=0.277). Eggs giving rise to male chicks averaged larger (511 ±28 g n=56) than female chicks (505 ±33 g n=78), but again non-significantly (GEE W=134, p=0.248).

Table 5.1 Wandering Albatross mean egg length, breadth and estimated fresh egg mass (± standard deviation, range) at Marion Island and South Georgia.

year	sample	length (mm)	breadth (mm)	estimated fresh mass (g)
Marion 2007	53	132 ±5.6, 118 - 147	81 ±2.1, 76- 85	498 ±35, 396 - 566
Marion 2008	51	133 ±4.9, 123 - 146	82 ±1.7, 79 - 86	518 ±29, 447 - 582
Marion 2009	69	131 ±5.7, 118 - 143	82 ±2.1, 77 - 87	501 ±34, 407 - 585
Marion total	173	132 ±5.3, 118 - 147	82 ±2.0, 76 - 87	505 ±34, 396 - 585
South Georgia	54[a], 1607[b]	131 ±5.6, 114 - 142[a]	81 ±1.9, 79 - 86[a]	490 ±40, 393-561[b]

[a] Tickell (1968)

[b] Croxall *et al*. (1992)

Breeding phenology

Laying date did not correlate with egg size but smaller eggs were incubated for shorter periods (GEE W=11.9, p<0.001; Figure 5.1) and hatched earlier (GEE W=8.7, p=0.003; Figure 5.1). Brood period did not vary with egg size. Inclusion of all terms in a GEE found incubation period was the only variable correlated with egg size in the best model. Hierarchical partitioning analyses including individual pairs, laying and hatching date and incubation period indicate that individuals or pairs account for 91% of the models variance, incubation for 5%, hatching date for 3% and lay date for <1%.

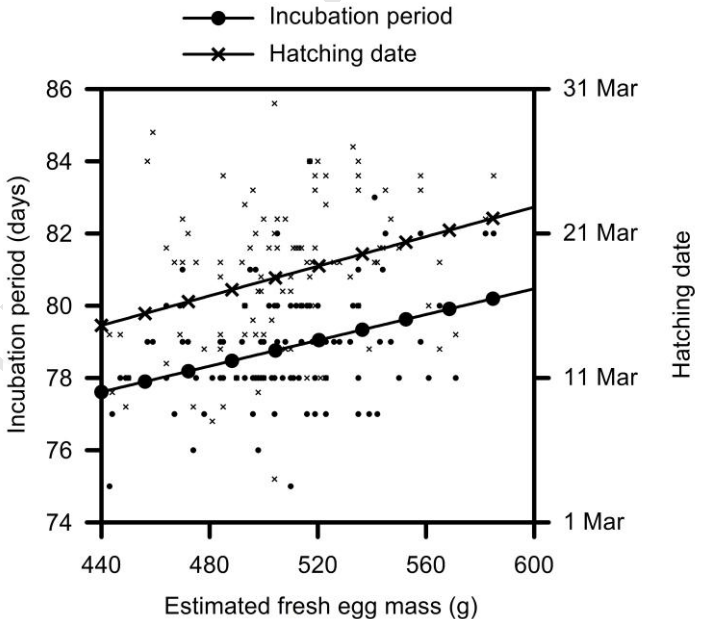

Figure 5.1 Larger eggs were incubated for longer (GEE W=11.9, p<0.001) and hatched later (GEE W=8.7, p=0.003) than smaller eggs.

Parental characteristics in relation to egg size

A null GLM was significantly improved when individual females (∆AIC=172) or pairs (∆AIC=166) were run against estimated fresh egg mass indicating that eggs of any two individuals are more dissimilar than eggs laid by the same individual. Egg size did not correlate with female body size (GEE W=2.628, p=0.105). Egg size also was not related to parent body condition indices upon arrival at the colony (males: GEE W=1.1, p=0.290; females: GEE W=0.2, p=0.650). Egg size tended to increase with breeding experience, but the difference was only significant when comparing experienced with new breeders (GEE males; W=27.6, p<0.001; females: W=16.3, p<0.001; pairs: W=16.6, p<0.001; Table 5.3). However, it should be noted that samples of first time breeders were small compared with experienced breeders. Female's age, as a continuous term, smoothed in a GAMM, was significantly related to egg size (GAMM F=93.0, p=0.004; Figure 5.2). Egg size increased with female's age up to age 20, then remained stable (Figure 5.2). There was some evidence of egg size being small in very old females (>30 years), but the sample size was too small to demonstrate this conclusively. However, models including parents' condition indices, age and experience (using all three categories) showed both females' and males' ages (GEE female's age: W=4.7, p=0.030; male's age: W=13.1, p=0.001;) and experience (GEE female's experience: W=46.8, p=0.001; male's experience: W=80.3, p=0.001) all influence egg size. Nevertheless, hierarchical partitioning indicates a strong influence of individual pairs on the variation in egg size, with individuals (females or pairs) accounting for 86% of the variance explained by the model, followed by female age (7%), male experience (3%) and male age and female experience (2% each).

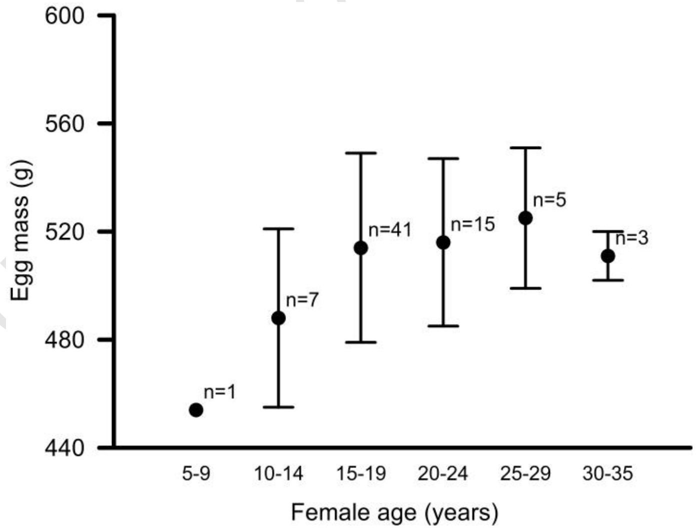

Figure 5.2 Egg size increased for females from ages 5 to 20, remained stable for females between 20 and 30 years but decreased when produced by females older than 30 (GAMM F=93.0, p=0.004).

Table 5.3 Estimated fresh egg mass in grams (mean ± standard deviation (n)) for females, males and pairs of different experience and GEE results of experience category comparisons.

	experienced breeders	limited experienced breeders	new breeders	W	p value
males	507 ±34 g (n=157)	497 ±34 g (n=11)	473 ±15 g (n=4)	0.08	0.780
females	507 ±34 g (n=158)	493 ±32 g (n=11)	475 ±18 g (n=3)	0.68	0.410
pairs	507 ±34 g (n=155)	500 ±34 g (n=12)	478 ±18 g (n=5)	0.00	0.980

Amongst experienced birds, there was no difference in egg size between categories of good, moderate or poor pairs in each year (Table 5.4) or between good, moderate and poor males, females and pairs in all three years combined (Table 5.6). Egg size did not correlate with the continuous measure of previous reproductive success either. Experienced parents tend to be older than less experienced birds, but amongst experienced birds, both males' and females' ages were positively correlated with egg size (GEE males: W=16.1, p<0.001; females: W=6.0, p<0.014) while body condition indices and previous reproductive success still did not correlate with egg size. Female age accounted for 4% of the model's variance, while males' ages accounted for 2% and the influence of individuals, once again, accounted for the largest portion of the models variance.

Table 5.4 Estimated fresh egg mass (mean ± standard deviation (n)) for categories of pairs with good, poor and moderate reproductive histories.

year	good pairs	moderate pairs	poor pairs	ANOVA F value	p value
2007	503 ±27 g (n=14)	506 ±31 g (n=16)	491 ±42 g (n=21)	0.92	0.400
2008	518 ±28 g (n=22)	515 ±35 g (n=19)	524 ±21 g (n=10)	0.25	0.780
2009	497 ±40 g (n=15)	500 ±28 g (n=16)	510 ±33 g (n=22)	0.82	0.450

Table 5.5 Estimated fresh egg mass over three years (mean ± standard deviation (n)) for females, males and pairs with good, moderate and poor reproductive pasts and GEE result of comparisons.

	good	moderate	poor	W	p value
males	509 ±34 g (n=40)	506 ±31 g (n=60)	507 ±36 g (n=57)	0.01	0.920
females	505 ±33 g (n=51)	508 ±32 g (n=51)	508 ±36 g (n=56)	0.01	0.920
pairs	508 ±33 g (n=51)	508 ±32 g (n=51)	505 ±37 g (n=53)	1.00	0.760

Discussion

At South Georgia, mean estimated fresh egg mass of Wandering Albatross eggs that failed to hatch were lighter than those that hatched (Croxall *et al.* 1992) hinting towards a correlation between egg size and reproductive success. In contrast to the South Georgian population, data from Marion Island provide only weak evidence for an influence of egg size on hatching success or chick survival. At South Georgia, Croxall *et al.* (1992) found that 55% of the variation in Wandering Albatross egg size was due to differences between individuals, suggesting that genetic differences between females cause variation in egg size. Similarly at Marion Island individual variation accounted for most variation in egg size. Yet surprisingly, at Marion Island, amongst experienced breeders neither maternal, paternal nor pair historic reproductive success (a surrogate measure of lifetime reproductive success) was related to greater egg size. A comparison between more and less productive Grey-headed Albatrosses (*Thalassarche chrysostoma*) also showed that reproductive ability does not correlate with egg size (Cobley *et al.* 1998). Thus, while egg size may be influenced by individual genetic characteristics it does not necessarily relate to quality measured in terms of historic reproductive success.

Wandering Albatrosses are a threatened species so I sought a non-destructive measure of egg quality but it is possible that egg size is not a primary characteristic that distinguishes egg quality in this species. Egg constituents, such as yolk and albumen chemical composition, shell thickness or membrane chemical composition (Williams 1994, Christians 2002, Whittow 2002), may be better measures of Wandering Albatross egg quality. Egg constituents are affected by oceanic pollutants and female nutrient balance during egg formation (Auman *et al.* 1997, Ludwig *et al*. 1998, Jones 1999, Tao *et al*. 2006) and it is feasible that they could also relate to body condition and long-term reproductive success.

At the Crozet and South Georgia Islands, Wandering Albatrosses' egg sizes increased with breeding experience (Lequette and Weimerskirch 1990, Croxall *et al.* 1992). Evidence from the Crozet Island Wandering Albatross population suggests that birds breeding for the first time are less efficient at breeding and foraging than those with more breeding experience (Weimerskirch 1992). Poorer breeding and foraging skills may restrict eggs produced by first time breeders at Marion Island. New breeders spend more time in the colony prior to laying (chapter 3), which may also lead to a deficient diet for inexperienced females during the egg formation period, potentially accounting for their reduced egg size (Perrins 1996).

Croxall *et al.* (1992) emphasized that egg size is associated with age more than breeding experience, and that most studies fail to differentiate between these factors (e.g. Lequette and Weimerskirch 1990). Teasing apart effects of age and experience is difficult since age is positively correlated with breeding experience. However, female age was identified as the parental characteristic most accountable for Wandering Albatross egg size variation at Marion Island. Wandering Albatross egg size increased with female age until 20 years at the Crozet Islands (Lequette and Weimerskirch 1990) and until 25 years at South Georgia (when the upper limit of egg size is reached; Croxall *et al.* 1992). Eggs produced by old females (>35 years) remained similar to the upper limit of egg size at South Georgia (Croxall *et al.* 1992). Weimerskirch (1992) reported a decrease in egg size in females older than 24 years suggesting that reduced egg size is a senescence effect (Weimerskirch 1992). Data suggest that this trend may be repeated at Marion Island, but greater sample sizes in the older age classes are needed to confirm the pattern. Paternal characteristics, possibly through mate selection, correlates with egg characteristics in some species (Fox *et al*. 1995, Gil *et al*. 1999, Cunningham and

Russell 2000). The association of egg size with male's age and experience may be an effect of age assortative mating (Jouventin *et al*. 1999).

It is feasible that eggs resulting in male chicks could be larger in sexually dimorphic species but in both Waved Albatrosses (*Phoebastria irrorata*; Awkerman *et al.* 2007) and Wandering Albatrosses (this study) there was no difference in egg size between male and female offspring. Larger eggs required longer incubation periods, suggesting that larger eggs were laid by Wandering Albatrosses able to invest more in the breeding event, both in terms of egg size and incubation investment. Since larger eggs require greater incubation effort (Tickell 2000, Whittow 2002), which in turn influences the chicks' development (Kim and Monaghan 2006, Olson *et al*. 2006), individuals may be limited in the size of egg they lay. Egg size appears to have limited effect on the outcome of the breeding event or subsequent breeding behaviour of the adults, barring the longer incubation periods. Since egg size is driven by individual variation in Wandering Albatrosses, as in many other species (e.g. Moss and Watson 1982, Williams 1990, Czapulak 2001, Christians 2002, González-Solis *et al*. 2004), it is justifiable to suggest that egg size is a trait controlled by genetic characteristics of the female. I caution against suggesting that egg size reflects parental quality since fitness in terms of reproductive ability did not correlate with egg size.

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Chapter 6

Sex allocation in Wandering Albatrosses at Marion Island

Abstract

While the adult population of Wandering Albatross, *Diomedea exulans,* at the Crozet Islands was male-biased, there was no consistent sex bias amongst offspring prior to 2004. I found the sex ratio of adults at Marion Island was consistently male-biased from 2007 to 2009. Differential fishing mortality of females has been proffered as a cause of the male-biased adult population but offspring sex ratio biases may drive biases in the adult population too. To enable an understanding of geographical and temporal variation in offspring sex bias I used molecular techniques to sex offspring from Marion Island from 2006 to 2009. More female than male young were raised in all four years, with an overall sex ratio of 1:1.29 males to females. Continued sexing of chicks and monitoring of sexed chicks from different populations is required to determine whether offspring sex ratios equalise towards a 1:1 ratio in the adult population (through differential mortality) or if they cause sex biases in the reproductive population. Further, since sex biases in fledgling populations may cause sex ratio skews in future breeding populations, offspring sex ratios should also be included in demographic modelling of Wandering Albatrosses.

Keywords

offspring sex bias, operational sex ratio, sex ratio

Introduction

Sex allocation theory predicts that parents differentially adjust investment in offspring sex according to the cost or benefit of producing the different sexes (Frank 1990, Kokko and Jennions 2008). Fitness can be maximised by biased sex production as an adaptive response to environmental conditions (West *et al*. 2002). With the development of molecular techniques, some studies on avian offspring sex ratio have strongly supported theories that parents differentially produce male or female offspring to their benefit (Komdeur 1996, Pike and Petrie 2003, Donald 2007) but others have not shown predicted offspring sex ratio biases (e.g. Watson 1982, Kojola and Helle 1994, Cockburn and Double 2008). Conflicting results, frequently confounded by small sample sizes, have left much debate regarding offspring sex adjustment. Further studies are needed to explain taxonomic patterns, mechanisms of sex determination and to explain why different organisms show variation in sex ratio adjustment (West *et al.* 2002). Understanding of offspring sex ratio adjustment requires studies of multiple populations over several years as well as investigation into factors driving individuals' differential investment in the sexes.

In Procellariiformes which produce single-egg clutches, a comprehensive study of Waved Albatrosses (*Phoebastria irrorata*) from 2002 to 2004 at Isla Española, Galapagos did not show deviation from the 1:1 sex ratio at hatching stage despite a bias towards females in the adult population (Awkerman *et al*. 2007). Offspring of the Crozet Island Wandering Albatrosses, *Diomedea exulans* were variably biased towards either sex or gender equal prior to 2004 (Weimerskirch *et al.* 2000, 2005, Blanchard *et al.* 2007). A male biased sex ratio has been reported for adult Wandering Albatrosses at breeding colonies at the Crozet Islands (Jouventin *et al*. 1999, Weimerskirch *et al.* 2005) due to an apparent excess of males within the reproductive non-breeders. A male bias in the adult population may result from the reportedly higher rates of long-line female fatalities than male fatalities (Weimerskirch and Jouventin 1987, Croxall and Prince 1990, Jouventin *et al*. 1999) but may also be driven by biased production of male offspring (Donald 2007). However, males are more likely to be recorded in a colony than females because prior to laying males are present at the colonies for longer than females (chapter 2). The resultant greater probability of detecting males may be influencing estimates of adult sex ratios and unbiased counts of breeding birds of both sexes are required to confirm a male-biased adult sex ratio (Donald 2007).

Understanding biases in sex ratios in fledglings, recruits and breeding adults provides information that can be used to increase accuracy of demographic models of Wandering Albatrosses (e.g. Inchausti and Weimerskirch 2002, Mills and Ryan 2003, Donald 2007). This in turn would enhance conservation protocols of this Vulnerable species (BirdLife International 2011). I sought to complement available offspring sex ratio data by establishing proportions of male and female Wandering Albatross chicks produced at the Prince Edward Islands, which support a significant proportion (44%) of the global Wandering Albatross breeding population (Ryan *et al*. 2009).

Methods

Offspring sex ratio

From 2006 to 2009, Wandering Albatrosses laid 981 eggs within three study colonies at Marion Island, the larger of the Prince Edward Islands (46º52'S, 37º41'E). Of these eggs, 711 (72%) chicks were sexed. Most samples were chick blood, collected at the end of the brood phase (April to May) but three were analysed from tissue samples (all in 2007) salvaged from crushed or predated eggs and 11 (one in 2006, four in 2007 and six in 2009) were analysed from tissue samples collected from chick carcasses. A further 44 chicks were sampled outside the study colonies in 2006 to boost sample size of that year.

Blood (100 µl) was collected from the tarsal vein, using 23 G needles, of post brood phase chicks and stored in lysis buffer (a Longmire's solution of proportions 100 mM Tris, 100 mM EDTA, 10 mM NaCl and 0.5% SDS) and duplicates were stored in 96% ethanol. Total genomic DNA was extracted using an extraction solution of 10% Chelex® 100 Resin (BioRad), 10 mM Tris, 0.2% SDS and 5 µl of Proteinase K (100 mg/mL). Approximately 20 µl of blood was added to 200 µl of the extraction solution and incubated at 65 ^{o}C for at least eight hours followed by boiling for 10 minutes. DNA was amplified using polymerase chain reaction (PCR) and sex-specific primers for birds (Fridolfsson and Ellegren 1999).

As the study ran over four years, some pairs produced multiple chicks that could be sexed. To assess whether pairs were biased towards the production of one sex or produced female and male chicks equally, a chi-squared contingency table was used to compare frequencies of the possible combinations of sibling sex. In a few cases pairs produced more than two chicks. To simplify the analysis, only the first two chicks produced were included in the analysis.

Non-breeder and operational sex ratio

The operational sex ratio includes the actual and potential reproductive individuals available for breeding (Emlen and Oring 1977) and was calculated at Goney Plain in 2007, 2008 and 2009. The adult sex ratio includes all breeding aged birds, including those that may not be available to breed in a given season (Donald 2007). I was not able to sample breeding aged birds that remained at sea during the breeding season and so I limit my investigation the operational sex ratio at the colony during specifics breeding season. Prior to laying, observers were present in the Goney Plain colony for an average of nine hours a day from the start of the pre-laying period until laying began (chapter 2). Breeding aged adults were recorded twice daily (morning and evenings) and new arrivals recorded when seen during the day. After the first egg was laid, birds present at the colony were recorded once a day. Numbers of non-breeders (adults who did not subsequently breed but had bred before and were present in the colony prior to mid-laying) were used to determine whether there was an excess of one sex in the unpaired reproductive sector of the population. As the Wandering Albatross breeding season extends over twelve months (Tickell 1968), parents feeding chicks from the previous season may be present during the pre-laying period of the next breeding season. These parents were excluded from annual sex ratio analyses unless they had previously failed at breeding and were thus likely to attempt breeding in successive years. Males are larger and have a whiter plumage than their mates and so paired males were distinguished from females according to Gibson’s (1967) plumage scores and via behavioural differences. Sexes of non-breeders were determined from historic breeding data using the same method. DNA sexing (Fridolfsson and Ellegren 1999) of a subsample of 91 adults verified that these sexing methods were accurate for all tested adults (chapter 4).

Since females spend short periods in the colonies during the pre-laying phase and males tend to stay for many days (Tickell 1968, 2000, chapter 2) it is possible that field observers recorded most males present whereas some females that actually visited the colony were not seen. This could result in an inaccurately estimated operational sex ratio (Donald 2007). In each year’s pre-laying period, daily numbers of females and males arriving for the first time in the colony are expected to decline after mean arrival date. To control for non-breeding females missed during the pre-laying period, I compared curves of the cumulative number of non-breeding males and females arriving per day to assess whether data collection has been biased towards recording males. I tested various S-shaped functions (Crawley 2008) and the Gompertz logistic equation,

$$Y = Ae^{-e^{-k(t-t_i)}},$$

fitted most suitably to the curve of cumulative number of breeders and non-breeders arriving per day ($r^2 \geq 99\%$). Y represents the number of birds that arrived by a specific day (t), k is the number of new birds seen per day and t_i is the day on which the number of new birds seen per day starts to decrease. The asymptote (A) was used as the estimated number of non-breeding males and females arriving each season. These estimated numbers were compared to the actual numbers of non-breeders recorded.

Results

Offspring sex ratio

Of 981 eggs laid in three study colonies over four years, a total of 270 (28%) could not be sexed due to failure at the egg stage (n=163); hatchling death prior to sampling (n=88) and failure of DNA extraction (n=19). Over all four years 166 (16%) eggs failed to hatch (of which three were sexed) and 149 chicks died during chick rearing (of which 61 were sexed). In 2006 and 2007 significantly greater numbers of female chicks were produced and this trend was repeated, non-significantly, in 2008 and 2009 (Table 6.1). With a ratio of 1:1.29 males to females there was an overall significant bias towards production of females (56%; Table 6.1).

Table 6.1 Numbers of chicks sexed and male and female chicks produced at study areas at Marion Island from 2006 to 2009. Values of significantly different ratios are highlighted in bold.

	% sexed (n=eggs laid)	% male chicks (n)	% female chicks (n)	$\chi^2_{0.05,2}$	p value
2006	83% (n=199[a])	41% (86)	59% (122)	**5.89**	**0.015**
2007	76% (n=258)	43% (84)	57% (113)	**3.98**	**0.046**
2008	65% (n=253)	48% (80)	52% (85)	0.10	0.756
2009	68% (n=271)	43% (80)	57% (105)	3.11	0.078
total	73% (n=981)	44% (330)	56% (425)	**11.70**	**0.001**

[a] This number excludes the additional 44 chicks that were sampled outside study colonies to boost the sample size of 2006.

A total of 225 pairs produced two chicks that could be sexed, 12 produced three and one pair produced four chicks. Of the 238 pairs, 47 successively produced two male chicks, 80 pairs produced two female chicks successively and 111 produced one of each sex. Sex of the second offspring was independent of the sex of the first offspring ($\chi^2_{0.05,2}$=0.4305, p=0.752). Since pairs were not biased towards the production of a specific sex, multiple chicks from the same pairs are unlikely to affect the female biased sex ratio.

Non-breeder and operational sex ratio

Modelled numbers of non-breeders present prior to laying (from the asymptote of logistic equations performed on the cumulative number of birds arriving per day; Figure 6.1) slightly altered some of the sex ratios. However, these modelled numbers (Table 6.2) did not alter patterns of significance, so the

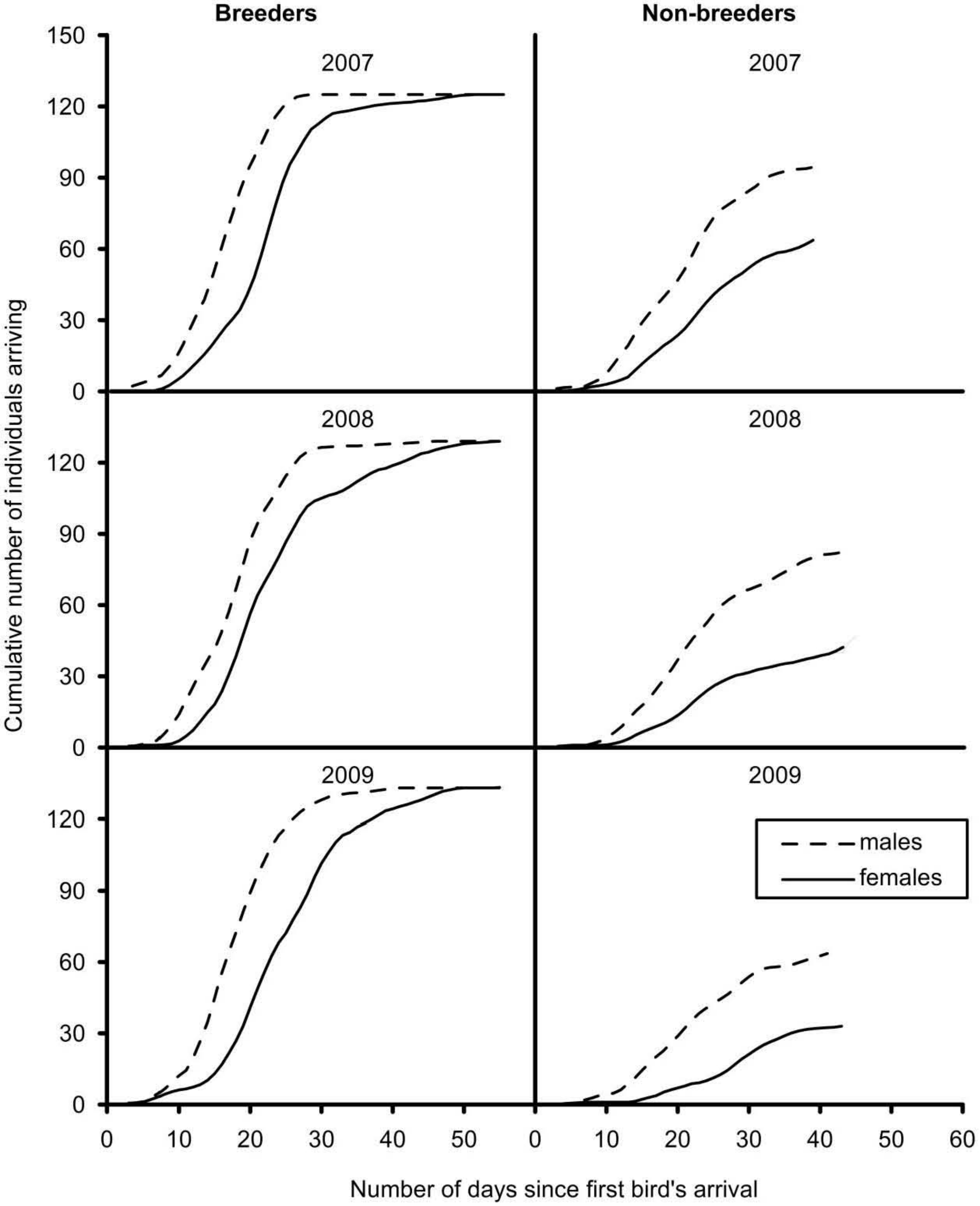

Figure 6.1 Cumulative numbers of breeding and non-breeding males and females arriving per day from the start of the pre-laying period (16 November).

ratios and statistics run on the observed numbers of non-breeders seen prior to laying are presented (Table 6.2). In each year, the numbers of non-breeding males at Goney Plain was significantly greater than that of non-breeding females (Table 6.2). The operational sex ratios were consistently male-biased, albeit non-significantly (Table 6.2). Some males that were unpaired in the study subsequently formed partnerships and bred, indicating that the unpaired males were not too old to breed.

Table 6.2 Numbers of adults at Goney Plain during the pre-laying period, the colony’s operational sex ratios and the ratio of non-breeding males to females (bold denotes significant differences). Numbers of non-breeding males and females in parentheses are the asymptote of Gompertz best fits models.

	breeding adults	non-breeding adults		operational sex ratio			non-breeders sex ratio		
	males:females	males	females	ratio	$\chi^2_{0.05,2}$	p value	ratio	$\chi^2_{0.05,2}$	p value
2007	130:130	97 (98.1)	67 (71.2)	1 : 1.2	1.98	0.145	**1 : 1.4**	**5.13**	**0.019**
2008	131:131	83 (85.3)	47 (43.8)	1 : 1.2	3.13	0.069	**1 : 1.8**	**9.42**	**0.002**
2009	138:138	65 (67.2)	34 (39.6)	1 : 1.2	2.09	0.134	**1 : 1.9**	**9.09**	**0.002**

Discussion

I found a consistent female-biased chick production by Wandering Albatrosses at the Prince Edward Islands. This contrasts with reports from Possession Island in the neighbouring Crozet Islands, where chick production was gender neutral in four years and the only significant deviation was for a male-biased production in one year (Table 6.3). Variations in offspring sex ratios stress the importance of monitoring different populations within a species. Concurrent investigations into offspring sex ratios at prominent Wandering Albatross breeding colonies (such as Crozet Island and South Georgia) would yield valuable information regarding geographical variation in sex ratios.

Table 6.3 Numbers of female and male chicks produced from subsamples of the 1986, 1994, 1999, 2002 and 2003 cohorts of Wandering Albatrosses at Possession Island of the Crozet Islands.

	number sexed	% male chicks	% female chicks	$\chi^2_{0.05,2}$	p value
1986[a]	59	56% (n=33)	44% (n=26)	0.61	0.362
1994[a]	28	50% (n=14)	50% (n=14)	0.04	1.000
1999[b]	256	57% (n=147)	43% (n=109)	**5.32**	**0.018**
2002[c]	41	56% (n=23)	44% (n=18)	0.39	0.435
2003[d]	90	42% (n=38)	58% (n=52)	1.88	0.140
total	474	54% (n=255)	46% (n=219)		

[a] Chick sexes inferred from birds that returned to breed, sexed as adults and using their growth characteristics prior to fledging (Weimerskirch *et al.* 2000).

[b] Results from Weimerskirch *et al.* (2005) using molecular sexing methods.

[c] Results reported in Weimerskirch *et al.* (2005) but methods unknown.

[d] Results from Blanchard *et al.* (2007) using molecular methods.

Evidence suggests that biased offspring production is unlikely to be a factor influencing the male-biased operational sex ratios. However, questions remain as to whether the current offspring sex ratio bias found at Marion Island is in response to current male biased operational sex ratios and whether differential female fishery mortality drives the male-biased operational sex ratio (Donald 2007). The sex-ratio of the entire adult population could not be determined since some adult birds do not return to the breeding colonies every year, however the annual operational sex-ratio in the colonies reflect conditions that breeding birds experience. Although the male bias in the colony is non-significant, birds experience a bias towards unpaired breeding aged males when present in the colony in each season. In a monogamous species, the same number of males as females will have the opportunity to breed. Thus, in a colony characterised by a male biased operational sex ratio, females are a limiting and currently more valuable resource. Under these circumstances one might expect that pairs have the potential to differentially increase their fitness by producing female chicks. However, age assortative mating prevails in Wandering Albatrosses (Jouventin *et al*. 1999): females usually mate with males of similar age. This means that, should the same proportions of males and females survive their juvenile years, future operational sex ratios will be female biased and over production of females will not improve an individual's fitness. On the other hand, should female biased mortality continue, future operational sex ratios may drift to equality. But in this situation, females suffer greater mortality and so producing females is a risky strategy unlikely to differentially increase fitness.

Increased male biased operational sex ratios may result in increased male aggressive competitive behaviour for mates (although aggressive competition decreases if the male bias is greater than 2:1; Weir *et al*. 2011). The tendency for birds to experience a male bias in the breeding colonies may explain aggressive behaviour associated with extra-pair copulations described in chapter 4. An increased male biased operational sex ratio also reduces courting and increases mate guarding and copulation (Weir *et al*. 2011). It facilitates monogamy in species requiring paternal care for rearing young because male bias operational sex ratios promote males monopolizing females, as they are a valuable resource (Ligon 1999).

West *et al.* (2002) predicted more extreme sex ratio adjustment in more predictable environments. Predictable environments increase accuracy of assessment of the costs and benefits involved in rearing the different genders (e.g. Komdeur 1996). Ability to predict these costs increases an individual's chances of gaining differential fitness benefits from rearing the more valuable or more energetically costly sex. Environmental and anthropogenic impacts causing differential mortality in adult Wandering Albatrosses may be temporary or unpredictable, particularly given changes in fishing effort and ongoing mitigation initiatives (BirdLife International 2011). If female-biased fishery mortality drives the male-biased operational sex ratio, and if this mortality is reduced, when the current cohort recruits into the breeding population the female-bias may still exist. In this case the operational sex ratio of the breeding population would swing towards a female bias. Offspring sex ratios, variation in environmental factors driving sex ratios (of offspring and adults) as well as naturally higher mortality rates that post fledging males suffer in comparison to females (Weimerskirch *et al.* 2005) may singly or in combination alter the population's future operational sex ratio.

Mills and Ryan (2003) make a case for including skewed sex ratios of the adult population (caused by female biased long-line mortality in Wandering Albatrosses) in demographic modelling since it reduces fecundity. Sex biased chick production can result in a skewed sex ratio in reproductive populations and, as such, sex biased offspring production should also be incorporated in demographic modelling. Continued monitoring of Wandering Albatross offspring sex ratios is necessary to understand patterns of sex ratio adjustment in response to changing and frequently unpredictable environmental conditions. This will enable realistic population demographic assessments and thereby enhance conservation protocols. Monitoring of adult and offspring sex ratios should be made in relation to continued and altered fishery activities to determine the effects of anthropogenic impacts on demography and to ensure that fishery activities are sustainable.

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Chapter 7

Sex-biased chick production in Wandering Albatrosses: Who produces the rarer sex?

Abstract

Manipulating offspring sex allows individuals to maximise their fitness by balancing characteristics such as body condition and reproductive ability with the requirements involved in raising more or less energetically costly young. There may also be fitness tradeoffs if the sex ratio of the population is skewed, especially for dimorphic, monogamous species such as Wandering Albatrosses, *Diomedea exulans,* which produced female-biased cohorts of offspring at Marion Island from 2006 to 2009. Males are larger and require more investment during rearing, yet mortality of male and female chicks is similar and does not alter the female biased offspring sex ratio. Newly formed pairs tended to produce greater proportions of female than male young, consistent with the smaller energetic investment required to produce female offspring. However, this bias was driven by individuals with previous breeding experience from prior pair bonds, as first time breeders produced males and females equally. Parent age, even when controlled for breeding experience did not significantly influence offspring sex. Amongst experienced pairs (stable pair bonds with at least eight years as breeders or four prior breeding attempts), birds with higher average reproductive success more commonly produced female young, whereas parents with poor reproductive histories produced a greater proportion of males. Parents with lowered reproductive ability who produce males may be taking risky reproductive approaches that results in lowered chick production rate. Offspring sex was related to the body condition indices of experienced mothers. Better condition mothers produced male offspring, as predicted by Trivers and Williard theories.

Keywords

age, body condition, breeding experience, offspring sex ratio, reproductive success, sex ratio bias, Trivers and Williard Theory

Introduction

Annual production of Wandering Albatross, *Diomedea exulans*, chicks at Marion Island between 2006 and 2009 was skewed towards females (chapter 6). Trivers and Willard (1973) predicted that when ecological or parental conditions differentially influence benefits gained from producing either male or female chicks, parents should adjust productions of sons or daughters during a specific breeding event to maximise their fitness (Frank 1990, Kokko and Jennions 2008). This suggests that female chick production in Wandering Albatrosses at Marion Island maximised fitness from 2006 to 2009.

Sex-biased chick production may depend on factors such as the species' ability to manipulate offspring sex, their life history traits (West *et al.* 2002) as well as environmental conditions (Komdeur 1996). An ability to manipulate offspring sex increases fitness through enabling parents to balance the cost of rearing a more energetically expensive offspring and differentially increasing their fitness or failing to successfully rear the offspring (Trivers and Williard 1973). This balancing should consider factors such as parent condition, age, experience, reproductive ability and conditions specific to each breeding event. In species in which females are smaller and require less energy to raise, parents with decreased body condition may skew their offspring production to females (Trivers and Williard 1973, Nager *et al.* 1999, 2000). Old parents with lowered reproductive viability due to senescence and young parents with relatively less chance of breeding successfully also tend to produce female young (Weimerskirch *et al*. 2005, Lecomte *et al*. 2010). Similarly, if breeding experience increases reproductive efficiency, first time breeders may be expected to produce more of the least costly sex. Parents with low rates of historic reproductive success may be indicative of individuals with inherently lowered reproductive ability and have been shown to skew offspring production to the less costly sex (Weimerskirch *et al*. 2005).

Wandering Albatrosses are sexually dimorphic and Weimerskirch *et al.* (2000) concluded that rearing the larger male chicks was more costly than rearing a female chick. Wandering Albatrosses are long-lived, socially monogamous biennial breeders and produce a single-egg per breeding season, which simplifies investigation into causes and effects of producing the different sexes. I investigate whether, in a population deviating from a Fisher 1:1 offspring sex ratio production, individuals maximise their fitness by balancing their individual characteristics with the cost of raising chicks. Parents of lower historic reproductive success, in poorer body condition, with less breeding experience and young and the very old are expected to rear females, the less energetically costly sex.

Methods

Molecular techniques (Fridolfsson and Ellegren 1999) were used to sex 711 Wandering Albatross chick samples collected over four years (2006-2009) from 981 eggs laid in three long-term monitored colonies at Marion Island (chapter 6). In 2006 a further 44 samples were collected from outside the study colonies to boost sample size of that year. The fates of all eggs and chicks were followed through to fledging stage or until the egg failed or chick died.

Parents' ages, past breeding experience and historic reproductive success were determined from long-term monitoring of uniquely banded individuals from the three study colonies (chapter 1). Age was known for a subset of mothers (49%, n=349) and fathers (58% n=415). Adult sex was determined using their behaviour and Gibson's (1967) plumage scores compared between mates (chapter 2) and genetically confirmed for a subsample of birds (chapter 4). For ease of communication I distinguish sex of offspring from sex of parents by referring to female parents as mothers and male parents as fathers through out this chapter. Mass-size regression analyses were used to calculate parent body condition indices upon arrival at the Goney Plain colony (chapter 3).

Chi-square goodness of fit with Yate's correction was used to identify sex ratio biases amongst chicks for each year and for the different categories of breeding pairs. Chicks that were cross-fostered between parents with differing levels of previous reproductive success were excluded from breeding success analyses (although including them did not change the results). Parent age, body condition indices, breeding experience and historic reproductive success were tested in binomial generalised estimating equations (GEEs) to identify factors affecting differential production of male or female chicks. Individual pairs were included as a random effect because some pairs produced more than one chick over the four year study. Models were compared using ANOVA and higher order terms were removed via a backwards stepwise procedure based on significance until the most parsimonious representative model was found (Zuur *et al*. 2009). All statistics were run in R software package (R Development Core Team 2010) and GEE models were run using the package geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2005).

Results

A significantly greater number of female than male chicks were hatched ($\chi^2_{0.05,2}$=10.6, p=0.001) and fledged ($\chi^2_{0.05,2}$=8.8, p=0.003) in the three study colonies at Marion Island, from 2006 to 2009. The observed ratio of male to females chicks hatched was 44:56 (1:1.28). Of the 402 female chicks sexed, 89% (n=359) fledged compared to 90% (n=283) of the 314 male chicks. Chick sex did not affect breeding success (GEE W=2.41, p=0.121). The ratio of male to female chicks at fledging did not differ from that at hatching stage ($\chi^2_{0.05,2}$=0.13, p=0.714).

Effects of age and breeding experience on offspring sex

Parents' ages had no significant influence on chick sex. Pairs breeding together for the first time produced a greater proportion of female than male young in all years, but due to small sample sizes only numbers summed over three years differed significantly from a 1:1 ratio (Table 7.1). However, the ratio of male to female produced by these pairs did not differ from the observed population ratio of 1:1.28 (Table 7.1). Newly formed pairs composed of parents with breeding experience from a previous pair bond produced a significantly greater proportion of females compared to a 1:1 ratio and also to the 1:1.28 population ratio. Newly formed pairs comprised of two naïve parents, on the other hand, produced equal numbers of males and females (Table 7.2). Neither experienced pairs nor pairs with limited experience produced biased offspring sex ratios (Table 7.1). Multivariate GEEs combining both mothers' and fathers' ages and experience showed that even when controlling for experience, parents' ages did not influence offspring sex.

Table 7.1 Male and female chicks produced by newly formed pairs and those with limited or extensive breeding experience from 2006 to 2009 (significantly different $\chi^2_{0.05,2}$ p values are in bold).

	eggs laid	percent sexed	male chicks	female chicks	1:1 p value	1:1.28 p value
new pairs	210	66%	53 (38%)	85 (62%)	**0.008**	0.216
limited experience	358	77%	121 (44%)	153 (56%)	0.061	0.994
experienced pairs	403	74%	139 (46%)	160 (54%)	0.247	0.418

Table 7.2 Offspring sex ratio of new pairs comprised of two naïve parent or two parents with breeding experience (significantly different $\chi^2_{0.05,2}$ p values are in bold).

new pairs: parents' breeding experience	number sexed[a]	male chicks	female chicks	1:1 p value	1:1.28 p value
naïve	57	29 (51%)	28 (49%)	1.000	0.361
prior experience	46	11 (24%)	35 (76%)	**<0.001**	**0.009**

[a] Sample size does not equal the total number of new pairs because new pairs in which parents have different degree of breeding experience are not included here.

Parent body condition indices influencing sex of offspring

Average body condition indices of all fathers' were significantly higher for those producing female chicks than those producing male chicks (GEE W=4.74, p=0.030; Table 7.3) whereas average body condition indices of all mothers' did not correlate with offspring sex (GEE W=0.79, p=0.375). However, average body condition indices of mothers in experienced pairs was significantly greater for those mothers producing males than those producing females (GEE W=4.65, p=0.031; Figure 7.1) but there was no difference in average body condition indices of experienced fathers producing males or females (GEE W=0.08, p=0.770). Of parents in new pair bonds, body condition indices of mothers and fathers were not significantly associated with offspring sex regardless of whether the parents were naïve breeders or had breeding experience in previous partnerships (Table 7.3). The stepwise reduction of GEEs including all parents' body condition indices, confirmed fathers' body condition indices were significantly greater for those producing females (GEE W=5.05, p=0.025). When this model was run on only experienced pairs, mothers' body condition indices, again, had a significant relationship with offspring sex; experienced mothers with greater body condition indices tended to produce males (Figure 7.1).

Table 7.3 Patterns of parent body condition indices linked to offspring sex. Parents are divided into experienced and newly formed pairs and newly formed pairs are further subdivided according to the experience of both parents in the new pair bonds. Significantly different GEE Wald and p values are shown in bold.

	father's condition	W (p) value	mother's condition	W (p) value
all parents	**male < female**	**4.74 (0.030)**	male = female	0.79 (0.375)
new pairs	male = female	2.39 (0.120)	male = female	2.55 (0.110)
new pairs: naïve parents	male = female	0.06 (0.800)	male = female	2.53 (0.110)
new pairs: parents with experience	male = female	1.70 (0.192)	male = female	1.31 (0.253)
experienced parents	male = female	0.08 (0.770)	**male > female**	**4.65 (0.031)**

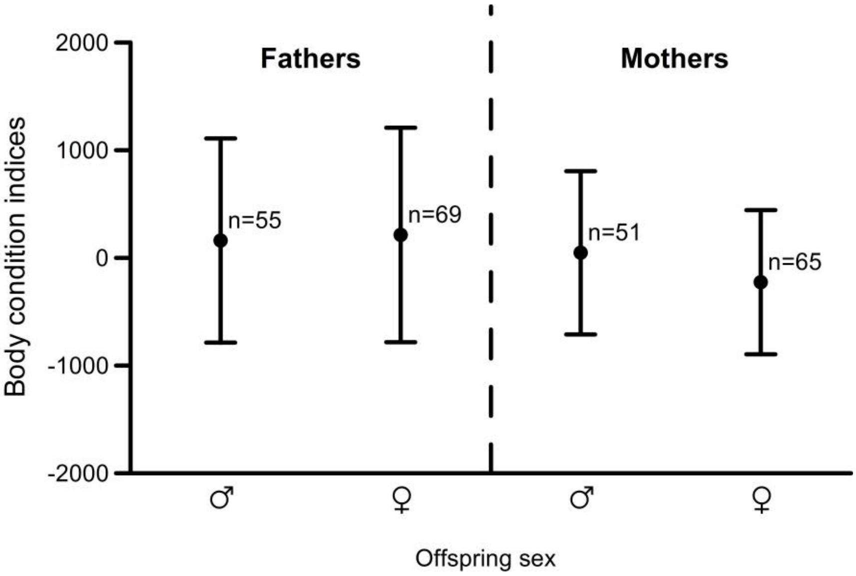

Figure 7.1 Experienced mothers body condition indices (mean ± standard deviation) were greater for those producing male offspring (GEE W=5.45, p=0.020) while body condition indices of experienced fathers producing males and females did not differ significantly.

Relationship between offspring sex and previous reproductive success

Amongst pairs with extensive breeding experience, those with high levels of previous reproductive success (good pairs) tended to produce more females than males (Table 7.4). Pairs with low rates of previous reproductive success, produced more males than expected from the observed population ratio (but not from a 1:1 ratio; Table 7.4). Pairs with moderate levels of previous reproductive success produced significantly more females than would be expected from a 1:1 ratio, but as with good pairs the ratio of male to female chicks did not differ from the observed population ratio (Table 7.4). Biased female chick production appears to be driven by good and moderate pairs more so than by poor pairs.

GEEs also did not show significant relationships between offspring sex and pairs (GEE W=1.21, p=0.270), fathers (GEE W=0.56, p=0.460) or mothers (GEE W=0.04, p=0.840) previous reproductive success run as a continuous variable. Furthermore, GEEs including both parents' body condition indices, age and previous reproductive success yielded no significant model or terms in relation to offspring sex.

Table 7.4 Male or female offspring produced by parents with varying levels (good, moderate and poor) of previous reproductive success (significantly different $\chi^2_{0.05,2}$ p values are in bold).

	eggs laid	percent sexed	male chicks	female chicks	1:1 p value	1:1.28 p value
good pairs	135	82%	50 (45%)	60 (55%)	0.391	0.833
moderate pairs	139	71%	39 (39%)	60 (61%)	**0.044**	0.411
poor pairs	129	70%	50 (56%)	40 (44%)	0.343	**0.036**

Discussion

Wandering Albatross male offspring at the Crozet Islands received larger meals (fathers delivered almost twice as much food to male chicks than those rearing female chicks), had faster growth rates and reached higher asymptotic masses, making them the more costly sex to rear (Weimerskirch et al. 2000). Life history theory predicts that very young birds and very old birds are more likely to be affected by the costs of reproduction than are middle-aged birds (Stearns 1992, Møller *et al*. 2005). At Marion Island, Wandering Albatross reproductive performance is relatively poor in birds <10 years and >25 years old (Nel *et al*. 2003). At the Crozet Islands, male foraging efficiency decreases in birds >25 years old (Lecomte *et al*. 2010), and older birds tend to produce less costly female chicks (Weimerksirch *et al*. 2005). Daunt *et al*. (2001) predicted that optimal sex ratio varies with age when costs of rearing the sexes differ. They found that male Shags, *Phalacrocorax aristotelis*, which are larger and more energetically costly to raise than females, fledge in poorer condition when reared by young as opposed to older parents. In contrast to predictions that old and young birds tend to produce female offspring, age did not influence offspring sex amongst Wandering Albatrosses at Marion Island.

Contrary to expectation that naïve parents should produce more female chicks, they raised equal numbers of the sexes. However individuals with previous breeding experience forming new pairs did show a strong female bias. Successive breeding with the same individual potentially enables breeders to control for aspects that they are less able to predict in newly formed pair bonds, such as their partner's parenting skills. With lowered predictability comes the greater risk of failure when attempting to raise more costly male offspring. Thus, experienced mothers in new pair bonds may tend to produce female offspring to offset the potential unpredictability of a new partner. Individuals breeding for the first time, on the other hand, do not control for their naïvety in this way, in accordance with studies showing that first time breeders are less efficient than experienced breeders (Croxall 1990, Lequette and Weimerskirch 1990).

Parents with lowered body condition were expected to increase their chances of breeding successfully by producing less costly female offspring (Trivers and Willard 1973). Supporting the theory, Blanchard *et al*. (2007) showed better condition Wandering Albatross mothers produce sons at the Crozet Islands. At Marion Island, experienced, but not naïve, mothers also compensated for poor body condition by producing females. Although body condition indices of experienced fathers, in particular, were not significant predictors of chick sex, overall fathers in better body condition (regardless of their experience) were more likely to produce females. That fathers do not compensate for poor body condition by producing the less costly sex suggests that the ability to gauge body condition and manipulate offspring sex is limited to females. The pattern of better condition mothers producing male offspring, occurring in two separate populations of Wandering Albatrosses (Crozet and Marion Islands), lends support to the Trivers and Willard (1973) theory that mothers adjust offspring sex according to their body condition (Blanchard *et al*. 2007).

Teasing apart the effects of age and experience is not simple as naïve breeders are naturally younger than experienced breeders (Croxall *et al.* 1992). Naïve breeders, while producing equal proportions of male and female chicks, also tend to have lower body condition indices than experienced breeders, further confounding the assessment of characteristics controlling offspring sex. Offspring sex appears to be driven by individual experience rather than pair bond experience, because parents with breeding experience, regardless of the length of their concurrent pair bond, produced more females. Body condition indices of only experienced mothers predict offspring sex, suggesting that breeding experience is required by mothers to be able to adjust offspring sex in relation to their body condition.

Consistent differences in reproductive success suggest some parents are better at producing young than others (chapter 1). Although Weimerskirch *et al.* (2005) found that birds with higher levels of past reproductive performance at the Crozet Islands produced more male offspring, at Marion Island pairs with higher and intermediate levels of previous reproductive success more frequently produce females. Parents with poorer reproductive pasts produced more males, which suggests that parents do not control for their reproductive ability by producing the less costly sex. It may be argued that pairs have higher levels of previous reproductive success merely because they take a less costly (and hence less risky) approach by producing female chicks. However, there is no evidence that pairs successively produce same sex chicks (chapter 6). Mortality of post brood phase chicks did not alter the sex ratio bias, suggesting that differential parental ability to provision or protect chicks did not influence offspring sex ratio, despite male chicks being more costly to rear (Weimerskirch *et al*. 2000). I believe that the female sex bias amongst newly-hatched offspring is a result of sex biased egg production. This assumes that failures at the egg stage and that the 9% of hatchling chicks that could not be sexed (most of which died prior to sample collection) would not swing the sex bias (chapter 6).

Egg sizes of male and female chicks are similar (chapter 5) limiting the opportunity for parents to use egg size as a cue to reduce parental incubation investment in either sex.

Although there is little evidence that parents with good reproductive histories attempt to maximise their fitness by producing male offspring, my data support the Trivers-Willard theory because mothers in poor condition were more likely to produce female offspring (Trivers and Willard 1973). Factors that impact on food resources (e.g. fishery impacts on food availability) have the potential to influence parental condition. Indirectly these environmental characteristics could affect offspring sex ratios in species in which offspring sex is influenced by parental condition.

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Chapter 8

Influences of genetic and behavioural parental characteristics on chick survival and growth in Wandering Albatrosses

Abstract

Growth and survival of altricial young are influenced by their parents' abilities to invest in a breeding attempt. Parental care and chick growth in Wandering Albatrosses, *Diomedea exulans,* were correlated with parents' historic reproductive success to determine whether individual variation in long-term reproductive success is driven by differential breeding investment. Experimentally cross-fostering eggs between parents of poor and good reproductive histories showed an increase in reproductive success for poor breeders and a decrease for good breeders. This suggests that both individual egg characteristics and parent breeding behaviours influence the success of a breeding attempt. However, the lack of differences between growth rates and fledging size of chicks despite cross fostering indicates that chick development is largely independent of parents' reproductive histories. This was confirmed by a lack of correlation between parent's long-term reproductive success and chick growth rates and fledging mass or size of chicks. Longer brooding of chicks increased their survival, but chick brooding did not differ between historically unproductive and successful breeders. Better parental body condition indices (mass–size indices) neither increased brooding period nor enhanced chick growth rates, final mass or size. Older and more experienced parents brooded chicks for longer and their chicks grew faster suggesting that breeding competence is a learnt skill.

Keywords

body condition, chick brooding, cross fostering, growth rate, historic reproductive success, parental investment

Introduction

In species producing altricial young, greater investment by parents in a breeding attempt increases their chances of breeding successfully (Gebhardt-Henrich and Richner 1998, Stearns 1992). Greater investment in each breeding attempt could culminate in higher lifetime reproductive success provided the greater investment does not reduce survival or the ability to invest in future breeding attempts (Stearns 1992). Parental investment in a specific breeding event may distinguish parents of different reproductive ability and indicate their potential lifetime reproductive success. Behaviourally influenced investments include pre-laying and gestation or incubation activities as well as offspring protection and provisioning (Gubernick and Klopfer 1981, Prince and Ricketts 1981, Clutton-Brock 1991, Lewis *et al*. 2006, Gardner and Smiseth 2011). Provisioning skills (influencing meal size, frequency, prey quality and pair provisioning co-ordination in biparental species) are reflected in offspring growth rate and final mass or size (Wendeln and Becker 1999, O'Dwyer *et al*. 2007). Some individuals are likely to be more competent at nurturing their young than others, with better parents providing larger or more frequent and better co-ordinated meals resulting in accelerated growth and larger chicks (Gebhardt-Henrich and Richner 1998, O'Dwyer *et al*. 2007). Protecting young against predators and environmental conditions are other forms of investment (e.g. Amat *et al*. 2000, Lewis *et al*. 2004). Protection may be measured as the time spent guarding offspring or the size at which parents leave offspring unattended.

Inter-individual variation in chick development may result from differences in diet, reflecting individual variation in parenting skills or varying food availability (Phillips and Croxall 2003). Developmental variation may also result from inherent differences amongst offspring, reflecting their genetic makeup. In some birds, growth may vary less between chicks produced by the same parents than between chicks produced by different parents, suggesting that chick growth rates are inherited (van Noordwijk and Marks 1998). If growth rate is heritable, siblings from more successful parents should display superior development than siblings from reproductively impoverished parents. For example, Cobley *et al.* (1998) showed, in years of low food availability, chicks from reproductively successful Grey-headed Albatrosses (*Thalassarche chrysostoma*) had a higher hatching mass and attained greater peak mass than those from less successful parents.

Wandering Albatrosses (*Diomedea exulans*) are monogamous, biparental and a single-chick-per-year producing species. Using historic breeding records of Marion Island birds with extensive breeding experience I establish whether historically less productive parents provide less post hatching protection than more successful parents. I also investigate whether chicks from highly successful and less successful parents differ in terms of growth rate and asymptotic mass and size, predicting that; (1) chicks of more successful breeders attain higher growth rate than chicks from less successful breeders, and (2) chicks of highly successful breeders attain greater asymptotic mass and size than chicks from less successful breeders. By cross fostering eggs between historically more and less successful parents I determine whether chick survival and development is dependent on chicks' genetic characteristics or whether survival and development are driven by parental breeding behaviours. If genetic traits are more important, chicks of successful parents are expected to have greater survival and faster growth rates despite being fostered by less successful parents. Alternatively, if parental behaviour is the dominant factor chicks from less successful parents should have enhanced survival and growth rates when fostered by more successful parents.

Wandering Albatrosses are sexually dimorphic (Shaffer *et al*. 2001) and chick development is influenced by sex (Lequette and Weimerskirch 1990, Weimerskirch *et al*. 2000) as well as environmental conditions (e.g. Prince and Ricketts 1981). Thus both offspring sex and year of study must be taken into account when investigating chick development. Age and experience affect foraging and influence provisioning and offspring development across species (e.g. Lequette and Weimerskirch 1990, Weimerskirch 1990, Benton *et al*. 2008, Bell 2010, Lecomte *et al*. 2010). Better conditioned parents are able to invest more in their offspring (e.g. Wendeln and Becker 1990, Lavery and Kieffer 1994). In birds, provisioning is influenced by parental ability to maintain their own condition and offspring of parents in better condition grow faster and to greater size (Wendeln and Becker 1990, Takahashi *et al*. 1999, O'Dwyer *et al*. 2007). Better condition and greater skill obtained through experience or maturity may increase the ability to invest in breeding in Wandering Albatrosses. Condition, age and experience should be considered when relating previous reproductive success to parental investment. Thus, I test whether more experience, better condition and older age result in longer chick brooding, faster chick growth and greater fledging size of chicks.

Methods

Parents' ages, past reproductive experience and long-term breeding success were determined from historic breeding records of uniquely ringed birds at Goney Plain at Marion Island (methods described in chapter 1). Adult sex was determined from behaviour and comparative plumage. These methods were confirmed to be accurate by genetic sexing of a subsample of birds (chapter 4). From 2007 to 2009 parent arrival condition was determined from mass-size residuals as described in chapter 3. Breeding phenology data was obtained through daily checks of the colony from the start of egg laying until the end of chick brooding (detailed in chapter 2). Briefly, these checks provided laying and hatching date (giving chicks' ages) and the period for which parents brooded or guarded their chick directly after hatching. Chicks were weighed and measured (culmen and tarsus length) at the end of the brood phase and blood samples were collected so that chicks could be sexed from DNA (Fridolfsson and Ellegren 1999; chapter 6).

Cross fostering experiment

Eggs were swapped between nests on average 34 days into incubation (but timing of swaps ranged from 6 to 59 days into incubation). Forty eggs were swapped between experienced parents of good and poor reproductive histories. A cross-fostering control included 43 eggs that were swapped between parents of the same level of previous reproductive success (19 between two good pairs, 22 between two moderate pairs and 8 eggs between two poor pairs). Eggs were removed from the first nests, measured (chapter 5), and replaced under the adults in the selected foster nests. A white resin egg of similar weight to a Wandering Albatross egg was placed under parents' of the first nests when their real eggs were removed so that these parents continued to incubate. When the foster parents received their new eggs, their own eggs were measured and then replaced for the false resin egg. Average time out the nest for each swapped egg was six minutes (eggs were protected in a container and cushioned in thermal fleece during translocation to maintain their temperature). Most (89%) swapped eggs were laid within one day of each other but three pairs of eggs were laid within two days of each other and one pair within three days of each other. A non-fostering control was included where eggs were removed from the nest for two minutes, measured, and then returned to their original parents (19 good pairs, 28 moderate pairs and 24 poor pairs). Even though the experiment ran over three separate seasons (2007-2009) in a colony supporting in excess of a hundred nests per year, numbers of pairs with the required breeding experience were limited, which restricted the sample of pairs available for cross fostering.

Chick growth rates

From 2006 to 2009, 352 known age chicks were weighed every 10 days from May to July and every 15 days from July to November, when the chicks began to fledge. Depending on chick size, 5 kg (accuracy 50 g), 10 kg (accuracy 100 g) or 20 kg (accuracy 200 g) Salter macro-line spring balances were used. In 2006 exact hatching date was not recorded so age was calculated from hatching dates assumed to be the mid-point between colony checks made every three to five days. Each chick's growth rate (k), asymptotic mass (A) and time taken to reach asymptotic mass (t_i) were determined using a Gompertz growth curve using mass (M) and age (t) in days:

$$M = Ae^{-e^{-k(t-t_i)}}$$

Gompertz curves are sigmoidal, readily interpretable and resilient to changeable (and less precise) data (Zach 1988). They are deemed suitable for slow-growing Procellariiformes in which chick peak weights exceed adult weights, decreasing shortly before fledging (Richards 1959, Ricklefs 1968, 1973, Ricketts and Prince 1981). The average proportion of variation in mass explained by the fitted Gompertz growth curves was 96% in 2006, 92% in 2007 and 95% in 2008 and 2009.

Chick culmen and tarsus lengths were measured using Vernier callipers (accuracy 0.1 mm). Three commonly used logistic curves were tested for suitability on culmen and tarsus growth curves; Michaelis-Menten, two-parameter and three-parameter functions (Crawley 2008). The coefficients of determination (r^2) of the two- and three- parameter equations were similar and superior to those of the Michaelis-Menten equation. Accordingly, I selected the two-parameter equation as the simplest function that adequately fitted the data (average proportion of variance explained was >97% for both culmen and tarsus growth curves). The two-parameter curve is:

$$L = A\left(1 - e^{-kt}\right)$$

where k is the growth rate, A represents asymptotic length (or final length) of culmen or tarsus and L is the length at age t. This equation predicted more realistic final culmen and tarsus lengths than the 3-parameter model. Growth curves could not be accurately modelled on chicks that died prior to fledging because their growth data was usually incomplete so growth analyses are restricted to chicks that fledged.

Statistical analyses

Statistical analyses were run in R (R Development Core Team 2010). G tests were used to identify differences in survival and Mann-Whitney tests and t-tests differences in chick growth between cross fostered groups (Crawley 2008). Parental breeding effort in terms of chick brooding period, chick growth rate, weight and size at fledging were examined in relation to parents' previous reproductive success, breeding experience, ages and condition using generalised estimating equations (GEEs) from the package geepack (Yan 2002, Yan and Fine 2004, Højsgaard *et al*. 2005). Offspring fostered between parents of different categories of previous reproductive success were excluded from the latter analyses. It should be noted that the reduced sample sizes negatively influenced the robustness of some GEEs but I have included these results as they give insight into the observed trends. A plethora of models was run via a backwards stepwise removal of least significant terms. I present the most parsimonious, best fitting models selected using ANOVA comparisons (Zuur *et al*. 2009). Year and chick sex were included as a fixed effect when they were significantly associated with the response variables. Individuals or pairs were used as a random effect since some pairs and individuals produced two chicks in the study. This also provided the opportunity to examine variation in offspring growth within pairs for a species with a single egg clutch. For this I used generalised linear models compared using Akaike's Information Criterion (AIC; Crawley 2008). Relative variance of variables included in models was determined using hierarchical partitioning (Chevan and Sutherland 1991) via the R package hier.part (Walsh and MacNally 2008).

Results

Breeding success of eggs fostered between pairs of the same quality was the same or higher in all three categories (good, poor and moderate) than those not cross fostered (Table 8.1), indicating that handling eggs and fostering did not impact breeding success. The success of 'good eggs' reared by poor pairs (65%) was lower than 'good eggs' reared by good pairs (88%; Figure 8.1) Poor pairs with 'good eggs' had greater success (65%) than poor pairs rearing 'poor eggs' (56%; Figure 8.1), but neither effect was significant due to limited sample size. Eggs fostered from poor to good pairs had a greater likelihood of succeeding (75%) compared to those cross fostered to poor parents or left with their original parents (56%; Figure 8.1). However, good pairs with 'poor eggs' were less successful (75%) than good pairs rearing good eggs (88%; Figure 8.1), but again effects were not significant due to sample size. A greater sample size may have produced significant differences between the breeding success of 'good eggs' raised by poor pairs and 'poor eggs' raised by good pairs.

Table 8.1 Comparison of breeding success of pairs rearing chicks fostered between parents of the same level of previous reproductive success and those rearing their own offspring. Significantly different levels of breeding success are indicated by bolded G-test and p values.

	Control cross-fostering	*Control without fostering*	G-test value	p value
total	84% n=43	63 % n=71	**5.696**	**0.017**
poor	63% n=8	54% n=24	0.171	0.679
moderate	86% n=22	53% n=28	**5.318**	**0.021**
good	92% n=13	84% n=19	0.488	0.485

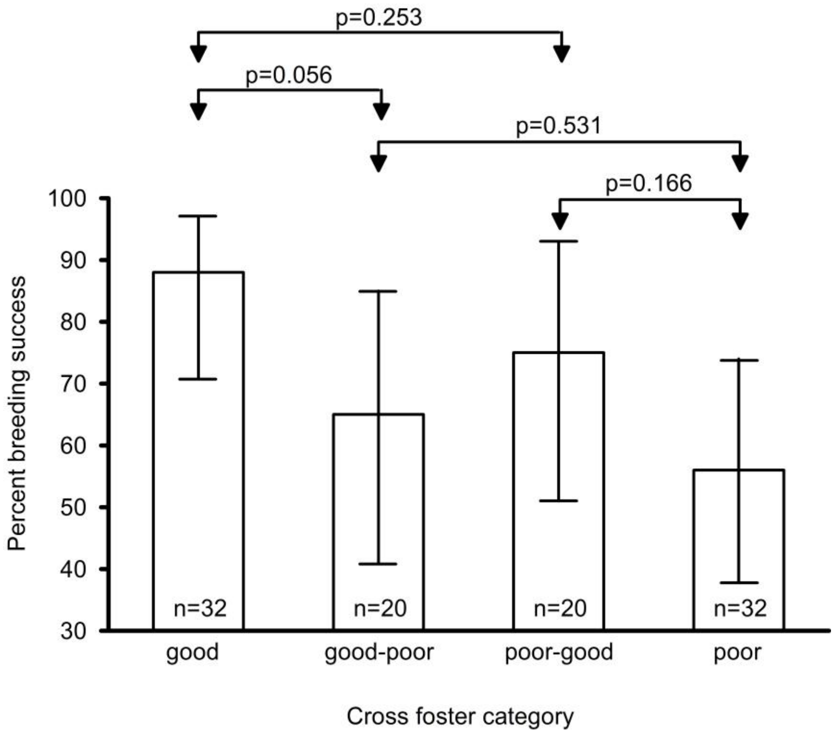

Figure 8.1 Breeding success of experimental cross fostering between pairs of different levels of historic reproductive success (i.e. eggs from ‘good to poor’ pairs or from ‘poor to good’ pairs) compared to success of control eggs (including both eggs fostered between pairs of the same reproductive success category and eggs not fostered). Confidence intervals are also provided because sample size was limited.

Poor parents with good eggs frequently failed as a result of inappropriate behaviours by one or both partners in the poor pair. For example, a female of a poor pair incubated for 49 consecutive days. When her mate finally returned he lost the apparently viable egg (remains from the egg showed signs of an embryo) within ten days, suggesting that he was the weak link in this pair.

One pair with a recent poor reproductive history (they raised three chicks between 1995 and 1999 but between 2002 and 2006 failed at the egg stage five years running) received an egg from parents with a good reproductive history. The 'poor pair' successfully reared a chick from the fostered egg, but their own egg was incubated beyond expected hatching date by the 'good pair'. When it was eventually abandoned, the egg was addled (interestingly 51% of egg failures were addled eggs, mostly incubated beyond hatching date; chapter 2). The 'poor pair' subsequently took off two breeding seasons before attempting to breed again. Perhaps the usual single sabbatical season was not enough for them to recover from the stress of successfully rearing a chick. Thereafter, they failed at egg stage once again. The female’s age is unknown but the male hatched in 1983, making him 19 in 2002 when their string of failures began. Since the pair had reared chicks previously, it is likely that they were genetically compatible and fertile (although extra-pair paternity could also account for the success of these early breeding attempts). These observations suggest that poor incubation techniques, lowered egg quality (possibly due to the females foraging behaviour) or genetically impoverished embryos results in their repeated breeding failures.

There was no difference in growth rate or final size between good to good (n=12) fostered chicks compared to non-fostered ‘good chicks’ (n=16). Neither was there a difference between poor to poor (n=8) fostered chicks compared to non-fostered ‘poor chicks’ (n=15), indicating that cross fostering did not negatively affect chick development. Chicks from moderate parents did have significantly higher culmen growth rate when they remained with their original parents (n=20) than those fostered between moderate pairs (n=18; Mann-Whitney W=227.5 p=0.038). However, final mass was greater for chicks that were fostered (n=18; Mann-Whitney W=64 p=0.006), providing little evidence for an influence of experimental design on chicks’ development.

No difference in growth rates of chicks reared by good versus poor parents was detected. Chicks from poor parents reared by good parents grew at similar rates and to similar sizes as those reared by poor parents. Chicks from parents of good histories reared by those of poor histories did not suffer lowered growth and were similar in size when compared to those reared by good parents. Overall, the cross fostering experiment provided no support to either the theory that chick development is related to parental reproductive histories or that it is related to genetic differences between chicks produced by different parents.

Duration of chick brooding influence on breeding success and relation to parent characteristics

Chick brood period averaged 32 days but varied greatly from 19 to 42 days, 8 to 24 days and 16 to 45 days in the 2007, 2008 and 2009 seasons. Shorter brood periods were associated with later laying and hatching, and longer incubation periods (GEE laying date: W=22.7, p<0.001; hatching date: W=31.2, p<0.001; incubation: W=16.7, p<0.001). Chicks brooded for longer were significantly bigger in tarsus (GEE W=83.9, p<0.001) and culmen length (GEE W=9.7, p=0.002) and heavier (GEE W=134, p<0.001; Figure 8.2) at the end of the brood phase than chicks left alone earlier.

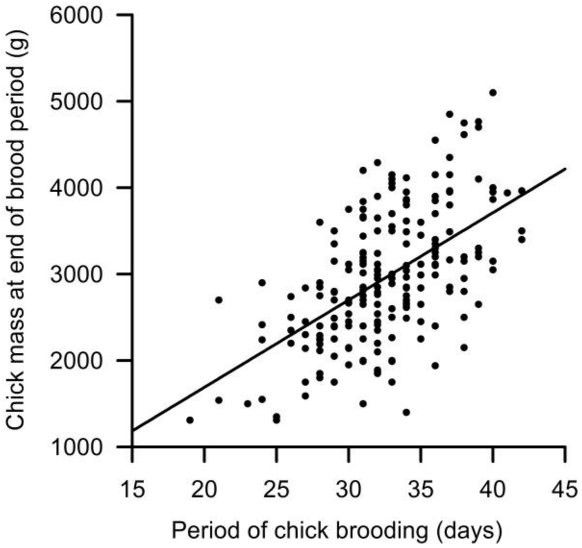

Figure 8.2 Chicks brooded for longer were heavier than chicks that were left alone earlier (GEE W=134, p<0.001).

Chicks that fledged tended to be brooded longer (33 ±4 days n=214) than chicks that subsequently died (31 ±6 days n=33; GEE W=3.2, p=0.074). Amongst chicks that failed, those that were brooded for shorter periods failed earlier (GEE W=4.8, p=0.028). However, brood period was not correlated with pairs' previous reproductive success. Experienced pairs brooded their chicks for longer than breeders with no or limited experience, but new pairs brooded chicks longer than those with limited experience (GEE W=8.9, p<0.003; Figures 8.3). Brood period increased significantly with male's age (GEE W=4.1, p=0.043) and female's body condition index (GEE W=5.5, p=0.019). Hierarchical partitioning including parents' condition indices, ages and experience showed pairs' breeding experience (7%) followed by males' ages (6%) accounted for greater proportions of the variation in brood length than females' ages and parents' condition indices (≤2%). The pairs themselves accounted for 81% of the variation. Multivariate GEEs found pair breeding experience to be the only variable associated with chick brood period, with experienced pairs brooding chicks for significantly longer than those with less experience (Tables 8.2; Figure 8.3). But when the analysis was confined to experienced breeders, male's age was the only significant effect and was negatively related to brood period (Table 8.3; Figure 8.4).

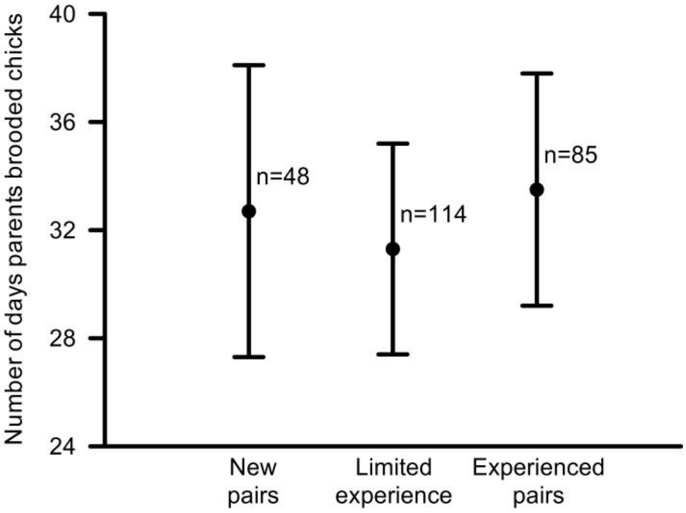

Figure 8.3 Pairs with extensive breeding experience brooded chicks for longer (mean ± standard deviation) than both pairs with limited experience and newly formed pairs (W=8.9, p<0.003).

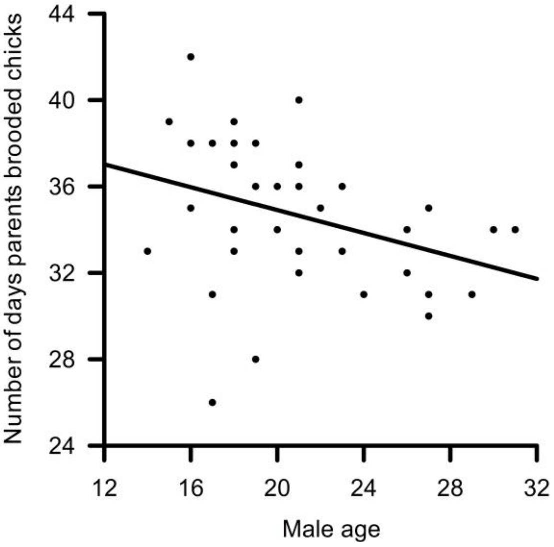

Figure 8.4 Linear models show that amongst experienced pairs, chicks of older males were brooded for fewer days than those of younger males (GEE W=6.2, p=0.013).

Table 8.2 Significant terms in best fitting GEEs explaining chick brood period (n=63), growth rates and size or mass at fledging (all n=56) derived through stepwise removal of terms from a primary model which included pairs' experience, parents' ages and body condition indices.

response variable	terms in best fitting model	effect	W	p value
	pairs' experience:			
brood period	new pairs	positive	6.7	0.010
	limited experienced pairs	positive	19.6	<0.001
growth rate				
mass	females' ages	positive	11.4	<0.001
tarsus	females' ages	positive	9.8	0.002
culmen	females' ages	positive	10.4	0.001
fledging size				
mass	No significant terms other than chick sex and year			
tarsus length	No significant terms other than chick sex and year			
culmen length	No significant terms other than chick sex and year			

Table 8.3 Significant terms in best fitting GEEs examining only experienced pairs. GEEs explain chick brood period (n=21), growth rates and size or mass at fledging (all n=19) and terms included were parents' ages, body condition indices and pairs' previous reproductive success.

Response variable	Terms in best fitting model	effect	W	p value
brood period	male's age	negative	6.2	0.013
growth rate				
mass	females' condition indices	negative	6.2	0.013
tarsus	females' condition indices	negative	7,6	0.006
culmen	No significant terms in final model	-	-	-
fledging size				
mass	No significant terms in final model	-	-	-
tarsus length	No significant terms in final model	-	-	-
culmen length	females' ages (and chick sex and year)	negative	8.7	0.003

Parent characteristics associated with offspring growth rate

Mass, tarsus and culmen growth rates differed between male and female chicks (GEE mass W=8.2, p=0.004; culmen W=7.1, p=0.008; tarsus W=14.8, p<0.001) although their growth rate means were similar (Table 8.4). Mass growth rate was affected by the year in which the chick was reared (GEE W=14.2, p<0.001). Chicks gained weight faster in 2006 and 2009 compared to 2007 and 2008. Thus the year was included as a fixed affect in multivariate models associated with mass growth rate and chick sex as a fixed term in all models associated with growth rates (Tables 8.2, 8.3). Growth rates were not influenced by parent reproductive ability or body condition indices. Culmen growth rate was greater for chicks of older females (GEE W=7.4, p=0.007; Figure 8.5) and tarsus growth increased with both parents' ages (GEE females: W=7.0, p=0.008; males: W=7.2, p=0.008). Tarsi of chicks of experienced breeders grew faster compared to those of first time breeders (GEE females W=14.3, p<0.001; males W=7.5, p=0.006). Multivariate GEEs showed female's age was the variable best associated (positively) with growth (of mass, tarsus and culmen; Figure 8.5; Table 8.2). Amongst experienced parents, females' condition indices were negatively correlated with mass and tarsus growth rates (Tables 8.3). Hierarchical partitioning showed that the pair was responsible for the greatest proportion of the models' variances with at least 73% of the variances attributed to the pair in models of tarsus, culmen and mass growth rates.

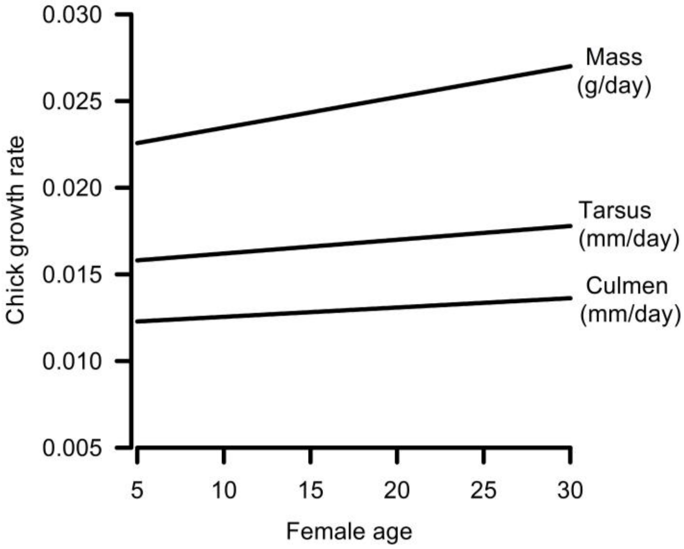

Figure 8.5 Linear models illustrate that chicks of older females grew faster in mass, tarsus and culmen than those of younger females.

Table 8.4 Growth rates and peak values plus estimated asymptote values of mass, culmen and tarsus length amongst Wandering Albatross chicks at Marion Island from 2006 to 2009.

	male chicks ($\bar{x}$ ±SD (n), range)	female chicks ($\bar{x}$ ±SD (n), range)
mass		
growth rate	0.026 ±0.007 g/day (128[a]), 0.014-0.051	0.024 ±0.007 g/day (165), 0.010-0.065
asymptotic	13.9 ±1.4 kg (128[a]), 9.8-17.0	12.3 ±1.4 kg (165), 8.2-16.0
peak	14.6 ±1.5 kg (132), 10.6-18.8	12.9 ±1.3 kg (165), 9.9-17.2
culmen		
growth rate	0.013 ±0.001 mm/day (132), 0.01-0.02	0.013 ±0.001 mm/day (165), 0.01-0.02
asymptotic	181.9 ±7.8 mm (132), 160.1-212.5	174.3 ±8.3 mm (165), 125.1-194.2
final	169.5 ±4.5 mm (132), 156.0-180.1	163.9 ±4.3 mm (165), 154.0-176.4
tarsus		
growth rate	0.016 ±0.002 mm/day (132), 0.01-0.02	0.017 ±0.002 mm/day (165), 0.01-0.02
asymptotic	136.9 ±4.8 mm (132), 123.3-159.4	130.0 ±5.4 mm (165), 117.9-168.3
final	131.2 ±3.3 mm (132), 121.2-142.6	125.4 ±3.0 mm (165), 117.0-133.3

[a] Four samples were removed as the modelled estimates were not realistic.

Parental influence on chick fledging mass and size

Peak mass and size give real measures of fledging chicks (Table 8.4) whereas modelled asymptotic mass, culmen and tarsus from growth curves provide comparatives measures (Table 8.4) and the latter were used for analyses. Male chicks were larger and their final mass was greater than that of female chicks (GEE mass: W=73.5, p<0.001; culmen length: W=56.5, p<0.001; tarsus length: W=126.0, p<0.001; Table 8.4). Chick mass and size were significantly influenced by the year of study (GEE mass: W=17.3, p<0.001; culmen length: W=6.1, p=0.014; tarsus length: W=5.9, p<0.015). Both chick sex and year were included as fixed terms in multivariate models (Table 8.2, 8.3). Parent condition indices and previous reproductive success were not significantly associated with mass and tarsus length of chicks but culmen size was negatively correlated with males' body condition indices (GEE W=5.38, p=0.020). Fledging chick mass was greater for chicks reared by older parents (GEE females: W=47, p=0.030; males: W=7.6, p=0.006; Figure 8.6). Experienced parents produced heavier chicks than first time breeders (GEE females: W=3.98, p=0.046; males W=7.3, p=0.007). Experienced pairs produced chicks with longer tarsi than first time breeders (GEE W=4.8, p=0.029). Multivariate GEEs did not show a correlation between parent condition indices, age or pair experience and estimated chick fledging mass and size (Table 8.2). However, amongst experienced parents, females' ages were negatively associated with fledging culmen length (Tables 8.3). Once again in models of final size of tarsus, culmen and mass variance attributed to the pair (>80%) exceeded that of other terms (age, body condition index, experience or previous reproductive success).

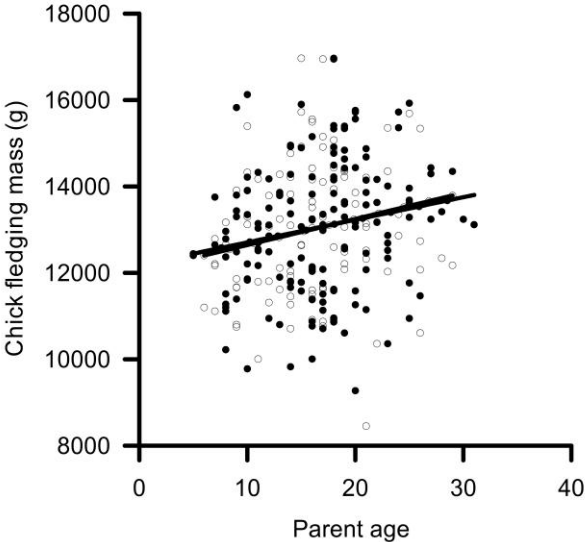

Figure 8.6 Females' (open circles) and males' (closed circled) ages were positively correlated with chick fledging mass (GEE females: W=4.7, p=0.030; males: W=7.6, p=0.006).

Individual pair effect on brood period and chick development

Hierarchical partitioning showed that the pair unit accounted for the greatest proportion of variance of models run on brood period, chicks' growth rates, size and mass at fledging. Percent of models variance attributed to the pair far exceeded (by 60% or more) the influence of age, breeding experience, previous reproductive success, body condition indices, year or chick sex. Pair as the dependent term in generalised linear models run on brood period and chick development characteristics significantly improve the null models when run on brood period (ΔAIC=142), final chick mass (ΔAIC=1442), fledging tarsus (ΔAIC=625) and culmen length (ΔAIC=659).

Chicks that failed usually did so before sufficient growth data could be obtained and so incomplete growth data were obtained for 21 failed chicks. Eight of these chicks decreased in body mass prior to death, suggesting that insufficient provisioning was a factor in their deaths. In one instance, a hatchling was found dead underneath the male parent. The male had incubated for 25 days followed by only one days relief before he resumed incubating for another 20 days. The 20 day shift was followed directly by another 11 days of brooding the newly hatched chick (a total of 31 days without relief from nest attendance by his mate who has not been seen since). The chick starved to death because the male had been sitting on the nest for so long he apparently had no food to regurgitate for the chick once it hatched (although he continued to brood and protect the chick even after it died). In this case the breeding failure was primarily driven by the female's absence.

Discussion

The increased reproductive success of 'poor pairs' receiving good eggs compared to those with poor eggs suggests that some 'poor pairs' suffer decreased success due to genetic or egg inadequacies.

This was supported by the reduced success of ‘good pairs’ who received ‘poor eggs’. However, that success of ‘poor pairs’ with ‘good eggs’ was lower than ‘good pairs’ with ‘good eggs’ indicates that some poor pairs also fail because of behavioural inadequacies. Furthermore, ‘good pairs’ had greater success than ‘poor pairs’ when raising chicks from ‘poor eggs’ indicating that good pairs display better reproductive behaviours.

The cross fostering experiment suggested that breeding behaviour of parents in more or less productive pairs differs enough to alter the outcome of a breeding attempt, suggesting that breeding success is related to variation in individual breeding behaviour. However, addled eggs may be a result of infertility of either parent, a naturally inviable embryo, or parent genetic incompatibility resulting in an aborted foetus (Cabezas-Díaz and Virgós 2007). Parents may also fail at the egg stage owing to poor quality eggs, possibly due to females in poor condition during egg formation (Chastel *et al*. 1995). Failure at the egg stage may be driven by parental genetics as well as incubation and foraging behaviours. Chick death may reflect lowered parental investment in protection and provisioning as well as genetically disadvantaged chicks. Studies examining causes of egg failure and particularly examining egg composition, incubation behaviours and genetic variability of parents with a repeated history of failure at the egg stage may further elucidate differential effects of behaviour and genetics on reproductive success.

Young offspring are frequently more vulnerable to predation and severe weather events than older offspring (Koskela *et al*. 2000, Tickell 2000, chapter 2). Wandering Albatross chicks regurgitate stomach oils as a means of defence against predators (Tickell 2000). Yet, when handled in the first few weeks after hatching, most chicks did not regurgitate and may have been unable to do so at these early ages. Greater chick vulnerability during the post hatching phase may explain benefits of longer brood periods (with associated longer parental protection from predators and environmental conditions; Lewis *et al.* 2004). Longer brooding may be required for chick survival in harsh climatic conditions (Catry *et al*. 2010). However, mean brood periods at Marion and Crozet (34 days, ranging from 25 to 44; Fressanges du Bost and Segonzac 1976) Islands are similar to the mean brood period recorded in the more climatically extreme South Georgian population (32 days, ranging from 21 to 43; Tickell 1968). Brood period and chick size at the end of brooding was associated more with breeding experience than parent condition indices or past productivity, suggesting that, in part, competence at protection of young chicks is learnt.

In contrast to chick brooding behaviour that impacts on young chicks and determines their survival, provisioning behaviours (reflected as growth and final chick size) impact throughout chick development. Poor provisioning can result in chick death due to starvation. Yet, the lack of differences in the growth rates and in the final sizes of chicks reared by experienced parents with different levels of historic reproductive success suggest that chick development is not influenced by parent breeding behaviours or differences in chick genetic characteristics.

Wendeln and Becker (1990) found that body mass, reflecting parental condition, influences chick growth rates (as well as breeding success) and that Common Terns (*Sterna hirundo*) in better condition invested more in their offspring. After punctuated fasting during incubation shifts, parents are likely to have lost some body condition and longer brooding must be balanced against their mounting need to forage for both their own and their chicks' sustenance (Lewis et al. 2004, Catry *et al*. 2010). It is expected that parents starting to breed in better condition should be able to withstand the effects of enforced fasting during incubation and thus brood for longer. However, body condition upon arrival at the colony neither influenced the duration of the brooding period nor was it positively correlated with chick development. Once again, age and parent experience were found to be most influential in determining chick growth characteristics, supporting evidence of improved ability during an individual's lifetime (Weimerskirch 1992, Lewis *et al*. 2006). Wandering Albatross chicks reared by inexperienced parents at South Georgia and Crozet Islands, grow more slowly during early chick development, but fledge at similar weight and size to chicks reared by experienced parents (Lequette and Weimerskirch 1990, Berrow *et al*. 2000). The difference between inexperienced and experienced birds is diminished during chick rearing, suggesting that the inexperienced birds attained the same degree of efficiency as more experienced birds during their first breeding attempt.

In Common Guillemots (*Uria aalge*), Lewis *et al.* (2006) found that breeding success was related to female and pair characteristics and that pair 'quality' operates through the female during chick rearing. Selecting a good quality mate is of particular relevance in albatrosses because they are socially monogamous and biparental care is required to rear chicks: The few rare records of chicks reared by single (widowed) parents, suggest chick growth was hindered (Tickell 1968, Brown and Adams 1984). While individual males' and females' reproductive abilities may influence chick development independently (e.g. Weimerskirch *et al*. 2000, Lewis *et al*. 2006), investigating the effects of the pair unit establishes the total parental investment impact that chicks experience (Lewis *et al*. 2006). The strong influence of pairs on brood period and growth characteristics suggests that chick protection and development differs more between families than within families.

Cross fostering also indicates that chick growth and final size is not improved when chicks from unproductive parents are raised by highly productive breeders, further evidence that provisioning behaviours influencing development do not vary between birds of differing reproductive success. Chick growth rate and fledging mass may influence post fledging survival (Gebhardt-Henrich and Richner 1998). Thus, while impacts of parental investment may be assessed via chick development, they may also be assessed via post fledging survival or offspring recruitment into the breeding population in the future (Gebhardt-Henrich and Richner 1998).

Overall, pair experience and parental age characteristics influenced parental care in terms of brooding and chick development. While reproductive ability, determined from historic reproductive productivity, was not related to parent investment of the studied breeding attempts, parent investment measures did differ from pair to pair suggesting that individual variation influences parental investment. Cross fostering indicates that pairs’ reproductive success is influenced by a combination of inherent (genetic or egg characteristics) and behavioural characteristics.

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Chapter 9

Synthesis

The long distances breeding seabirds typically commute between feeding and breeding grounds enforce biparental care and monogamy (Hamer *et al.* 2002). Slow prey delivery rates to chicks also result in small clutch sizes, encouraging seabirds to invest more in survival than reproduction. Albatrosses are particularly long-lived and exhibit the associated life history traits of delayed maturity, high partner fidelity, slow reproductive rates and production of slow growing altricial young, with successful breeding forfeited over survival (Stearns 1992, Schreiber and Burger 2002, Tickell 2000). They have long held fascination for humans as they travel remarkably long distances (Tickell 2000) and parallels between albatrosses and humans engender an appreciation of them. Their wingspan allows for efficient dynamic soaring and some birds circumnavigate the globe between breeding events (Ryan and Bester 2008, Percy FitzPatrick Institute, unpublished data). They return to land (usually oceanic islands) for breeding and rearing a seasons' single chick requires a combined parental effort as they must forage at sea between incubating shifts and chick survival depends upon regular provisioning by both parents (Tickell 2000).

After time spent in the Wandering Albatross (*Diomedea exulans*) colonies at Marion Island, I learnt to identify individuals, not solely from their unique ring numbers, but also from a mixture of their appearance, behaviour and, perhaps, their unique nature. One bird had a particularly ear piercing vocal pitch, another was diligent and meticulous at patting her nest, some merely shuffled their feathers, peering at me sidelong while I checked their rings, while others had the tendency to tattoo indelible marks, with voluble accompaniments, onto my wrists. Knowing the individuals prompted me peruse their breeding histories where I discovered some patterns more akin to adultery and serial romances than textbooks descriptions of 'mate for life' fidelity. Further, systematic, scrutiny of those records left me impressed by some parents, so good at rearing young, but also pitying others that never managed to hatch their eggs. The main goal of this thesis was to search for characteristics that might explain the variation in their reproductive histories but along the way other interesting aspects of their breeding behaviour came to light. In this chapter I highlight some of my key findings on sex ratios (chapters 6 and 7), extra-pair paternity (EPP; chapter 4) and finally draw together conclusions from investigations into parental characteristics influencing reproductive success and findings from a cross fostering manipulation (chapter 8).

Sex ratios

Male albatrosses are slightly larger than females (Tickell 1968) and male chicks attain greater size and mass prior to fledging (Weimershirch *et al*. 2000, chapter 8), requiring a greater parental investment. My Wandering Albatross data supported the Trivers-Willard theory that predicts individuals should invest in the more costly sex when in better condition (Trivers and Willard 1973) as experienced mothers producing male chicks had better body condition than those producing females (chapter 7). Factors that impact on food resources (e.g. fisheries affecting food availability) have the potential to influence parental condition. Indirectly these environmental characteristics could influence offspring sex ratios in species in which offspring sex is influenced by parental condition.

An excess of unpaired males in the colony prior to laying (chapter 6) supports the notion that Wandering Albatrosses may have a male biased adult population (Weimerskirch and Jouventin 1987, Jouventin *et al*. 1999). This has been linked with female biased mortality associated with their more northerly foraging ranges, which overlap more extensively with long-line fishing (e.g. Weimerskirch and Jouventin 1987, Croxall and Prince 1990). However, sex biases in an adult population may be caused by both differential sex-biased offspring production and sex-biased mortality. An examination of offspring sex ratios at Marion Island from 2006 to 2009 indicated a bias towards production of female chicks (56%; chapter 6). Continued monitoring of these cohorts as they recruit into the breeding population is needed to determine effects of offspring sex ratios on adult sex ratios and also to verify whether sex-biased mortality influences operational sex ratios.

In a monogamous species, an excess of one sex reduces that sex's opportunities of forming pair bonds, potentially reducing chick production and hence fitness. Testing whether male Wandering Albatrosses (in a male biased population) suffer lower long-term reproductive success in comparison to females, due to repeated years of non-breeding, could confirm whether sex ratios influence variation in long-term reproductive success. If anthropogenic activities are responsible for biased sex ratios, we should consider that human activities reduce effective population size by reducing the number of breeding pairs (e.g. Mills and Ryan 2005) as well as artificially skewing individuals' long-term reproductive success. A general association of skewed sex ratios with threatened species (Donald 2007) is of particular relevance for albatrosses since most are listed as threatened (BirdLife International 2011). Given that extinction risk is increased with more heavily skewed sex ratios (Donald 2007), sex ratios should be included in conservation-oriented monitoring of albatrosses.

Extra-pair paternity: balancing costs and benefits

One of the most entertaining aspects of the project has been examining the 'hidden' mating strategy of this monogamous bird. Diamond (1991) reports on human families tested for blood molecule heritability, which inadvertently revealed 10% of fathers were cuckolded (formerly unpublished as 'that kind of thing did not happen' in the 1940s). More recent studies report EPP rates of <1% to 35% in human babies (Diamond 1991, Simmons 2004, Brooke 2011) revealing distinct similarities to

Wandering Albatrosses, which range from 6% to 24% (chapter 4). In seeking to explain human mating systems, we often turn to monogamous birds that display similar mating systems to humans.

EPP is predicted to be low in species displaying long-term pair bonds (Wink and Dyrcz 1999). In albatrosses, judicious mate selection is necessary since their pair bonds usually last for life (Tickell 2000). Delayed maturity and the extended period of pair bond formation should enable selection of a good mate (Tickell 2000), yet, moderate levels of EPP occur in albatrosses (and other monogamous birds; Griffith *et al.* 2002, Abbott *et al.* 2006, Burg and Croxall 2006, Huyvaert *et al.* 2006, chapter 4). The rate of EPP may be influenced by the evolutionary history of avian lineages (Griffith *et al.* 2002). EPP has been recorded in all five species of albatrosses that have been tested (Huyvaert *et al.* 2000, Abbott *et al.* 2006, Burg and Croxall 2006, Huyvaert *et al.* 2006, Jouventin *et al.* 2007), suggesting that EPP is typical of this group. If EPP is related to phylogeny, it may not be explained solely by ecological explanations such as breeding density or synchrony (Griffith *et al*. 2002). In fact, Griffith *et al*. (2002) suggest that evidence supporting the hypothesis that synchoronous breeding increased EPP is limited or, at most, disproves the theory. Amongst albatrosses, support for the synchronous breeding hypothesis is equivocal, with pre-laying arrival correlating with EPP rates in Waved Albatrosses (*Phoebastria irrorata;* Huyvaert *et al*. 2006) but breeding timing unrelated to EPP in Wandering Albatrosses (chapter 8). Currently there is little evidence supporting the notion that breeding density influences EPP in birds (Griffith *et al.* 2002). Investigation of EPP rates in Wandering Albatross populations of differing densities, and also the influence of within colony inter-nest distance on EPP, would be valuable in testing this theory.

The persistent and widespread occurrence of extra-pair paternity in monogamous species suggests that there should be evolutionary advantages to cuckoldry (Griffith *et al.* 2002). Life history characteristics hypothesised to inflate EPP include reduced longevity and paternal parental care (Griffith *et al.* 2002). Yet, this does not explain the EPP rates in Wandering Albatrosses or EPP occurring in other albatrosses (Abbott *et al.* 2006, Burg and Croxall 2006, Huyvaert *et al.* 2006, chapter 4). Genetic theories for EPP suggest adaptive advantages to extra-pair behaviour as it insures against mate infertility or incompatibility (Wink and Dyrcz 1999, Griffith *et al.* 2002). Genetic theories also pose the 'good genes' hypothesis in which EPP offspring are of higher genetic quality than within-pair paternity young (predicting that females with poor mates will seek extra-pair copulations; Wink and Dyrcz 1999, Griffith *et al.* 2002). However, evidence supporting behavioural and genetic hypotheses explaining EPP is inconclusive in birds and probably EPP cannot be explained by a single hypothesis (Griffith *et al.* 2002, Akçay and Roughgarden 2007). There was no evidence that within-pair and extra-pair half siblings differed genetically at Marion Island nor that unfaithful females and cuckolded males were of lower genetic diversity than parents producing within-pair chicks. There was at most a weak indication that mate incompatibility may inflate EPP rates. Overall, Wandering Albatrosses provide limited support for the notion that EPP has genetic benefits (Jouventin *et al.* 2007, chapter 4).

Males siring EPP offspring may benefit by increasing their lifetime reproductive success with minimal effort. In the case of Wandering Albatrosses, the larger size of males (Tickell 1968, chapter 3, appendix 1) enables forced copulations (chapter 4) and a male biased sex ratio at the colony during the copulation period (chapter 6) may intensify EPP occurrence. Observations of females soliciting or consensually cooperating in extra-pair copulations (chapter 4) suggest that females also may benefit from EPP. However, Wandering Albatross females are unlikely to derive direct social benefits (e.g. food or access to male territories) from extra-pair copulations as occurs in some birds (Wink and Dyrcz 1999, Griffith *et al.* 2002). In the absence of genetic advantages (chapter 4), the benefits of EPP for females remain unclear. She may gain from cooperative extra-pair behaviour as it initiates a pair bond relationship providing a back-up mate should she lose her current partner (through divorce or widowhood). Mate swapping is costly in terms of the missed breeding years devoted to pair bond formation (Jouventin *et al*. 1999, Bried and Jouventin 2002). There was no evidence of discrimination against extra-pair offspring (in chick growth or mortality) indicating that costs to EPP are low (chapter 4). With costs to EPP being low, genetic polyandry may be an adaptive alternative to mate swapping (Jouventin *et al*. 1999, Bried and Jouventin 2002).

Characteristics influencing variation in reproductive success

Life history characteristics must be taken into account when considering an organism’s reproductive success. Short-lived organisms may produce vast numbers of offspring (e.g. insects) whereas long-lived organisms usually produce few young, requiring extensive parental care (Clutton-Brock 1989, Stearns 1992). Some mating strategies also skew reproductive success. For example, very few males in polygynous species get the chance to mate, but in monogamous birds the lifetime reproductive success of the two sexes might be equal (Clutton-Brock 1989). However, amongst socially monogamous species, EPP skews reproductive success amongst males, highlighting the importance of understanding genetic as well as social mating strategies.

That age and experience improve breeding behaviours and reproductive success is well documented in seabirds as well as other taxa (Lequette and Weimerskirch 1990, Weimerskirch 1990, Sydeman *et al.* 1991, Croxall *et al.* 1992, Jouventin *et al.* 1999, Berrow *et al.* 2000, Weimerskirch *et al.* 2000, Sagar *et al.* 2005, Lewis *et al.* 2006). However, reproductive success also may decline with age (e.g. Lecomte *et al*. 2010) and experience (Newton 1989). Age-related decreases in reproductive output occur due to senescence (and are genetically influenced) whereas experience-related decreases occur due to ‘burn out’ (with costs of early reproductive effort reducing survival; Newton 1989). The phenomenon of birds dying after their first breeding attempt (Newton 1989) is indicative of differential reproductive ability. Positive influences of experience and age were confirmed for the Wandering Albatross at Marion Island. Experienced males were in better condition than inexperienced birds, yet spent less time in the colony and fewer days with their partners prior to laying (chapter 3) suggesting that efficiency, derived through experience, enabled economy in breeding behaviours. Older females produced larger eggs (except the very old females who tended to produce slightly smaller eggs; chapter 5), suggesting that maternal investment increased with age (but was limited by effects of senescence). Eggs of pairs with experienced males were laid earlier (chapter 5), experienced parents brooded chicks for longer and offspring grew faster when reared by older females (chapter 8) further indication that age and experience increase parental investment and breeding efficiency.

In chapter 1, I established that two thirds of fledged Wandering Albatrosses do not survive to even attempt to reproduce. Reproductive individuals may be divided into birds that produce no offspring, those that produce few young and those very good parents that produce most of the next generation (Newton 1989, Moreno 2003). I concentrated on reproductive success amongst experienced breeders and used their breeding histories to compare the extremes of highly productive and unsuccessful birds. Parents with better reproductive pasts were more likely to continue breeding successfully than those who had poor reproductive histories (chapter 1) indicating that individuals vary in their ability to successfully rear young. However, Wandering Albatross traits differentiating successful and impoverished breeders remained elusive. Parents with productive and impoverished breeding histories could not be distinguished by most breeding phenology characteristics, although good parents had shorter incubation periods (chapter 3). Parental investment (in terms of egg size, chick care, growth and fledging size) did not correlate with reproductive ability (chapter 5 and 8). Mating strategies of good and poor parents did not differ and there was no evidence to suggest that females in pairs with poor reproductive histories employ EPP to counteract their unproductive pasts (chapter 4). Paradoxically, pairs with good reproductive histories tended to produce females; the more commonly produced sex, rather than the more energetically costly male offspring (chapter 7). Also counter intuitively, pairs with poor histories tended to produce more male offspring (chapter 7). It might be suggested that good pairs are productive merely because they take the less risky approach by producing females, thereby increasing their reproductive output. However, there was no tendency for pairs to repeatedly produce same sex offspring. Nor did offspring sex apparently influence breeding success (chapter 7). If the factors determining good breeding are heritable, selection should soon fix these characteristics within a species unless they carry other costs such as reduced survival (Stearns 1992, Møller *et al*. 2005). With only one third of offspring (who largely come from very good parents) attempting to breed, selection pressures for better breeders will be strong. This in turn could limit variation in the successful breeding behaviours making it difficult to detect phenotypic differences between the good and poor breeders.

Amongst adults, the decision to breed or defer breeding was associated with early arrival and a longer presence at the colony prior to laying. Both early arrival and longer presence were linked to better body condition upon arrival. So, body condition, indirectly at least, also influenced an individual's decision to breed. Decisions to defer breeding beyond the usual single sabbatical year may be a key feature driving variation in long-term reproductive success. The evident distinction in pre-laying behaviour and body condition between birds that went on to breed and those that did not, suggests that pre-laying behaviour and characteristics of non-breeding birds could distinguish the good from the poor breeders. Prior to laying, experienced males with good breeding histories were present at the colony for longer than poorer breeders (chapter 3) and productive females spent more time with their mates, supporting the idea that pre-laying behaviour may distinguish good from poor breeders. A future study, concentrating on breeder versus non-breeder differences may reveal phenotypic characteristics driving variation in reproductive success. Besides condition and pre-laying presence, loss of mate or nest site also results in non-breeding (Newton 1989). Pair bond characteristics (e.g. pair bond duration) may be more important than breeding characteristics when it comes to determining lifetime reproductive success which also indicates that effects of sex-ratios should be considered when examining characteristics of non-breeding birds.

Demographic models used for conservation purposes typically rely on average parameters. Relying on average parameters may lead to biased inferences if the variance amongst individuals is strongly skewed, or if traits correlated with differential breeding performance also influence the likelihood of human-induced mortality. Including variation in breeding performance, extra-pair paternity rates (that cause skews in male reproductive success; chapter 4) and biased operational and offspring sex ratios (chapter 6) would increase the predictive power of Wandering Albatross demography modelling.

Genetic and behavioural influences on reproductive success

The cross fostering experiment in chapter 8 suggests that both genetic and behavioural traits might influence reproductive success, confirming the results of the classic natural twin studies expanded upon by Ridley (2003): Adopted children retain some of their parents' genetic traits, but the traits are tempered by their upbringing. Characteristics associated with variation in long-term reproductive success in Wandering Albatrosses have been elusive, but the benefits of parental care, the influence of parental phenotypic characteristics (e.g. body condition on offspring sex; chapter 7), as well as genetic and innate differences lead to the conclusion that genetic and behavioural traits are interconnected in their influence on reproductive success.

Wandering Albatrosses differ in reproductive success and ability but reproductive efficiency is also increased through age and experience, suggesting that learnt skills increase breeding competency. That characteristics such as egg size, chick growth and size differ more between families than within families gives evidence for variation between individuals' reproductive abilities. Nevertheless, characteristics that distinguish the most productive individuals from those with poor breeding pasts were frustratingly difficult to find, suggesting that there is little variation in breeding characteristics, possibly driven by strong selection for successful breeding behaviours. The cross fostering manipulation provided two exciting results in this regard: It revealed that parental behaviour is a driving factor behind reproductive success in some individuals. Pertinently, it also confirmed that individual variation in reproductive ability is influenced by inherent (genetic) characteristics, thereby giving support to the notion that successful breeding behaviours are heritable.

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