

**Effects of Investigator Disturbance
on the Reproductive Success of
Short-tailed Shearwaters *Puffinus tenuirostris***

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A thesis submitted in fulfilment of the requirements for the Degree of
Doctor of Philosophy

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March 2011

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Carey, M.J., Phillips, R.A. and Silk, J.R.D. Post-breeding migration of Short-tailed Shearwaters – testing old theories with new technology. 1st World Seabird Conference. 7-11 September 2010, Victoria, British Columbia, Canada.

Gonzalez-Solis, J., Felicísimo, A., Tremblay, Y., Reid, T., **Carey, M.**, Hodum, P., Takahashi, A., Muñoz, J., Sigurðsson, I., Thompson, D., Ryan, P., Cuthbert, R., Hedd, A., Montevecchi, W., Trathan, P., Phillips, R., Shaffer, S. Global migration dynamics of trans-equatorial shearwaters. 1st World Seabird Conference. 7-11 September 2010, Victoria, British Columbia, Canada.

Carey, M.J. The effects of data-logger attachment on breeding Short-tailed Shearwaters. 5th Australasian Ornithological Conference, 29th Nov - 4th December 2009, Armidale, NSW, Australia.

Carey, M.J. Incubation routine, body mass regulation and egg neglect in Short-tailed Shearwaters (*Puffinus tenuirostris*). 5th Australasian Ornithological Conference, 29th Nov - 4th December 2009, Armidale, NSW, Australia.

Carey, M.J. The effects of investigator disturbance on the hatching success, chick survival and quality of Short-tailed Shearwaters (*Puffinus tenuirostris*). 36th Annual Meeting of the Pacific Seabird Group, 22 – 25th February 2009, Hakodate, Hokkaido, Japan.

Carey, M.J. and Meathrel CE. The effects of investigator disturbance on the hatching success of Short-tailed Shearwaters *Puffinus tenuirostris* on Great Dog Island, Tasmania. 4th Australasian Ornithological Conference, 3 - 5 2007, University of Western Australia, Perth.

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Abstract

Despite long-held concerns about the effects of researchers on breeding birds, comparatively few experimental studies have focused on the impact of investigators on Procellariiformes. Published investigations concerning the effects of investigators on physiology, behaviour, reproductive success, offspring quality, and population trends of procellariiform seabirds are lacking. However, anecdotal evidence suggests that many of the smaller procellariid taxa, such as storm-petrels (Hydrobatidae, and some shearwater *Puffinus* species) are particularly sensitive to handling during the incubation period, resulting in lowered reproductive success, burrow shifts, and increased divorce between pairs. Knowledge of these impacts are important as any factor that reduces reproductive success in small or threatened populations may only hasten their decline and interfere with the accurate assessment of demographic parameters.

In this thesis, the frequency of investigator disturbance on Short-tailed Shearwaters (*Puffinus tenuirostris*) was examined experimentally throughout the incubation period to determine if disturbance influences hatching success, pre-fledging chick survival and chick body size. Handling of incubating birds at intervals of every day, every three days and once a week, reduced hatching success by 100, 61 and 39%, respectively, compared to pairs that were not disturbed. Most failures resulted from egg abandonment by the parents, particularly during the early stage of incubation. Chick survival did not differ between treatment groups, but control chicks were significantly heavier and had larger bill depths and a longer wing length. These results demonstrate that investigator disturbance during incubation greatly reduced the hatching success of Short-tailed Shearwaters while having no discernible effect on chick survival. The difference in chick body mass and size observed between the control and disturbed chicks might be due physiological or behavioural mechanisms in adults or carry-over effects from the incubation stage to the next life-history stage. Reduced offspring quality has the potential to affect post-fledging survival and recruitment.

The disturbance experiment was followed into the next year to determine the effects of handling in the subsequent breeding season. The results showed that one year after investigator disturbance, disturbed birds returned in lower numbers, divorced their partners and recorded a lowered breeding success than birds in the

control group. These results suggest that investigator disturbance during the incubation stage can have long-lasting effects and could be costly to an individual's lifetime reproductive success. These findings are significant in broader terms because any investigator disturbance that reduces reproductive success, survival and offspring fitness could interfere with the accurate assessment of demographic parameters and exacerbate population declines, particularly of rarer species or small populations.

In addition to the effects of direct handling of adult birds, this thesis also evaluated the possible effects of deploying global location-sensing (GLS) data-loggers on a 500 – 600 g seabird. Recent advances in tracking technology (i.e. smaller and lighter devices) have enabled long deployments, of up to 12 months or more, on shearwaters (Procellariidae). These deployments have been successfully used to examine migration patterns, wintering sites and non-breeding ranges as well as at-sea activity. Hence, an effective method for the long-term deployment of tracking devices that is able to withstand UV radiation, saltwater immersion and terrestrial abrasion while reducing any adverse effects of the attachment of the logger to the bird is needed. In this thesis, a method for attaching global location-sensing (GLS) data-loggers to Short-tailed Shearwaters on a modified aluminium band is described. GLS loggers were attached for 12 months from the 2007–08 austral summer and 74% of geolocated birds returned the following season. The 21st bird returned in December 2010, increasing the return rate to 77%. This finding provides further evidence that this new method can be used for long-term deployments on medium sized seabirds. No adverse injuries to the birds were observed. The application of this method with its high rate of return can be applied to all species of shearwater and will not only assist researchers in future tracking studies but help minimise any adverse effects the logger has on the birds' behaviour.

To ensure tracked birds were acting 'normally' and not biased by the attachment of the GLS devices, equipped and non-equipped birds were monitored in the year of deployment and in the year post recovery of the GLS devices. Of particular concern were potential alterations to birds' reproductive, flight, diving and foraging performances. Return rates, breeding success and body condition were compared between equipped and non-equipped birds over the two breeding seasons of 2007/08 and 2008/09. In the year of deployment, no evidence of negative effects of attaching data-loggers on hatching success, pre-fledging chick mass or survival was found. However, chicks reared by non-equipped adults were skeletally larger. In the

year of recapture, significantly more GLS equipped than non-equipped adults returned to the colony. There were no differences in adult body condition, egg size, hatching or fledging success between the two groups. Chick mass and size at pre-fledging were equal between those raised by GLS equipped and non-equipped adults. These results suggest that appropriate sized data-loggers are a relatively benign method of obtaining at-sea foraging and behavioural information from seabirds.

This thesis provides a considerable amount of new knowledge on the effects of investigator disturbance on Short-tailed Shearwaters. Results from this study could be used to develop initial research protocols for other species until a species-specific study is undertaken. Techniques should be developed that ensure the accurate recording of birds' natural behaviour while minimising the impact of investigator disturbance. If investigators are willing to study disturbance problems, it should be possible to reduce biases caused by their activities. Therefore, researchers seeking unbiased estimates of demographic and ecological parameters of birds should be encouraged to measure their own impact and report the findings in the literature, even if they detect no adverse effects of investigator disturbance.

Statement of Authorship

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis for any other degree or diploma.

No other person's work has been used without due acknowledgment in the main text of the thesis.

This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Mark J. Carey

DATE

Acknowledgements

This project has been one long journey that started in 2006 and there are a number of people that I would like to thank, as without them, this research would never have gone ahead. First, to the staff and students of La Trobe University, Department of Environmental Management and Ecology, I would like to thank them for helping me through this PhD. In particular I would like to acknowledge Dr Susan Lawler in her role as Post-graduate Co-ordinator and more recently, as Head of Department, for initiating the monthly postgraduate meetings. Setting monthly goals and reporting back to my post-graduate peers was a terrific way to determine ‘the next most important thing’. Please continue this wonderful initiative and hopefully other students will find it as rewarding as I did. To Dr Peter Pridmore for helping me develop various research hypothesis based on our current understanding of the natural world. I also thank you for encouraging me to get that first publication out when the opportunity arose. I thank Dr Warren Paul for various statistical advice particularly power analysis. The PhD wouldn’t have been the same without the input of Dr Dennis Black, for his field assistance and initiating thought provoking scientific discussions on Great Dog Island. I loved working with you in the Animal Diversity practicals, I have learnt so much from you and I hope you continue to share your wisdom with each student you have. In many ways you became a pseudo-supervisor, I consider you a close friend and mentor. I thank Nick May for his technical assistance and helping me design new bands so that we could attach the data-loggers. I also thank Nick for his work in the laboratory and helping set up so many Plant Science and Animal Diversity practicals. I could not have finished the PhD without the extraordinary administration services of Rachel Gorman. Thank you for answering my stupid questions, teaching me how to use the fax machine and listening to my regular venting sessions. Rachel you are an absolute legend! Lastly, to former and present post-graduates Dean Heinze, Cassandra Bloye, Dr Sarah Avitabile, Dr Petina Love, Dr Dale McNeil, Aaron Troy, Dr Janice Kerr, Dr Nathan Ning, Stephanie Suter, Vicki McCartney, Michael Shackleton, Nirmala Wijeratne and Julia Mynott for advice on PhD timelines, coffee breaks and intellectual conversations. All of you are doing amazing things. For those of you, who have just started your PhD, never give up, and just push through the pain!

To my academic co-supervisor and former Head of Department, Associate Professor Phil Suter, I thank you for your thoughtful insights into the progress of the PhD, employing me as a Teaching Fellow, funding significant holes in my project during the early years and supporting me 100% throughout the PhD tenure. There were a number of times where I could have easily walked away from it all, I think it was our regular chats in your office and in the ourtyard that kept me going. To Dr Catherine Meathrel my principal academic supervisor, well what can I say? You certainly showed me plenty of ‘goodwill’ over the years, but it hasn’t been easy. You really are a horrible vindictive person and a very poor researcher who has, despite all the potential, failed as a scientist. Working under you has undoubtedly prepared me for the ‘real world’. I am leaving La Trobe a much better person and researcher than when I entered it. I wish you all the very best in your teaching and fieldwork on Fisher Island.

I would also like to acknowledge the many field assistants that have helped me along the way particularly, Felix De Natris, Julia Mynott, Victoria McCartney, Dr Bruce Robertson, Sophie Kennedy, Dr Dennis Black, Danielle Smith, Terry Karis, Michael North, Laura Savige, Bronwen Grutzner, Rodney Newall, Steve Mason and Jono Thompson. I thank you all for the hard work you put in on Great Dog and Flinders Islands, it certainly was not a holiday!

Significant amounts of funding were secured during the scope of this research. Without it, the majority of the equipment and expenses would have been paid out of my own pocket. I thank all the funding bodies including; Birds Australia (\$450), ANZ Charitable Trust Australia – Holsworth Wildlife Research Endowment (\$15,270), 1st World Seabird Conference Organising Committee (\$850USD) and DEME (\$9,000). Staff at Research Services (formally known as Research and Graduate Studies Office), Caroline Northwood, Louise Frances, Robyne Manallack, were vital in reading draft proposals, and securing money.

A very memorable time in the PhD was spending six weeks at the British Antarctic Survey, Cambridge, United Kingdom with Dr Richard Phillips and Janet Silk. Passing on yours skills in downloading and analysing the geolocation data was much appreciated. Welcoming me into your home and giving me a nice cold beer was very generous. I would also like to thank James Fox (BAS) for manually downloading several GLS loggers. Dr Scott Shaffer (Department of Biological

Sciences, San Jose State University, USA) also helped analyse and interpret the geolocation data. All of you have been very generous with your time and advice.

To my friends and family I thank you for your support and encouragement over the last several years. I would particularly like to thank my dad for his financial assistance and letting me stay at home for all these years!! Lastly I thank and acknowledge the wonderful people of Flinders Island. Their generosity and interest in this project was at times overwhelming. In particular I would like to thank Margie Goss and Steve Mason, whom opened up their house each time I returned to Flinders Island. Thank you for the hot showers, tasty food, clean bed and copious amounts of champagne! I promise I won't stop coming down to Flinders, in fact, I've even got a trip planned, you'll be seeing me again soon. I would also like to acknowledge the generosity of the Newall family who allowed access to their land and shed on Great Dog Island. Very special thanks to Leigh and Paul Cox for diving me back and fourth from Great Dog Island over a number of seasons.

Preface

This doctoral dissertation is composed of a general introduction (Chapter 1), general material and methods (Chapter 2), and six experimental chapters (Chapters 3-8). The general discussion (Chapter 9) includes a summary of major findings, implication of the research and directions for future studies. Finally, a list of conference presentations arising from this research is given in Appendix I and printed copies of published/accepted papers are given in Appendix II. The author, Mark J. Carey, has written all of these chapters and performed the statistical analyses and therefore is lead author on all manuscripts. Where appropriate and where there has been a significant contribution to the project, and in all aspects of manuscript preparation, authorship is shared among those persons, as is outlined by La Trobe University's *Guidelines for the Conduct of Research and Handbook for Candidates and Supervisors for Masters Degrees by Research and Doctoral Degrees*. Supervisors Dr Catherine Meathrel and Associate Professor Phil Suter have provided advice and editing on specific chapters. Dr Robert Trevethan has provided additional editing and advice on where improvements could be made to the dissertation.

The review paper and experimental chapters submitted to/accepted in journals are:

CHAPTER 1.

Carey, M.J. (2009) The effects of investigator disturbance of procellariiform seabirds: a review. *New Zealand Journal of Zoology* 36: 367-377.

CHAPTER 3.

Carey, M.J. (2011) Sexual size dimorphism, assortative mating and with-in pair comparisons of the Short-tailed Shearwater. *Notornis* **58**: 8-16.

CHAPTER 4.

Carey, M.J. (2011) Investigator disturbance reduces reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. *Ibis* **153**: 363-372.

CHAPTER 6.

Carey, M.J. (2011) Incubation routine, foraging trip duration and body mass regulation in Short-tailed Shearwaters. *Emu* **111**: 166-171.

CHAPTER 7.

Carey, M.J., Meathrel, C.E., May, N.A. (2009) A new method for the long-term attachment of data-loggers to shearwaters (Procellariidae). *Emu* 109: 310-315.

Carey, M.J., Shaffer, S, Phillips, R.A., Silk, J, (in review) Migration and wintering of Short-tailed Shearwaters. *Marine Biology*

Gonzalez-Solis, J., Felicísimo, A., Tremblay, Y., Reid, T., **Carey, M.**, Hodum, P., Takahashi, A., Muñoz, J., Sigurðsson, I., Thompson, D., Ryan, P., Cuthbert, R., Hedd, A., Montevecchi, W., Trathan, P., Phillips, R., Shaffer, S. (in prep) Global migration dynamics of trans-equatorial shearwaters. *Biological Conservation*

CHAPTER 8.

Carey, M.J. (in press) Leg mounted data loggers do not affect the reproductive performance of short-tailed shearwaters (*Puffinus tenuirostris*). *Wildlife Research*

CHAPTER 1: General Introduction

1.1 The effects of investigator disturbance on procellariiform seabirds: A review

Ideally, in ecological studies of wildlife, researchers strive to obtain data that represent animals' normal behaviour by reducing stress to the organism during the research process (Götmark 1992). In doing so, researchers believe that they make observations under natural conditions and do not bias their results. However, this belief may not be well founded and should be examined.

Carney and Sydeman (1999) regarded 'investigator disturbance' simply as all activities affecting individual birds or nests (marking nests, trapping, banding, and handling of adults and their young) (Götmark 1992; Carney and Sydeman 1999). Nisbet (2000, p. 313) defined disturbance as "... any human activity that changes the behaviour or physiology of one or more individuals within a breeding colony of waterbirds". He drew a distinction between 'research procedures' (e.g., banding, trapping, and taking blood) and 'investigator intrusions' (e.g., counting nests or walking through the nesting area for population monitoring).

Studies of breeding waterbirds, including gulls, penguins, boobies, gannets, and cormorants, emphasise the dangers of disturbance to colonial breeding seabirds (see reviews by Götmark 1992, Carney and Sydman 1999, and Nisbet 2000). These studies have shown that human-induced effects include predation of eggs and young, desertion of nests, and behavioural changes in adult birds (see Götmark 1992).

Visiting the nests of Atlantic Puffins (*Fratercula arctica*) by researchers, and researchers' handling of Least Auklets (*Aethia pusilla*), reduced breeding success by 38% and 30% respectively (Piatt et al. 1990; Rodway et al. 1996). Tufted Puffins (*F. cirrhata*) disturbed by investigators temporarily deserted their eggs for longer periods

of time than did undisturbed birds (Pierce and Simons 1986). Activities in that colony reduced fledging success from 94% in undisturbed areas to 18% in the heavily disturbed areas. Harris and Wanless (1984) and Hatchwell (1989) reported that breeding success, growth rate and age at departure of Guillemont (*Uria aalge*) chicks were reduced by daily human disturbances. Hatchwell (1989) went on to propose that the effect of disturbance might be due to reduced provisioning of chicks by parents, increased energy demands for thermoregulation in the absence of brooding, and/or increased energy expenditure due to stress of being handled. Negative effects on physiology, behaviour, and breeding success have been observed in penguin populations (Wilson et al. 1989, 1991; Giese 1996; Regel and Pütz 1997; Walker et al. 2008); in some gull and tern species, handling of adult or young birds, and checking nest contents, significantly reduced reproductive success (Gillett et al. 1975; Robert and Ralph 1975; Brubeck et al. 1981; Fetterolf 1983; Nisbet 2000). By contrast, other studies of seabirds indicted no negative impact or even positive outcomes associated with the presence of humans (Hill and Rosier 1989; King et al. 1992; King 1993; Brown and Morris 1994; Dunlop and Jenkins 1994; Nisbet 2000).

Procellariiformes (albatrosses, shearwaters, and petrels) are particularly long-lived seabirds, some with declining populations (Warham 1990; Baker et al. 2002). Populations may be decreasing for a number of reasons. These include their island breeding habitat being lost or degraded due to human development or disturbance (Brothers and Harris 1999; Taylor 2000; Micol and Jouventin 2001; Le Corre et al. 2002; Keitt et al. 2003; Priddel et al. 2006a); predators having been introduced to their breeding islands (Simons 1985; Cooper et al. 1995; Booth et al. 1996; Gaze 2000; Taylor 2000; Twyford et al. 2000; Copson and Whinam 2001; Cuthbert 2004; Martínez-Gómez and Jacobsen 2004; Schulz et al. 2005; de León et al. 2006; Igual et

al. 2006); or because of mortality associated with long-line fishing (Baker et al. 2002; Baker and Wise 2005; Ryan et al. 2006; Sullivan et al. 2006). Investigator disturbance that reduces reproductive success in already-stressed populations might not only hasten these population declines but might also interfere with the accurate assessment of demographic parameters (Blackmer et al. 2004).

This chapter provides a review of the current literature relating to investigator disturbance on procellariiform seabirds from Australia, New Zealand, Antarctica, North America, South America, and Europe. While most previous studies of investigator disturbance have measured only the effects on hatching success (Götmark 1992), others include the birds' physiological condition (e.g., elevated stress hormone levels), behaviour (e.g., chick provisioning), survival, and future reproductive performance. Unfortunately, few studies report the effect of investigator disturbance on procellariiform seabirds. This chapter provides a summary of the research that deals with the effects of investigator disturbance (as opposed to human disturbance more generally) on physiology, behaviour, reproductive success, offspring quality, and population trends of procellariiform seabirds.

1.1.1 Short-term effects of handling adult birds

Generally, researchers consider the effects of their actions as being insignificant and not worth reporting in the literature, but some results suggest an unacknowledged negative effect on procellariiform seabird behaviour and reproduction. For example, handling of storm-petrels during the incubation period has been associated with permanent abandonment of breeding attempts (Allan 1962; Morse and Buchheister 1979; Warham 1990; Huntington et al. 1996). Boersma et al. (1980) found that daily handling of Fork-tailed Storm-petrels (*Oceanodroma furcata*) caused a significant

number of adults to desert their nests, and even a slight disturbance by researchers was associated with a reduction in hatching success (58% for nests checked daily, compared with 84% for nests visited only four times late in the incubation period). Marks and Leasure (1992) found that adult Tristram's Storm-petrels (*O. tristrami*) readily abandoned their eggs when disturbed by handling and nest visits. Of the 22 nests that failed during incubation, 55% failed between the first and second visits and 23% between the second and third visits; only 33% of eggs hatched, and overall breeding success rate was 18%.

In one of the few studies to quantify the frequency of investigator disturbance and its effects on reproduction, Blackmer et al. (2004) found that handling Leach's Storm-petrels (*O. leucorhoa*), whether daily or weekly, significantly reduced hatching success compared with a control group that was not handled. By the subsequent breeding season, divorce was common between unsuccessful, disturbed pairs, and 37% more disturbed pairs than control pairs deserted the nesting burrows that they had used in the previous year (Blackmer et al. 2004). In this case, investigator disturbance may have had a long-term negative effect on the birds' lifetime reproductive success as changes in pair bonding and nest site fidelity are known to affect reproductive output (Boersma et al. 1980; Wooller et al. 1989, 1990; Wooller and Bradley 1996). These findings complement those of Richdale (1963), who had previously noted that disturbance of nesting Sooty Shearwaters (*Puffinus griseus*) caused burrow shifts and divorces between pairs the following season, and even increased the likelihood that immature birds would emigrate from their natal colony.

1.1.2 Long-term effects of handling adult birds

Long-term research programs on seabird ecology are rare (Bradley et al. 1991; Wooller et al. 1992). In particular, the impact of handling adults during the breeding period and over a number of breeding seasons is not well known for most procellariiform seabirds. Furthermore, although population estimates and demographic data are vitally important for conservation efforts, the reliability of these data is unknown. In one study on Fisher Island in Bass Strait, Australia, Serventy and Curry (1984) documented a case of investigator disturbance, and suggested that handling Short-tailed Shearwaters (*P. tenuirostris*) at night resulted in a decline in the number of occupied burrows by 71% during the first 25 years. Serventy and Curry (1984) suggested that night patrols by investigators reduced attendance of immature and prospecting birds, and caused them to abandon Fisher Island as a potential future breeding site and relocate on nearby Little Green Island to breed. Not only had investigator disturbance reduced potential recruits into the population, but it also increased burrow desertion, decreased breeding success, decreased recruitment of young birds, and delayed the start of some birds breeding (Serventy and Curry 1984). The implication is that the well-known Fisher Island study (see Bradley et al. 1991, and references therein), does not correctly describe either the Short-tailed Shearwaters' natural 'undisturbed' behaviour or their population trend on Fisher Island. In another long-term study, Ollason and Dunnet (1978, 1980) reported that handling of adult Fulmars (*Fulmaris glacialis*) caused an increase of breeding failures of around 10% and also reduced the likelihood of the birds returning to breed in the subsequent year. In both long-term studies, prospector and young breeders were particularly affected by investigator handling, and that in turn affected recruitment.

Other long-term studies report that monitoring and banding birds during incubation reduced the hatching success of Leach's Storm-petrels (Huntington et al. 1996), but not that of southern hemisphere albatrosses (Croxall et al. 1990; Baker et al. 2002).

1.1.3 Handling of chicks

Few studies have investigated whether handling young seabird chicks interferes with growth rates or survival (Götmark 1992). Investigator handling of incubating adult birds might also affect the quantity and frequency of food brought back by parents to their chicks, and that may influence subsequent chick growth and survival (Warham 1990), but evidence is scarce. On Great Dog Island, Tasmania, Saffer et al. (2000a) reported no discernable effects from low (handled 3-6 times during the study), medium (handled 18-20 times), or high (handled 136 times) levels of investigator handling on Short-tailed Shearwater chick growth rates, although this study included no true 'control' group (i.e., chicks that were never handled). Similarly, handling of adult Gould's Petrels (*Pterodroma leucoptera*) every 7-10 days during the incubation stage did not appear to affect chick growth rates or survival (O'Dwyer et al. 2006a), suggesting that parental provisioning rates, though not measured, were normal despite handling during the incubation stage.

Handling of young may elicit defensive responses (e.g., regurgitating stomach contents, in particular proventricular oil, as an anti-predator mechanism or a response to handling [Quillfeldt and Peter 2000]), generate physiological changes (e.g., increased heart rate and energy expenditure), and ultimately affect growth rate and peak body mass. The regurgitation of stomach contents by many petrel species when handled (but not Great Shearwater (*P. gravis*) chicks [see Cuthbert 2005]) could have

growth implications as the chick loses a meal (or part meal) each time it occurs. Neither Saffer et al. (2000a) nor O'Dwyer et al. (2006a) made any attempt to quantify whether growth rate was affected by regurgitation of stomach contents associated with handling. For some highly pelagic species, whose chicks are fed infrequently, such losses could be serious, particularly in the early stages of chick development. Gangloff and Wilson (2004) investigated chick provisioning and growth in Pycroft's Petrel (*P. pycrofti*) and found that control chicks were significantly heavier than were 'study' chicks during the latter part of the chicks' development. The authors concluded that disturbance due to daily handling of chicks may have affected the study birds, but acknowledged that there may also have been an age difference between the two groups.

1.1.4 Effects on physiology

Only two studies have explored the impact of researcher disturbance on the heart rate and associated metabolic rate of incubating albatrosses and petrels. Weimerskirch et al. (2002) found that heart rates of Wandering Albatrosses (*Diomedea exulans*) doubled upon initial detection of human presence, and increased further on handling. These responses lasted for up to three hours, suggesting that energy expenditure was increased as a result of the disturbance. Males reacted more strongly to handling than did females, but females took longer to recover after handling (Weimerskirch et al. 2002).

The increased energy expenditure associated with approach and handling, and the prolonged recovery period after handling, could have potentially serious consequences, particularly if birds are handled several times and/or for prolonged periods of time (Weimerskirch et al. 2002). Wheeler et al. (2009) tested the effects of

disturbance frequency and approach distance on 148 brooding/guarding Wandering Albatrosses at Marion Island. Frequency of approach did not influence short-term behavioural responses, but was significantly associated with chick survival. The birds that were approached most frequently (twice a day, for three consecutive days) at a distance of 2 m had the highest percentage of nest failures (Wheeler et al. 2009). Wandering Albatrosses did not habituate to short- or long-term disturbance (as did Laysan Albatrosses [see Burger and Gochfeld 1999]) so, though not reflected in their behaviour, the sensitivity of these birds to disturbance may have induced physiological changes. Thus heart rate may have been a better indicator of stress than was direct observation (Ely et al. 1999; Weimerskirch et al. 2002; Wheeler et al. 2009).

In Northern Giant Petrels (*Macronectes halli*), de Villiers et al. (2006) used heart rate to measure response to human approach and subsequent nest manipulation. The birds' heart rate increased upon detection of a researcher 40 m away, and continued to increase until the human was 5 m away. The maximum increase over the resting heart rate in response to a natural disturbance was 97%, while the response to human approach was 204%. As in Wandering Albatrosses, a likely consequence of the considerable increase in heart rate following investigator disturbance is an increase in energy expenditure (Weimerskirch et al. 2002). The sensitivity of Southern Giant Petrels (*M. giganteus*) to human disturbance at their breeding sites has caused a decline in some populations (Woehler et al. 2003; Pfeiffer and Peter 2004), and breeding success at sites used for extensive research is lower than in other colonies of this species (Cooper et al. 2001). The disappearance of this species from around the research station on Marion Island is also thought to be the result of human activity (Nel et al. 2002).

The above findings have implications not only for researchers studying these birds but also for the growing ecotourism market. Guidelines specifying the minimum distance to which tourists can safely approach nesting birds are essential to protect seabird populations (Great Barrier Reef Marine Park Authority 1997; Pfeiffer and Peter 2004; de Villiers et al. 2006). Although above-ground nesting seabirds can habituate to the presence of humans (Burger and Gochfeld 1999), their breeding biology needs to be closely monitored to ensure that they suffer no long-term negative consequences.

Heart rate and metabolism are not the only physiological effects of disturbance on birds. Variation in stress-related hormones such as corticosterone in response to investigator or tourist disturbance have been researched across seabird taxa, particularly in penguins (for a review, see Walker et al. 2008), but no research of that kind appears to have been conducted on procellariiforms.

1.1.5 Effects of satellite telemetry and data loggers

Over the last twenty years advances in tracking technology have greatly advanced some areas of research, for example in satellite and geolocation studies of albatrosses and larger petrels (Falk and Møller 1995; González-Solís et al. 2000a; Phillips et al. 2003 for a review). In addition, recent improvements in the size and mass of devices to be carried by shearwaters and petrels (Iguar et al. 2005; Burger and Shaffer 2008), have given researchers more information about foraging locations, breeding and wintering ranges, migratory directions and pathways, and important staging points used by these birds (Burger and Shaffer 2008). These tracking devices have provided extremely important information about the lifestyles and habits of some seabirds,

particularly about the overlap between fisheries and the birds' foraging ranges— matters of great concern to research scientists and conservationists (Baker et al. 2002).

While acknowledging these advances, researchers must realise that tracking devices may themselves have an effect on birds' behaviour, reproductive success, and survival. The size, mass, location, and method of attachment have all been raised as possible problems affecting flight, swimming, and diving efficiencies (Wilson et al. 1986; Phillips et al. 2003). Length of deployment on a bird may also affect its behaviour, body condition, and reproductive success (Igual et al. 2005).

Empirical evidence documenting these potential problems is mixed. Imitation satellite transmitters attached to Sooty Shearwaters decreased colony attendance and affected adult body mass, but it did not affect chick condition (Söhle et al. 2000; Söhle 2003). Data loggers had only slight short-term negative effects on the body condition of equipped Cory's Shearwaters (*Calonectris diomedea*), but were not related to the birds' demographic parameters or feeding ecology (Igual et al. 2005). For Black-browed and Grey-headed Albatrosses (*Thalassarche melanophris* and *T. chrysostoma* respectively) trip duration, meal mass, breeding success, and rate of return in the next season were not affected when birds were equipped with satellite transmitters (Phillips et al. 2003).

In other studies, extended trip duration and nest desertion were observed if transmitter loads were greater than 3% of adult body mass (Falk and Møller 1995; Klomp and Schultz 2000; Freeman et al. 2001; Phillips et al. 2003). Use of satellite transmitters has been associated with significantly longer foraging trips during the chick rearing stages in Grey-headed Albatrosses (Waugh et al. 2000), Campbell Island Albatrosses (*T. impavida*) (Waugh et al. 2000), White-chinned Petrels (*Procellaria aequinoctialis*) (Berrow et al. 2000; Catard et al. 2000), Westland Petrels (*P.*

westlandica) (Freeman et al. 2001), Pink-footed (*P. creatopus*) (Guicking et al. 2001), and Sooty Shearwaters (Söhle et al. 2000), but not in Wandering Albatrosses (Weimerskirch et al. 1992; Arnould et al. 1996), Black-browed Albatrosses (Phillips et al. 2003), or Short-tailed Shearwaters (Klomp and Schultz 2000). Attachment of satellite tags had no effect on reproductive success of Waved Albatrosses (*Phoebastria irrorata*) (Anderson et al. 1998) or Light-mantled Sooty Albatrosses (*P. palpebrata*) (Weimerskirch and Robertson 1994). However, attachment of harnesses caused a 100% failure of breeding attempts by Northern Fulmars (Falk and Møller 1995), and breeding failure was also observed in Antipodean Albatrosses (*D. antipodensis*) (Nicholls et al. 2002), but not in Wandering Albatrosses (Weimerskirch et al. 1992). All the Northern Fulmar pairs abandoned their nests for unknown reasons, but Falk and Møller (1995) believed that capture procedures, energetic constraints, or the attachment of the harness were responsible rather than impaired flight performance. Recently, in an experimental study Navarro et al. (2008) found that by adding 45 g of weight to produce an increased wing loading of 6% in Cory's Shearwaters, equipped birds spent longer foraging, had a lower rate of mass gain while at sea, and had an increase in plasma levels of creatine kinase and lactate dehydrogenase activity indicating muscular damage. These results suggest that there are physiological stresses to an individual as a result of adding extra mass.

1.1.6 Summary

Over the past several decades, a number of studies have indicated that research activities such as monitoring nest attendance, banding, and handling of birds during incubation reduce the reproductive success of some petrel species (Warham 1990).

Yet, in their otherwise comprehensive review concerning the conservation and management of albatrosses and petrels in Australia, Baker et al. (2002) did not mention the potential impact of scientific investigations on vulnerable seabird populations. Given that little is known about the effects of investigator disturbance on most procellariiforms, documentation of any disturbance effects caused by researchers may be crucial for designing future research programs, particularly those that are intended to advance conservation efforts. Most studies make no mention of these effects, but that does not mean they are not operating. Therefore, it is imperative that researchers studying these birds understand how their research affects their study animals, and that they take precautions to mitigate any adverse effects, particularly when threatened species or small populations are involved.

Clearly, more research on the effects of investigators on procellariiform seabirds is necessary. The effect of handling is well established for several populations, but for most species many questions remain. For example, at what distance from the nest, at what frequency, at what stage of the breeding season, and for how long will particular species of birds accept investigator disturbance before negative consequences occur? Very few studies have been able to quantify disturbance adequately, and this gap in our knowledge offers opportunities for further research, possibly in conjunction with existing or new projects.

Answering some of these questions is likely to benefit a variety of bird species, as well as provide practical information for scientists and managers. Both outcomes may be particularly important for limiting the impact of the growing ecotourism industry in the sub-Antarctic islands and Antarctica. Managers of these areas should be encouraged to enforce strong precautionary guidelines to protect breeding seabirds against human disturbance and to ensure that there are minimal or

no impacts from visits by researchers and tourists (Great Barrier Reef Marine Park Authority 1997).

Measuring the effects of investigator disturbance will require studies of physiology, behaviour, and breeding biology as well as parallel studies of other known variables, such as predation and food availability, which affect bird populations. Appropriate methods should be used in these studies, and more attention needs to focus on minimising the unwanted effects associated with attempts to collect accurate data. The publication of these studies should be widely advocated, even if no negative outcomes are found. Ethics committees and government agencies should also promote research concerning disturbance, and encourage best practice methods in order to minimise any negative outcomes arising from research on the species being studied.

In this review I have raised some important issues. First, there are too few studies detailing the effects of investigators on most procellariiform seabirds, particularly those that *quantify* investigator disturbance (Götmark 1992; but see Blackmer et al. 2004). Second, the value of measuring investigator disturbance, and mitigating investigator impact, especially on threatened species, cannot be underestimated. Third, as Götmark (1992) has pointed out, such things as variation in investigator visitation rates can produce misleading comparisons between studies of species unless the data can be corrected for the influence of investigator disturbance. Researchers need to be more aware of this when designing research programs. Fourth, research on the effects of investigator disturbance on nesting birds might not have a high priority among researchers or funding agencies, but it should be easy to combine the exploration of these effects with both short- and long-term studies of other aspects of avian ecology or behaviour. Researchers willing to study problems

caused by investigator disturbance improve our knowledge and correct for biases caused by our activities.

1.2 Aims and organisation of this thesis

In light of the literature review and subsequent experimental studies, in this thesis new information will be provided about the effects of investigator disturbance on a long-lived seabird. I specifically address two topics identified in Chapter 1. First, I quantify the effects of handling adults during incubation and assess their reproductive success in the short (in the year of disturbance) and long term (one year after disturbance). Second, I investigate the effects of attaching GLS devices to adult birds by assessing their body condition, return rate, and reproductive success. For this research I used the Short-tailed Shearwater (*Puffinus tenuirostris*) to represent other members of its family (Procellariidae). By using an abundant procellariiform such as the Short-tailed Shearwater (estimated 23 million breeding birds; Skira et al. 1996) I also aimed to mitigate adverse investigator impacts in future studies especially on threatened species or small populations.

This research delivers a contribution of knowledge regarding the biology of the Short-tailed Shearwater and provides a better understanding of life-history strategies in general. That new knowledge can be used to improve future management of a species (and arguably a family: Procellariidae) that is known to be vulnerable to anthropogenic processes. Therefore, the outcomes of this research could have wide ranging implications for the way researchers undertake their research in the future.

This thesis consists of nine chapters. Chapter 1 has introduced the context of the thesis in the form of a literature review of investigator disturbance on

procellariiform seabirds. The intention was to provide background information to aid in the interpretation of data and observed behaviour. Chapter 2 contains general information about the Procellariiformes, particularly the Short-tailed Shearwater, as the study species, in order to describe its biology. This chapter also contains information about the study site and general methods used to conduct the research (specific methods are introduced in the subsequent chapters). Chapter 2 also describes the permits and licences under which this research was conducted.

Chapters 3 to 6 focus on the effects of handling Short-tailed Shearwaters during the breeding season and the associated effects on their breeding biology. In some cases, overlap of material occurs between chapters particularly with material in the introduction. This was unavoidable given the complexity of the topics covered.

Reducing handling time for the purpose of sexing live birds for the thesis, outside the egg laying period, is examined in Chapter 3. In that chapter an investigation of assortative mating and sexual size dimorphism is included. The short-term effects of handling incubating adults are examined in Chapter 4, and Chapter 5 details these effects in the long term by investigating return rates, pair-bond and nest-site fidelity. In Chapter 6 the results from Chapters 4 and 5 are explored in a typical scientific study and data are gathered about the incubation routine and body mass regulation of Short-tailed Shearwaters while an attempt is made to minimise the effects of handling.

In Chapters 7 and 8 the effects of attaching data-loggers to breeding adults are examined. Chapter 7 outlines a new method of long-term attachment of data-loggers to Short-tailed Shearwaters while presenting new information on their extraordinary trans-equatorial migration path. This is followed in Chapter 8 by an examination of

the effects that data-logger attachment has on chick size, return rates, adult body condition, and reproductive success.

Finally, in Chapter 9 there is a general discussion in which results of this investigation are summarised and discussed in relation to similar published studies. This chapter also contains comments about directions for future research.

CHAPTER 2: General Materials and Methods

2.1 Study species

2.1.1 The Order Procellariiformes

Procellariiformes is an Order of seabirds that comprises four families: Diomedidae (the albatrosses), Procellariidae (petrels and shearwaters), Hydrobatidae (storm-petrels), and Pelecanoididae (diving petrels). Formerly called Tubinares, and still called tubenoses in English today, they are often referred to collectively as ‘the petrels’ — a term that has been applied to all Procellariiformes, or more commonly all the families except the albatrosses (Warham 1990).

Procellariiformes range in size from the very large Wandering Albatross (*Diomedea exulans*), at 8.5 kg and a 3 m wingspan, to the tiny Least Storm-petrel (*Halocptena microsoma*), at 20 g and a 32 cm wingspan (Warham 1990). Their wings are long and narrow, their feet are webbed, and the hind toe is undeveloped or non-existent. Plumage is predominantly black, white, and grey. The Order has a few unifying characteristics, including their tubular nasal passage which is used for olfaction (Warham 1990). Their highly developed ability to smell helps to locate patchily distributed prey at sea and may also help to locate their nests within nesting colonies. The structure of the bill, which contains seven to nine distinct horny plates, is another unifying feature, although there are differences within the Order (Warham 1990). Petrels have a plate called maxillary unguis that forms a hook on their upper bill. The smaller members of the order have a comb-like lower bill, made by the tomia plate, for plankton feeding. Finally, these birds have stomach oil stored in their proventriculus that can be used as a food source during their long flights and also as a defence mechanism (Matthews 1949).

Procellariiformes are colonial, mostly nesting on remote predator-free islands (Brooke 2004). The larger species nest on the surface, while smaller species nest in natural cavities and burrows. They exhibit strong philopatry, returning to their natal colony to breed and returning to the same nesting site over many years (Serventy 1967; Croxall et al. 1990; Warham 1990). Procellariiformes are monogamous and form long-term pair bonds that are formed over several years and may last for the life of the pair. Only a single egg is laid at each nesting attempt, and usually only a single nesting attempt is made each year, although the larger albatrosses may nest only once every two years (Croxall et al 1990). Both parents participate in incubation and chick rearing. Incubation times and fledgling periods are long compared with those of other birds. Once a chick has fledged there is no further parental care.

Most albatrosses and procellariids use two techniques to minimise exertion while flying, namely dynamic soaring and slope soaring (Pennycuick 1982; Warham 1990). The albatrosses and giant petrels share a morphological adaptation to aid in flight. This is a sheet of tendon that locks the wing when fully extended, allowing the wing to be kept up and out without any muscle effort (Pennycuick 1982). Most who are unable to walk well on land, and many species visit their remote breeding islands only at night. The exceptions are the huge albatrosses, several of the gadfly petrels, shearwaters, and the fulmar-petrels. The latter can disable even large predatory birds with their stomach oil, which they can project some distance (Warham 1990). This stomach oil is a digestive residue created in the foregut of all tubenoses except the diving petrels, and is used mainly for storage of energy rich food as well as for defense (Matthews 1949).

Procellariiformes have had a long relationship with humans. They have been important food sources for many indigenous people, and they continue to be hunted in

some parts of the world (Elliott 1957; Skira 1990; Skira 1993; Bragg et al. 2009; Moller et al. 2009a, b, c; Newman et al. 2009). Procellariiformes are one of the most endangered bird taxa. Many species are threatened with extinction due to introduced predators in their breeding colonies, marine pollution, and the danger of fisheries' by-catch (BirdLife International 2004a).

2.1.2 The Family Procellariidae

The procellariids are the most numerous family of tubenoses, and the most diverse (Warham 1990). Sibley and Ahlquist's (1990) taxonomy included all the members of the Procellariiformes within the Procellariidae, and that family in an enlarged Ciconiiformes, but this categorisation has not been widely accepted (Tickell 2000). The procellariid family is usually broken up into four fairly distinct groups: the fulmarine petrels, the gadfly petrels, the prions, and finally the shearwaters. The fulmarine petrels include the largest procellariids, the giant petrels, the two fulmar species, the Snow Petrel (*Pagodroma nivea*), the Antarctic Petrel (*Thalassoica antarctica*), and the Cape Petrel (*Daption capense*). The fulmarine petrels are a diverse group with differing habits and appearances, but they are linked morphologically by their skull features, particularly the long prominent nasal tubes (Warham 1990). The gadfly petrels are the 37 species in the genus *Pterodroma*. They have traditionally included the two species in the genus *Bulweria* (Brooke 2004). These species vary from small to medium sized birds, and they all have long wings and short hooked bills. The genus *Pterodroma* is now split into four sub genera (Imber 1985), and some species have been split out of the genus (Bretagnolle et al. 1998). The prions include six species of true prion in the genus *Pachyptila* and the closely related Blue Petrel (*Halobaena caerulea*) (Kuroda 1983). Often known in the

past as whalebirds, three species have large bills filled with lamellae that they use to filter plankton much as baleen whales do, although the former name derives from their association with whales, not their bills (Warham 1990). Prions are small procellariids, 25–30 cm, with grey, patterned plumage, all inhabiting the Southern Ocean (Warham 1990; Brooke 2004). The shearwaters include the 20 or so species of the genus *Puffinus*, as well as the five large *Procellaria* species and the three *Calonectris* species (Warham 1990). While all these three genera are known collectively as shearwaters, the *Procellaria* are called petrels in their common names. Shearwaters are well adapted for diving after prey instead of foraging on the ocean's surface (Skira 1979, 1986; Morgan 1982; Wood 1993). Shearwaters are also well known for the long trans-equatorial migrations undertaken by many species (Shaffer et al. 2006; Guilford et al. 2009).

2.1.3 The *Puffinus* shearwaters

The taxonomy of this group is the cause of much debate, and the number of recognised species depends on the source (Warham 1990; Austin 1996; Brooke 2004). It is currently believed to comprise about 20 small to medium-sized species, but that may be revised with further research (Austin 1996; Austin et al. 2004; Penhallurick and Wink 2004). For example, Onley and Scofield (2007) recently recognised 28 species of shearwater (three in *Calonectris* and the rest in *Puffinus*). Currently, there are two other shearwater genera: *Calonectris*, which comprises three large shearwaters and *Procellaria* with another four large species. The latter are usually given the name 'petrels', although they are thought to be more closely related to the shearwaters than to the other petrels. A recent study splits the shearwater genus *Puffinus* into two separate clades or subgroups, "Puffinus" and "Neonectris"

(Penhallurick and Wink 2004). The “Puffinus” subgroup are the smaller *Puffinus* shearwaters (Manx, Little and Audubon's Shearwaters, for example), and the “Neonectris” subgroup are the larger *Puffinus* shearwaters (Sooty Shearwaters, for example). In 2004 it was proposed that the subgroup “Neonectris” be split into its own genus, *Ardenna* (Penhallurick and Wink 2004). This separation into two clades is thought to have occurred soon after *Puffinus* split from the other procellariids, with the genus originating in the north Atlantic Ocean and the “Neonectris” clade evolving in the southern hemisphere (Austin 1996). However, this taxonomic revision has been largely ignored (Austin et al. 2004; Rheindt and Austin 2005; Onley and Scofield 2007) and the genus *Puffinus* has been retained by most international taxonomic lists (except Australia; see Christidis and Boles 2008).

2.1.3.1 Distribution and status in Australia

In the Australasian region, eight species of *Puffinus* species breed, and of these four are endemic (Marchant and Higgins 1990): the Wedge-tailed Shearwaters, Flesh-footed Shearwaters (*P. carneipes carneipes*), Short-tailed Shearwaters, and Little Shearwaters (*P. assimilis tunneyi*) all breed within Australian territories (Figure 2.1). Sooty Shearwaters, Flesh-footed Shearwaters (spp. *hullianus*) and Little Shearwaters (spp. *assimilis*) breed in both Australia (on Lord Howe Island) and New Zealand. Buller's Shearwater (*P. bulleri*), Hutton's Shearwater (*P. huttoni*), and Fluttering Shearwaters (*P. gavia*) breed only on New Zealand and its offshore islands (Marchant and Higgins 1990; Brooke 2004). A further four species, the Pink-footed Shearwater



Figure 2.1 Distribution maps of *Puffinus* shearwaters breeding in Australia. (A) Wedge-tailed Shearwater, (B) Little Shearwater, (C) Sooty Shearwater, and (D) Flesh-footed Shearwater (*c.f.* Marchant and Higgins 1990). Filled circles indicate locations of offshore breeding colonies. Maps were generated with AUSMAP Global Map Data Australia 1M 2001 (AUSLIG 2001).

(*P. creatopus*), Great Shearwater, Manx Shearwater, and Audubon’s Shearwater forage but do not breed in Australian waters (Marchant and Higgins 1990).

Both Wedge-tailed and Little Shearwaters seem to be mainly sedentary, dispersing into waters near their breeding grounds soon after breeding (Asmussen 2006). Wedge-tailed Shearwaters are common off the western and eastern coasts of Australia, rare off the northern coasts, and very rare in southern Australia around Tasmania (Serventy et al. 1971; Rogers 1974). The breeding distribution for this

species is along eastern and western Australia, and the Coral Sea (Figure 2.1a) (Shipway 1969; Roberts et al. 1975; Floyd and Swanson 1983; Hill and Barnes 1983; Dyer and Hill 1992; Ogden 1994; Dyer et al. 1995; Carter et al. 1996; Dyer and Carter 1997; Garkaklis et al. 1998; Bancroft et al. 2004; Dyer et al. 2005). A small population also breeds on Lord Howe Island (Marchant and Higgins 1990). Throughout their range Little Shearwaters may be found at their colonies ten months of the year (Serventy et al. 1971). Fairly common in the seas south of Australia, flocks can be seen around Fremantle, and beach-washed birds have been found on the southern of Western Australia, Victoria, New South Wales, and southern Queensland (Serventy et al. 1971; Ross et al. 1996). The race *P. assimilis tunneyi* is restricted to south-western Australia breeding in the Recherche Archipelago, Eclipse and Saddle Islands, Cape Leeuwin, and the Abrolhos Group (Figure 2.1b). On Lord Howe Island *P. assimilis assimilis* breed in small numbers (Priddel et al. 2003).

Flesh-footed Shearwaters are common around their breeding grounds in Western Australia (Surman and Wooller 2000) and Lord Howe Island (Priddel et al. 2006a). The race *P. carneipes carneipes* breeds only in south-western Australia in the Recherche Archipelago, Doubtful Island, Albany area, islands near Point D'Entrecasteaux, Cape Leeuwin, and an islet of Cape Hamelin (Figure 2.1d) (Warham 1958; Burbidge et al. 1996; Powell 2004; Powell et al. 2007). The only breeding site in eastern Australia occurs on Lord Howe Island where there has been a 35.6% decline in nesting habitat and the total number of burrows has declined 19% since 1978 (Priddel et al. 2006a). The decline has been attributed to increased urbanisation on Lord Howe Island (Priddel et al. 2006a) and deaths caused by long-line fishing (Baker and Wise 2005) and ingestion of marine debris (Hutton et al. 2008; Bond and Lavers 2010).



Figure 2.2 Distribution of breeding Short-tailed Shearwaters (*c.f.* Marchant and Higgins 1990). Maps were generated with AUSMAP Global Map Data Australia 1M 2001 (AUSLIG 2001).

Short-tailed Shearwaters have a widespread breeding distribution, breeding on islands throughout south-eastern Australia (Figure 2.2) (Robinson 1962; Harris and Bode 1981; Brothers et al. 1996, 2001; Norman et al. 1996; Priddel 1996; Skira et al. 1996). A small isolated population also exists in the Recherche Archipelago, including Figure-of-Eight Island in south-western Western Australia (Lane 1983; Burbidge et al. 1996). Short-tailed Shearwaters are the only shearwater species to breed solely within Australian territories (Marchant and Higgins 1990). The total estimated population is 23 million breeding birds (Skira et al. 1985). It has been suggested that populations are increasing in Victoria (Harris and Bode 1981), New

South Wales (Marchant and Higgins 1990), and Tasmania (I. Skira pers. comm.). The stronghold of this species is the Furneaux Group of islands in eastern Bass Strait, where there are an estimated 11 million breeding birds (Brothers et al. 1996).

2.1.3.2 At-sea distribution, behaviour, and ecology

The Flesh-footed, Sooty and Short-tailed Shearwaters are trans-equatorial migrants. The Western Australian subspecies of Flesh-footed Shearwater (spp. *carneipes*) is believed to winter in the Indian Ocean, and at least one bird has been recovered in Sri Lanka (Serventy et al. 1971). Gibson-Hill (1953) proposed a migration route that takes them around Cape Leeuwin north to the Abrolhos Islands and then across the Indian Ocean to the Mascarene Islands. This migration trajectory is now supported by Powell (2009) who used satellite telemetry to track several birds. From here it would be possible to pick up monsoon winds in June that would carry them further north past the Seychelles and east of the Maldives. From Sri Lanka they return to their breeding grounds in Australia around September and October. Serventy et al. (1971) noted that these birds are common in the Gulf of Oman toward the end of May, and some are still present in October and November (Bourne and Radford 1961). The eastern Flesh-footed Shearwater subspecies (spp. *hallianus*) is fairly common off the coasts of North America and Japan during the Austral winter (Marchant and Higgins 1990; Brooke 2004). Several banded birds from Lord Howe Island have been recovered in the north Pacific, mainly off Japan and Korea, from May to August (Serventy et al. 1971). During their breeding period, Lord Howe Island birds are believed to engage in feeding off the coasts of southern Queensland and northern New South Wales (Hindwood 1945; Gibson and Sefton 1958; Marchant 1977; Thalmann et al. 2009).

Both Sooty and Short-tailed Shearwaters undertake an extraordinary trans-equatorial migration after breeding. Non-breeding birds are believed to leave earlier, in March (Richdale 1944; Serventy 1967), followed by breeding adults in April and May (Marchant and Higgins 1990; Chapter 7). Both species are found in large numbers in the northern Pacific off the coasts of Japan and North America. Sooty Shearwaters also travel into the northern Atlantic Ocean where they are frequently sighted in the English Channel (Serventy et al. 1971). In the Pacific Ocean, Sooty Shearwaters are abundant off the coast of California in May and September (Shaffer et al. 2006). In June and July they occur off northern Japan where they remain in warm current zones (Kuroda 1955). Short-tailed Shearwater adults depart their wintering grounds around late August, most during early September (Serventy 1956a, 1957, 1961; Marchant and Higgins 1990), with all but a few remaining by late September (Serventy 1956a, 1957, 1961). The first birds are seen back at their nesting islands from early September onwards, with landfall occurring in late September (Marshall and Serventy 1956; Robertson 1957; Serventy 1967; Marchant and Higgins 1990; Skira 1991; Norman 1992; Dann et al. 2003).

The remaining two species of *Puffinus* shearwaters breeding in Australia, Wedge-tailed and Little Shearwaters, are generally considered sedentary. However, no detailed tracking has been conducted on either species from Australian colonies. Little Shearwaters can be found at their breeding grounds almost 10 months of the year but little is known about their at-sea activity (Serventy et al. 1971; Asumussen 2006). It is believed that Wedge-tailed Shearwaters disperse into local waters near their breeding islands after nesting has concluded (Catry et al. 2009).

2.1.3.3 Breeding biology

The Little Shearwater is the only winter nesting *Puffinus* species in Australia. Adults return to their nesting islands from early January, and egg-laying peaks from the third week of June to mid-July (Serventy et al. 1971; Priddel et al. 2003; Asmussen 2006). The other four species (Sooty, Flesh-footed, Short-tailed, and Wedge-tailed) are summer breeders throughout their Australasian range. Adults return to their breeding islands in September and are present in great numbers through October (Marshall and Serventy 1956; Warham 1958; Serventy 1967; Lane and White 1983; Carter et al. 1996; Garkaklis et al. 1998; Powell et al. 2007). After a pre-egg laying exodus of one or two weeks, eggs are laid. The migratory species have a highly synchronised breeding timetable with egg laying occurring over a 2 – 3 week period from the third week of November through to the first week of December (Richdale 1963; Serventy 1963, 1967; Meathrel et al. 1993a). The egg-laying period is protracted for non-migratory species such as the Wedge-tailed Shearwater, with the earliest known egg date of 29 October until early December (Serventy et al. 1971).

Nests usually occur at the end of long burrows tunnelled in soft sandy or loamy soils. Burrows are located on flat to steeply rising ground and Sooty Shearwaters prefer ridges overlooking the sea (Richdale 1963). Some birds use rock crevices and coral sand. In the Abrolhos Islands, Wedge-tailed Shearwaters nest on the surface under low shrubs (Serventy et al. 1971). Nest chambers are often lined with grass, pig-face, or dried seaweed fragments (Asmussen 2006).

Only one egg is laid each year, and if it is lost it is not replaced. The eggs are coloured white, have no gloss, and are smooth. They are large and can weigh up to 20% of the female's body mass (Warham 1990; Meathrel et al. 1993b). Incubation is undertaken by both sexes in shifts of 10 – 14 days (for Short-tailed Shearwaters;

Serventy 1967) for approximately 50 – 55 days (Warham 1990). For summer nesting species, eggs hatch from mid-January to early February (Warham 1958; Serventy 1967; Garkaklis et al. 1998; Powell et al. 2007). For the winter nesting Little Shearwater, eggs hatch after a 52 – 58 day period in late August (Priddel et al. 2003; Asmussen 2006).

After they hatch, chicks are brooded by one parent for 2 – 3 days (Serventy 1967; Garkaklis et al. 1998; Powell et al. 2007). Brooding is then discontinued, and the chicks are fed nightly by both parents with increasing irregularity towards the end of the nesting period (Hamer et al. 1997; Saffer et al. 2000b). Chicks remain in their burrows for 70 – 100 days (Warham 1958; Saffer et al. 2000b; Priddel et al. 2003; Powell et al. 2007). They emerge from their burrows on consecutive nights before their departure to exercise their wings (Serventy 1967). For the summer nesting species, departure of chicks occurs during the April and May, and it occurs in October and November for Little Shearwaters (Warham 1958; Serventy 1967; Garkaklis et al. 1998; Priddel et al. 2003; Powell et al. 2007).

Beyond the basics, little is known about the principal population dynamics of most Australian *Puffinus* taxa (Table 2.1; Ross et al. 1996; Baker et al. 2002). Further work is required on all *Puffinus* species, first to determine their population status, and then to assess whether or not there have been any declines compared to historical population estimates. Knowledge of adult survival, breeding success, and recruitment rates is also urgently required (Ross et al. 1996; Baker et al. 2002).

Of the five *Puffinus* species that breed in Australia, only the Short-tailed Shearwater's breeding biology has been well studied (Farner and Serventy 1959; Hindwood and D'Ombrain 1960; Warham 1960; Lane 1961, 1962; Norman and Gottsch 1969; Norman 1970; Montague et al. 1986; Wooller et al. 1988, 1989, 1990,

1992; Bradley et al. 1989, 1990, 1991, 1995, 1999a, b, c; 2000; Serventy et al. 1989; Bradley and Wooller 1990, 1991a, 1991b; Meathrel et al. 1993a, 1993b; Brother and Harris 1999; Schultz and Klomp 2000; Fullagar and Heyligers 2001; Bradley and Meathrel 2006; Meathrel and Carey 2007). Virtually nothing is known about the breeding biology of the other four *Puffinus* species, which is of great concern given that many populations are not only considered threatened and but also subject to more than one serious threatening process (Table 2.1; Baker et al. 2002). Long-term studies on these species are needed, such as those on Fisher Island and Montague Island for Short-tailed Shearwaters (Wooller et al 1992; Knight et al. 2008). In most cases, 40 years will be needed to yield robust demographic data for these species (Serventy and Curry 1984; Baker et al. 2002).

As identified in Chapter 1, if and when these vital studies commence, a great deal of thought will be needed to avoid the problems encountered by Serventy and Curry (1984) and others. Excessive handling or other forms of investigator disturbance have the potential to cause population declines, decreased reproductive success, and increased burrow desertion, and they also call into question the legitimacy of the demographic data that are collected. Important consideration regarding the effects of investigator disturbance will be required in these studies if our conservation objectives are to be met.

Table 2.1 Demographic data for *Puffinus* shearwaters that breed in Australia (c.f. Baker et al. 2002).

Species	Body mass	Breeding season	Current monitoring in Australia	Breeding success	Age at first breeding	Adult survival	Juvenile recruitment	Longevity (yrs)
Sooty Shearwater	650-950 g	Summer	Montague Island, NSW	No data	9 years	No data	No data	9.11
Flesh-footed Shearwater (spp. <i>carneipes</i>)	533-750 g	Summer	?	No data	No data	No data	No data	No data
Flesh-footed Shearwater (spp. <i>hullianus</i>)	533-750 g	Summer	Lord Howe Island?	No data	No data	No data	No data	30.2
Short-tailed Shearwater	480 – 800 g	Summer	Fisher Island, Tas Montague Island, NSW	45.7 – 60%	5 – 8 years 4 – 15 years	Age dependent 96.7% 80 – 92.5%	14%	48.4
Wedge-tailed Shearwater	320-510 g	Summer	Montague Island, NSW	32 – 54%	No data	No data	No data	29
Little Shearwater (spp. <i>assimilis</i>)	220-260 g	Winter	?	No data	No data	No data	No data	No data
Little Shearwater (spp. <i>tunneyei</i>)	220-260 g	Winter	?	No data	No data	No data	No data	No data

2.2 Description of study site

2.2.1 The Furneaux Group

Named in honour of the English explorer Tobias Furneaux, the Furneaux Group consists of 52 rugged, windswept islands that emerge out of eastern Bass Strait, Tasmania, Australia (148°3'E, 39°58'S) (Figure 2.3). The island group was discovered in 1773 when Furneaux was commander of the *Adventure* on Captain James Cook's second voyage. Later in the century, Matthew Flinders explored the uninhabited islands and found enormous colonies of shearwaters, penguins, gannets, gulls, and cormorants. Cape Barren Geese (*Cereopsis novaehollandiae*), Black Swans (*Cygnus atratus*) and other birds were found on the lagoons that dotted the larger islands.

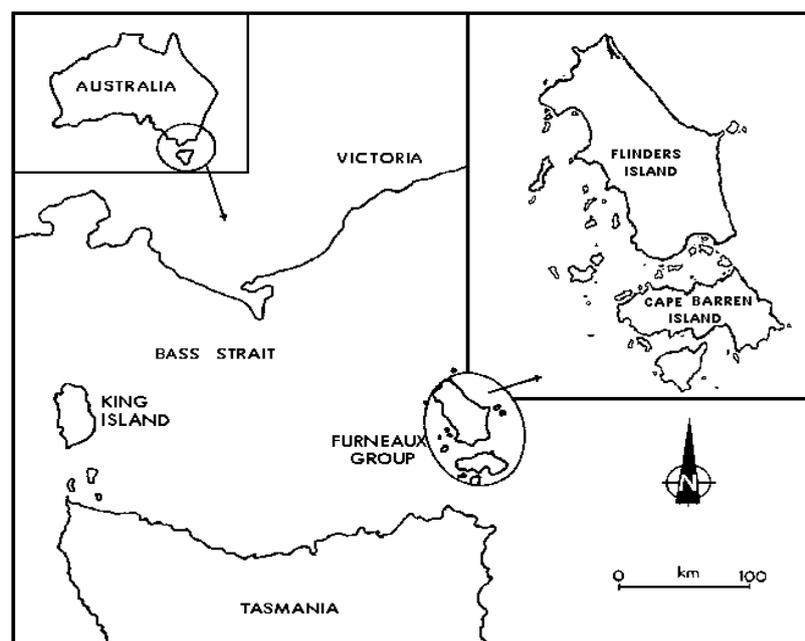


Figure 2.3. The location of Bass Strait and the Furneaux Group, Tasmania, Australia (after Bradley et al. 1991).

On the rocky headlands and islets there were thousands of seals, and it was that abundant availability of fur and oil that first brought permanent Europeans to the islands (Hope 1987; Kirkwood et al. 2009). Four species of seal were found in Bass Strait during early exploration: the Southern Elephant Seal (*Mirounga leonine*), Australian Sea Lion (*Neophoca cinerea*), New Zealand Fur Seal (*Arctocephalus forsteri*), and Australian Fur Seal (also known as Brown Fur Seal) (*Arctocephalus pusillus*) (Kirkwood et al. 2009). Exploitation quickly followed, in that between 1800 and 1806 approximately 100,000 seal skins from Bass Strait passed through Sydney (Hope 1987). By 1820 three of the four species of seal were almost completely extinct, and for over a century only Australian Fur Seals were thought to have continued breeding in Bass Strait. Recently though, New Zealand Fur Seals have re-established breeding populations there and colonies are growing steadily (Kirkwood et al. 2009).

Direct hunting of the Australasian Gannet (*Morus serrator*) caused the largest gannetry in Australia to become extinct. Cat Island, one of five gannet islands in Australia once supported between 5,000 and 10,000 birds (Warham and Serventy 1978). Fishermen found these birds a convenient source of crayfish bait because they were so easy to catch. By 1935, only 500 pairs remained, and by 1955 only 48 nests with eggs and young were counted (Warham and Serventy 1978). In 1983/84 there were 6 pairs, and following fires, human disturbance, and White-bellied Sea-Eagle (*Haliaeetus leucogaster*) predation, this species became extinct in the mid 1980s (Brothers et al. 2001). Cat Island is now a conservation area, ironically too late for the gannets.

The impact of human activities on the Furneaux Group flora has been equally dramatic. Harris et al. (2001) suggested that before European settlement of the Bass

Strait islands, the Furneaux Group was heavily forested with Drooping She-oak (*Allocasuarina verticillata*), Oyster Bay Pine (*Callitris rhomboidea*), Tasmanian Blue Gum (*Eucalyptus globulus*), Coastal Tea-tree (*Leptospermum laevigatum*), and Swamp Paperbark (*Melaleuca ericifolia*). With settlement, these ancient forests were exploited and their timber was used in shipbuilding and sealing activities. More recently, livestock grazing has further reduced the forest cover of many islands. With the decreased tree cover and the increased frequency of fire on many islands there has been an associated increase in the area of Coastal Tussock (*Poa poiformis*) grasslands. Recently, introduced woody weeds such as African Boxthorn (*Lycium ferocissimum*) and Mirror Bush (*Coprosma repens*) have also impacted on the Furneaux Islands. This has the potential to affect nesting seabirds by eliminating suitable habitats in which they breed (Lawley et al. 2005). Fortunately, on the main islands of Flinders and Cape Barren, and on smaller islands such as Great Dog Island, in the southern Furneaux Group, relatively intact forest survives and is of high conservation value (Harris et al. 2001).

Millions of Short-tailed Shearwaters (*Puffinus tenuirostris*) return to the Furneaux Group each year to breed over the summer months (Skira et al. 1996). The Furneaux Group is the species' stronghold, with an estimated 11 million birds breeding there every year (Brothers et al. 1996). Dominating the outer islands are dense colonies of Short-tailed Shearwaters. Babel Island, for example, reportedly has an estimated 2.8 million pairs (Towney and Skira 1985; Skira et al. 1996). Harvesting of Short-tailed Shearwater chicks (aka 'birding' or 'muttonbirding') began after the demise of the sealing industry and still occurs today with active harvesting sheds on Great Dog, Mt Chappell, Babel and Little Green Islands (Skira and Wapstra 1980; Serventy 1987). The birding season opens at the end of March and runs through to

April each year (Skira 1990). During World War II, birds were prepared as a tinned product and sold as ‘squab in aspic’ (Serventy 1987). The taste has been described as something resembling ‘fishy quail’ and is regarded as a local delicacy within the Flinders Island community. The Furneaux Group has had a long history of muttonbird harvesting in which the locals get actively involved each season (Skira 1990). However, the muttonbirding industry is declining with increasingly fewer birds taken (Skira 1990). Up until 1930, at the height of the industry, harvests were consistently over one million birds (Skira and Wapstra 1980; Serventy 1987). Now, rigorous regulations are imposed on the industry, and harvested numbers are now around 300,000 (Skira and Wapstra 1980; Skira 1991). It seems that shearwaters are resilient to harvesting and the Furneaux Group represents one of the few places in the world where this sort of commercial harvesting still survives (Skira and Wapstra 1980).

Today, the Furneaux Group is particularly important for the conservation of Australian seabirds, and many of the islands have been indentified as Important Bird Areas (IBAs) (Olsen 2008). IBAs are sites of global bird conservation importance. Each IBA meets one of four global criteria used by BirdLife International and is a priority area for bird conservation (BirdLife International 2004b). Brothers et al. (2001) indentified the islands of the Furneaux Group as an important refuge for Pacific Gulls (*Larus pacificus*), Little (Fairy) Penguins (*Eudyptula minor*), White-faced Storm-petrels (*Pelagodroma marina*), Sooty Oystercatchers (*Haematopus fuliginosus*), Pied Oystercatchers (*H. longirostris*), Hooded Plovers (*Thinornis rubricollis*), and several tern species such as the Caspian (*Hydroprogne caspia*), Crested (*Thalasseus bergii*), Little (*Sternula albifrons*), Fairy (*S. nereis*), and White-fronted (*Sterna striata*). Logan’s Lagoon, situated on Flinders Island, is also

recognised as an important RAMSAR wetland for waterbirds and thousands of migrating waders (Olsen and Weston 2004). The outer islands of the Furneaux Group are the stronghold of the threatened Cape Barren Goose (Brothers et al. 2001).

Many of the outer islands and large parts of Flinders Island are protected under various Tasmanian legislative agreements, but threats to the survival of the birds and their habitat remain (Olsen and Weston 2004; Olsen 2008). Weeds, fire, grazing, and human disturbance are the main current threats to the survival of many bird species in the Furneaux Group (Ross et al. 1996; Brothers and Harris 1999; Fullagar and Heyligers 2006). Climate change and associated rises in sea levels could potentially wipe out large areas of habitat required for foraging and nesting (Baker et al. 2006). An increase in sea surface temperature has the potential to cause catastrophic changes within the food web, resulting in declines of seabirds (Smithers et al. 2003; Surman and Nicholson 2009). Although researchers and managers have baseline information regarding the island vegetation composition, community structure and population status of breeding birds, many of the islands in the Furneaux Group have not been comprehensively surveyed for decades. Further research and surveying are needed to re-evaluate the status of these islands if conservation objectives are going to be met.

2.2.1 Great Dog Island

The research for this thesis was conducted on Great Dog Island ($40^{\circ} 15' 07''\text{S}$, $148^{\circ} 15' 08''\text{E}$), located in the southern Furneaux Group approximately 3 km south of Lady Barron on the south coast of Flinders Island (Figure 2.4). The island is approximately 370 ha in area, 3.7 km long, and up to 1.6 km wide. It is relatively flat, with the highest point, Great Dog Hill, 65 m above sea level.



Figure 2.4 Location of Great Dog Island within the Furneaux Group, Tasmania.

Map was generated with AUSMAP Global Map Data Australia 1M 2001 (AUSLIG 2001).

Great Dog Island is classified as a Conservation Area/Muttonbird (a.k.a. Short-tailed Shearwater) Reserve and is managed by the Tasmanian Parks and Wildlife Service in conjunction with the Tasmanian Aboriginal Lands' Council. It has an estimated 952,000 shearwater burrows and is Tasmania's third largest colony (Skira and Brothers 1988; Skira et al. 1996). Here, the recreational and commercial harvest of Short-tailed Shearwater chicks occurs during March and April each year just before chicks reach independence (Skira and Wapstra 1980; Skira 1990).

On the island, remnant forest is now restricted to the south-west, south-east, and north-east corners, and is protected under the Aboriginal Lands Act 1995 (Harris et al. 2001). It is this remnant vegetation that allows Great Dog Island to maintain a high

avian diversity (Olsen and Weston 2004; Olsen 2008). Within the forests Brown Thornbills (*Acanthiza pusilla*), Grey Fantails (*Rhipidura albiscapa*), Flame (*Petroica phoenicea*), Scarlet Robins (*P. boodang*), Silvereys (*Zosterops lateralis*), Olive Whistlers (*Pachycephala olivacea*), and Crescent Honeyeaters (*Phylidonyris pyrrhoptera*) can be found in the understorey. In the She-oaks, groups of Yellow-tailed Cockatoos (*Calyptorhynchus funereus*) feed on the abundant cones. Birds of prey are common and hunt for reptiles, small birds, and fish. Daily sightings of Swamp Harriers (*Circus approximans*), Brown Falcons (*Falco berigora*), Peregrine Falcons (*Falco peregrinus*), Australian Hobbies (*Falco longipennis*), Nankeen Kestrels (*Falco cenchroides*), and White-bellied Sea Eagles are common over the summer months. In the Coastal Tussock grasslands there are Striated Fieldwrens (*Calamanthus fuliginosus*), White-fronted Chats (*Epthianura albifrons*), Brown Quail (*Coturnix ypsilophora*), Skylarks (*Alauda arvensis*), and Cape Barren Geese. It has been suggested that Coastal Tussock, which is now the dominant vegetation on Great Dog Island, has facilitated the expansion of the current large Short-tailed Shearwater colony (Harris et al. 2001).

The earliest ornithological accounts of Great Dog Island come from Thomas Scott who described the island as “high, and well wooded, good grass is to be found in many places interspersed with thickets of brushwood, the small species of kangaroo called wallaby are numerous here, there is also a very large ‘rookery’ of muttonbirds...” (Scott 1828, p 606). Later in the century, Bishop Montgomery, the then Anglican Bishop of Tasmania, visited the Furneaux Group several times. He wrote several accounts of the Short-tailed Shearwater on Great Dog Island (Montgomery 1896, 1898). Mary Gilham (1963) worked on a number of islands in the Furneaux Group, including Great Dog, where she described the nesting habitats of

the White-faced Storm-petrel on the small island off the south-east end and named it Penguin Islet.

Banding of Short-tailed Shearwaters began on Great Dog Island in 1947 by Dr D.L. Serventy (Serventy 1957; 1961). Between 1947 and 1976, 84 adults and 16,665 fledglings were banded on the island. This program was used to estimate the number of chicks harvested using the Lincoln Index method. Frequent visits have been made by staff from Tasmanian Parks and Wildlife Service since 1969, during which the extent of the commercial harvesting between 1977 and 1980 was monitored (Skira and Wapstra 1980). Skira and Brothers (1988) visited the island in the Decembers of 1985 and 1986 and surveyed the island for seabirds as part of a wider survey of the Furneaux Group. More recently, investigations by researchers from Murdoch University and La Trobe University's Marine Ornithology Group have concentrated on various aspects of the breeding biology of Short-tailed Shearwaters (Meathrel et al. 1993a, b; Hamer et al. 1997; Saffer et al. 2000a,b; Carey 2005; Bradley and Meathrel 2006; Meathrel and Carey 2007), Silver Gulls (Auman 2007; Auman et al 2008; Auman et al. *in press*), and Pacific Gulls (Hollaway 2001; Lindsay 2004; Widdup 2004; Fergusson 2005; Lindsay and Meathrel 2008; B. Robertson).

2.3 Climate

The area in which the Furneaux Group occurs has a Mediterranean climate, with warm, dry summers and cool, wet winters (Harris et al. 2001). Great Dog Island has no long-term, published, climate averages. However, 40 km to the north, near the settlement of Whitemark, Flinders Island Airport has climate information dating back 67 years. Average rainfall is approximately 745 mm per year, with much of the precipitation occurring in winter months (Source: Bureau of Meteorology,

Melbourne). Rainfall totals for the first 10 years of the 21st Century suggest that Flinders Island experienced a dry period during that time, much as did most of south-eastern Australia (Figure 2.5).

The highest average monthly temperature for Flinders Island occurs in February and is 22.6°C; the lowest average monthly temperature of 13.2°C occurs in July (Source: Bureau of Meteorology, Melbourne). The islands experience strong westerly winds for much of the year, colloquially known as ‘the roaring forties’; at times wind gusts reach over 100 km/hr (Source: Bureau of Meteorology, Melbourne).

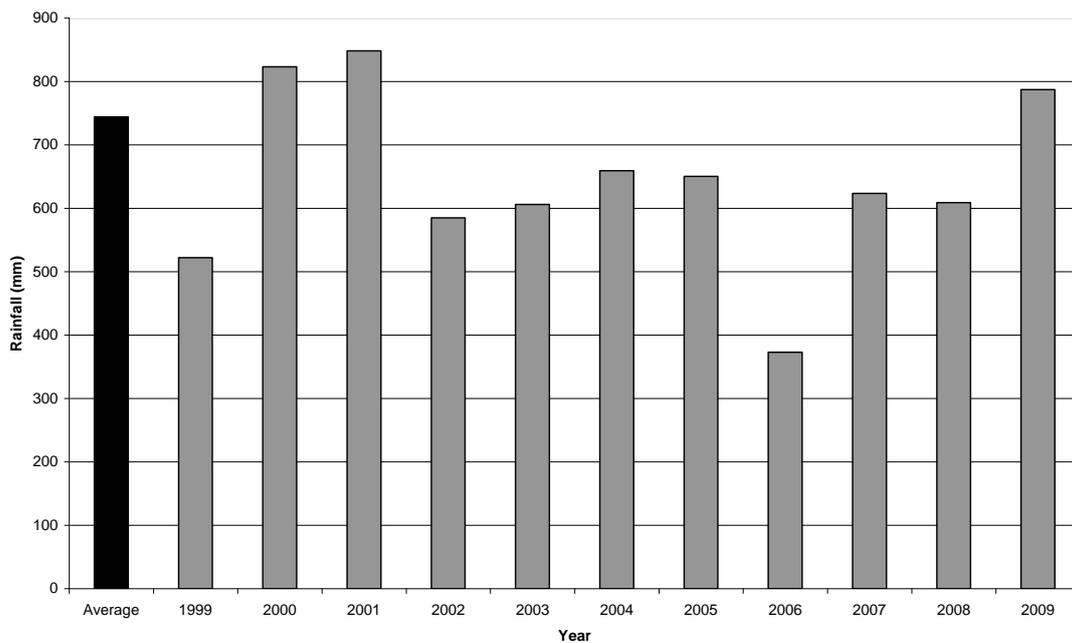


Figure 2.5 Rainfall totals for the past 10 years at Whitemark airport. Average rainfall indicated by solid black bar. (Source: Bureau of Meteorology, Melbourne).

2.4 Fieldwork

2.4.1 The breeding colony

Data for the present research were collected from a large Short-tailed Shearwater colony on Great Dog Island. The three sites used within this colony were located at South Beach, along the southern side of the island (Figure 2.6). Vegetation composition and structure have been well documented on this island (Harris et al. 2001). Here, the shearwaters nest in a range of habitats, including Coastal Tussock grasslands, Bower Spinach (*Tetragonia implexicoma*) herbfield, and dense Coastal Saltbush (*Rhagodia* spp.) shrubs. Burrow density averaged 0.47 m^{-2} (range $0 - 0.75 \text{ m}^{-2}$) (M. Carey, unpublished data). Skira and Brothers (1988) calculated burrow density for the entire island as 0.56 ± 0.08 burrows m^{-2} .

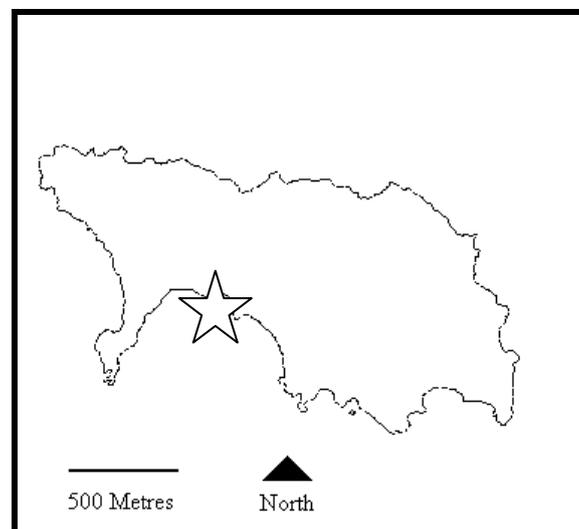


Figure 2.6 Location of study site on South Beach, Great Dog Island, Furneaux Group, Tasmania.

2.4.2 Burrow monitoring, capture and handling of birds

Adult Short-tailed Shearwaters return to the colony at the end of September. At that time they scratch out their burrow, re-unite with their partner, court, and copulate (Marshall and Serventy 1956; Serventy 1967). After a brief pre-egg laying exodus, females return in November to lay the egg (Serventy 1967). In this study, burrows were monitored for signs of activity over the 16 day period during egg laying. The burrows were mapped, assigned a unique identification code, and marked with a polyvinylchloride (PVC) pole. Poles were placed in the ground, upright, next to the burrow entrance. The markers were weatherproof and stayed in place for the duration of the research.

Adult shearwaters were captured by hand within the burrow during daylight hours, as prescribed by the research permits. Captive birds were removed and placed in a calico bag, then weighed and measured (see Section 3.3.3 Measurements). Once all the data had been collected, a bird was returned to its burrow. Handling time ranged from ~ 1 to 10 minutes depending on the procedure.

2.4.3 Measurements

2.4.3.1 Eggs

Eggs, if they could be reached, were measured at egg laying. They were removed from the burrow either by hand or with the use of a long handled plastic spoon. Each egg was measured with Vernier callipers to ± 0.02 mm (maximum length and breadth) and weighed with 300 (± 2) g Pesola scales. Egg volume was calculated using the equation $v = 0.51 lb^2$ (Hoyt 1979), where l = length and b = breadth.

2.4.3.2 Adults and chicks

All adults encountered for the first time were measured. Chicks were measured first at hatching and again at pre-fledging. Measurements (after Baldwin et al. 1931) taken of adults and chicks were head length from the tip of the maxillary unguis (upper nail of the bill) to the rear of the skull, bill length from the maxillary unguis to the posterior extremity of the nares (nasal tubes), bill depth measured vertically at the proximal base of the nares, and length of the tarsometatarsus (hereafter tarsus) with Vernier callipers to ± 0.02 mm. In addition, wing length, from the carpal joint to the end of the 10th primary feather, was measured with a standard, butt end wing ruler to the nearest 1 mm. Adult birds were weighed with 1000 (± 10) g Pesola scales. Chicks were initially weighed at hatching with 300 (± 2) g Pesola scales, then with 1000 (± 10) or 2500 (± 20) g Pesola scales before fledging.

2.4.4 Banding

All adults were banded in accordance with Australian Bird and Bat Banding Scheme (ABBBS) guidelines (Lowe 1989). All pre-fledged chicks were banded at the nest prior to their departure, except in the March 2009 fieldtrip due to logistical constraints.

2.4.5 Permits and licences

All procedures in the field were performed in accordance with the following permits and licences:

- Permit to Take Wildlife for Scientific Purposes: Permit No. F.A. 06494 (2006/07); F.A. 07166 (2007/08); F.A. 08145(2008/09); F.A. 09118

(2009/10). Department of Primary Industries, Parks, Water and Environment, Tasmania. Chief investigator: Dr Catherine Meathrel.

- La Trobe University Animal Ethics Approval: Approval No. AEC05-15-W ‘Breeding biology and ecology of seabirds in temperate Australia’. Chief investigator: Dr Catherine Meathrel.

- Australian Bird and Bat Banding Scheme ‘R’ Class Bird Banding Authority: No. 2670.

- Australian Bird and Bat Banding Scheme ‘A’ Class Bird Banding Authority: No. 2670.

CHAPTER 3: Sexual Size Dimorphism, Assortative Mating and Within-pair Comparisons of the Short-tailed Shearwater

3.1 Introduction

Identifying the sex of study individuals is vital in much ecological and behavioural research due to the importance of identifying the different role that each sex has in various aspects of breeding biology. However, as mentioned in Chapter 2, sex can often be difficult to determine in seabirds (Procellariiformes) because many exhibit monomorphic morphology or plumage characters (Warham 1990). In procellariids the sexes are similar in plumage, with males usually larger than females. However, there can be a considerable overlap between the sexes in their size ranges (Marchant and Higgins 1990; Warham 1990; Bradley and Meathrel 2006; Einoder et al. 2008). Monotypic birds such as shearwaters and petrels are sexed from a variety of methods such as dissection, observing copulation, cloacal examination at the time of egg-laying (Serventy 1956b; Boersma and Davies 1987), sexual voice dimorphism, particularly in the *Puffinus* group (Brooke 1978; Bourgeois et al. 2007) and, more recently, by molecular methods using polymerase chain reaction (PCR) amplification (Kahn et al. 1998). Alternative *in situ* methods are desirable, especially outside the breeding season, when knowledge of a bird's sex is required.

In studies outside the breeding season, where invasive techniques or molecular methods are not possible or undesirable, sex can be determined with a high degree of accuracy from external morphometric measurements. A discriminant function analysis (DFA) combining a number of morphometric measurements allow relatively accurate predictions of an individual's gender, even when there is considerable overlap in size ranges (Weidinger and van Franeker 1998). Body measurements have been used successfully to identify gender through predictive functions for Brown

Noddies (*Anous stolidus*) (Chardine and Morris 1989), Razorbills (*Alca torda*) (Wagner 1999), penguins (Amat et al. 1993; Renner et al. 1998), and gulls (Fox et al. 1981; Coulson et al. 1983; Hanners and Patton 1985; Evans et al. 1993, 1995; Torlaschi et al. 2000). The application of a DFA to sex adult birds using external body measurements can be particularly useful because of the non-invasive, cost effective, and efficient nature of the technique. The predictive function derived from the DFA is extremely useful as it is species-specific. However, caution must be observed when generalising more widely over the entire geographic range of the species owing to morphometric differences between colonies of the same species (Guicking et al. 2004; Einoder et al. 2008). It has been suggested, therefore, that a DFA should be used only in those studies of the local population from which it was derived (Evans et al. 1995). Analyses can also be confounded if individuals mate assortatively by size (Coulter 1986; Fletcher and Hamer 2003). For instance, in species where the sexes overlap in size but males are on average larger than females, assortative mating would lead to an increased likelihood of males in small pairs being sexed as females and females in large pairs being sexed as males. Problems in identifying individual sex may be greatly reduced by using within-pair comparisons of relative size. Such within-pair comparisons result in improved sex determination in South Polar Skuas (*Catharacta maccormicki*) (Ainley et al. 1985) and Cape Petrels (*Daption capense*) (Weidinger and van Franeker 1998). However the usefulness of this approach has not been widely evaluated (Fletcher and Hamer 2003).

Short-tailed Shearwaters (*Puffinus tenuirostris*) have no plumage differences between males and females, although published measurements suggest there may be some morphological dimorphism (Marchant and Higgins 1990; Meathrel *et al.* 1993a; Einoder et al. 2008). The life cycle and basic biology of Short-tailed Shearwaters

have been described by Serventy (1967) and Serventy and Curry (1984), but few studies examine differences in body size measurement of male and female birds. Within the context of the thesis, the aim of this chapter was to find an *in situ* method of identifying the sex of adult Short-tailed Shearwaters in the field that could be used outside the egg-laying period. This method provided rapid results and was cost effective compared to molecular sexing. In this chapter I evaluate data on sexual size dimorphism in body mass and five linear morphological measurements from random male and female birds as well as known pairs. I provide an equation that can be used to sex live birds and test whether a DFA derived from another colony, in South Australia (Einoder et al. 2008), can sex birds used in this thesis. Given the large number of pairs measured in this study, an assessment of whether Short-tailed Shearwaters mate choice is size-related is also examined.

3.2 Methods

Adult Short-tailed Shearwaters were captured during the breeding seasons of 2006/07, 2007/08, and 2008/09 within a large colony on Great Dog Island. Body mass (g), plus 5 external body measurements (after Baldwin et al. 1931) were taken by one person (MJC) in all three breeding seasons. This controlled for any researcher-induced variability or bias. The five morphological measurements were total head length, bill length (i.e., exposed culmen), bill depth, wing length, and tarsus length — as described in Chapter 2. As also described in Chapter 2, adults were weighed using Pesola 1000 (± 10) g scales and measured using Vernier callipers (± 0.02 mm), and wing length was measured using a standard butt ended wing ruler (± 1 mm). All birds encountered were banded with an individually identifying Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band. When birds were being handled

during egg-laying they were sexed by cloacal examination (Serventy 1956b; Boersma and Davies 1987). During this egg laying period, birds with an obviously distended, oedematous cloaca (i.e., evidence of an oviduct stretched by laying an egg) were presumed to be female. Birds that were partnered with females were presumed to be male, as no same-sex pairs of breeding Short-tailed Shearwaters have been recorded. Only those pairs in which the female had laid an egg were included in this study.

3.2.1 Statistical analysis

Statistical analyses were performed using SPSS (version 17.0: SPSS, Chicago, IL, USA, December 2008). All variables were tested for normality and homogeneity of variances before using appropriate tests. Principal components analysis (PCA) was used to characterise variability in body dimensions within the total sample. The first principal component (PC1) comprised head length, bill length, bill depth, wing length, and tarsus length, and was used as a single composite measure of body size.

Differences between the sexes for each measurement were assessed with *t*-tests. The sequential Bonferroni adjustment was needed as multiple measures of the same individual were used and thus a critical value of $P < 0.008$ was used for determining statistical significance (Sokal and Rohlf 1995). For all other tests the critical level for determining statistical significance was set at $P < 0.05$.

Sexual dimorphism (*SD*) was calculated as a percentage between the sexes in each measurement as:

$$SD = \frac{\bar{x}_m - \bar{x}_f}{\bar{x}_m} \times 100$$

where \bar{x}_m and \bar{x}_f were the mean values in males and females, respectively.

A DFA based on external morphometrics was performed according to the method of Dytham (2003). Body mass was not included in the analysis because it can vary greatly depending on time since last food ingestion and stage of breeding. The reliability of the discriminant function was estimated by checking the predicted sex against the actual sex determined in the field. To test the reliability of the prediction, a jack-knife procedure (cross validation) was performed, where each individual was classified using a function derived from the total sample omitting the individual being classified.

Because a number of known pairs were sexed and measured, the degree to which males and females mated assortatively with respect to their body measurements was examined. To test for assortative mating, Pearson correlation coefficients (r) were calculated between pairs in all linear morphometric measurements, body mass and, PC1 scores.

3.3 Results

In total, 390 adults were measured over the three years of the study: 178 in 2006/07, 177 in 2007/08, and 35 in 2008/09 (Table 3.1). Female body mass varied between years (Kruskal-Wallis $\chi^2 = 9.19$, $d.f. = 2$, $P = 0.01$) but were not statistically significant after the Bonferroni adjustment. There were also differences in male body mass ($F_{2,190} = 6.95$, $P = 0.001$) and tarsus length ($F_{2,190} = 5.85$, $P = 0.003$) between years. *Post hoc* least significant difference (LSD) testing (Fisher's LSD test) revealed that males that were weighed in 2007/08 were significantly lighter than were those in 2006/07 (mean difference -23.2 , $P < 0.01$) and 2008/09 (mean difference -41.2 , $P < 0.01$). Tarsus length of male adults was marginally longer in 2006/07 than in 2007/08 (mean difference -0.56 , $P = 0.01$) and 2008/09 (mean difference -1.29 , P

<0.01). No other differences were found between the sexes over the sampled years (Table 3.1).

3.3.1 Sexual dimorphism

All measurements except body mass met the assumptions of a two-sample *t*-test according to the results of Levene's test for equality of variances. For all variables other than body mass, males were larger than females in linear measurements and PC1 scores (Table 3.2). The largest proportional differences were in bill depth (7.5%), body mass (5.1%), and bill length (3.1%). The degree of sexual size dimorphism was least in wing length (1.1%). All differences were highly significant ($P < 0.001$) between the sexes and remained significant after the Bonferroni adjustment (Table 3.2). The prospective difference in body mass was tested using a Mann-Whitney *U*-test which showed that males were significantly heavier than females.

Table 3.1 Body measurements (\pm s.d.) of Short-tailed Shearwaters according to year of capture on Great Dog Island, Tasmania. Superscript letters denote significantly different means using Fisher's LSD *post hoc* testing.

	Male ($n = 193$)					Female ($n = 197$)				
	2006/07 ($n = 90$)	2007/08 ($n = 90$)	2008/09 ($n = 13$)	$F_{2,190}$	P	2006/07 ($n = 88$)	2007/08 ($n = 87$)	2008/09 ($n = 22$)	$F_{2,194}$	P
Head length (mm)	83.67 (± 1.9)	83.10 (± 2.1)	84.04 (± 1.4)	2.43	0.09	81.33 (± 1.7)	81.49 (± 2.0)	80.46 (± 2.4)	2.51	0.08
Bill length (mm)	32.74 (± 1.4)	32.5 (± 1.2)	32.98 (± 1.3)	1.21	0.30	31.54 (± 1.1)	31.73 (± 1.1)	31.41 (± 1.5)	0.87	0.42
Bill depth (mm)	8.93 (± 0.3)	8.88 (± 0.4)	9.09 (± 0.4)	1.64	0.19	8.27 (± 0.3)	8.23 (± 0.4)	8.28 (± 0.4)	0.30	0.74
Wing length (mm)	272.49 (± 5.7)	273.14 (± 6.7)	273.23 (± 6.3)	0.27	0.76	269.17 (± 6.2)	269.55 (± 5.6)	272.18 (± 5.6)	2.30	0.10
Tarsus length (mm)	58.84 (± 1.3) ^a	59.40 (± 1.6) ^b	60.13 (± 1.5) ^b	5.85	0.003	58.20 (± 1.7)	58.34 (± 1.3)	58.35 (± 1.5)	0.21	0.81
Body mass (g)	642.00 (± 50.9) ^a	618.78 (± 47.7) ^b	660.00 (± 60.4) ^a	6.95	0.001	583.41 (± 58.7)	612.30 (± 75.3)	615.45 (± 53.4)	9.19*	0.01

*Kruskal-Wallis (χ^2), d.f. = 2

Table 3.2 Descriptive statistics of the measurements of 390 adult sexed Short-tailed Shearwaters (\pm s.d.). Percentage of sexual dimorphism and level of significance between males and females according to the *t*-test in each variable are also shown.

	Males (<i>n</i> = 193)	Females (<i>n</i> = 197)	<i>t</i> _{2,388}	<i>P</i>	% dimorphism
Head length (mm)	83.42 (\pm 2.0)	81.31 (\pm 1.9)	10.51	<0.001	2.5
Bill length (mm)	32.65 (\pm 1.3)	31.61 (\pm 1.2)	8.24	<0.001	3.1
Bill depth (mm)	8.92 (\pm 0.4)	8.25 (\pm 0.4)	16.8	<0.001	7.5
Wing length (mm)	272.84 (\pm 6.3)	269.68 (\pm 5.9)	5.11	<0.001	1.1
Tarsus length (mm)	59.19 (\pm 1.5)	58.28 (\pm 1.6)	5.73	<0.001	1.5
Body mass (g)	632.38 (\pm 1.6)	599.75 (\pm 67.4)	-5.16*	<0.001	5.1
PC1 scores	0.60 (\pm 0.80)	-0.59 (\pm 0.80)	14.57	<0.001	n.a.

*Mann-Whitney *U*-test

3.3.2 Discriminant function analysis

Discriminant function analysis was applied to five morphometric characters of 390 adult Short-tailed Shearwaters (193 males and 197 females). Bill depth and head length were the most accurate variables for use in a discriminant function model, predicting sex with 83.8% accuracy (Table 3.3). The assumptions of the DFA were met as no significant differences between group covariance matrices or deviations from multivariate normality were found (Box *M* = 1.43, approximate *F* = 0.47, *P* = 0.70). Cross-validation classified adults marginally lower with 83.3% accuracy

(Wilks' $\lambda = 0.553$, $\chi^2 = 243.68$, $P < 0.001$). The discriminant function (D) obtained was the following:

$$D = 0.21 (\text{head length}) + 2.138 (\text{bill depth}) - 35.616$$

When D is greater than zero, the individual was classified as a male (mean 0.94 ± 1.03) and when less than zero as a female (mean -0.92 ± 0.97). Misclassification of some adults indicates a degree of overlap in the discriminant scores between the sexes resulting from a slight overlap in body size (Figure 3.1). When only one variable, either bill depth or total head length, was taken into account in the discriminant function, accuracy decreased to 82.1% and 69.7% respectively.

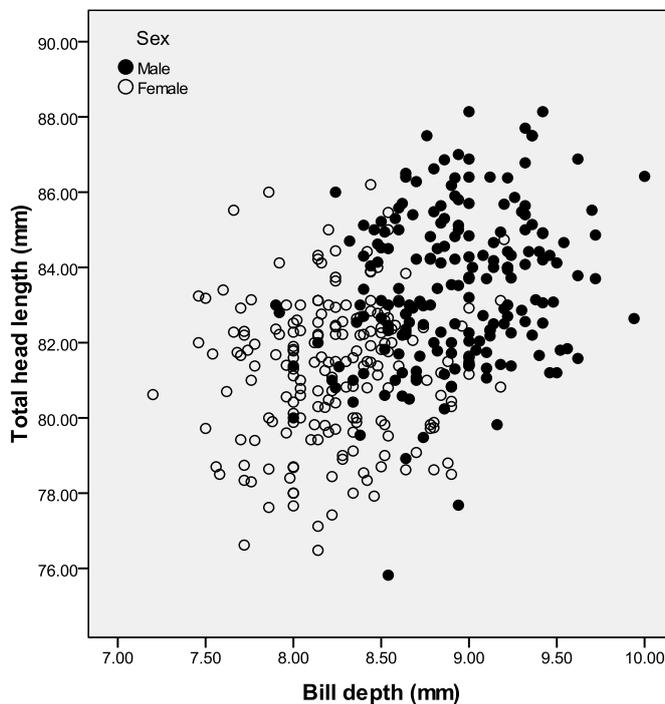


Figure 3.1 Segregation of male and female Short-tailed Shearwaters corresponding to the most accurate variables used in the discriminant function model that included bill depth and total head length.

Table 3.3 Accuracy of the discriminant function derived from measures of 390 Short-tailed Shearwaters. Frequencies and percentages (in parenthesis) of classified birds with the original function and with the cross validation shown.

		Predicted Sex	
	Sex	Male	Female
Original	Male	157 (81.3)	36 (18.7)
	Female	27 (13.7)	170 (86.3)
Cross validation	Male	156 (80.8)	37 (19.2)
	Female	28 (14.2)	169 (85.8)

To test the accuracy of a discriminant model developed by Einoder et al. (2008), their model was applied to the 390 known sexed birds used in this study. Of the 390 adults only 72.5% were accurately allocated the correct sex. This finding indicates some geographic size differences within the species.

Within-pairs, males were significantly heavier and larger than females in all linear variables tested but not based on their PC1 scores (paired *t*-tests; Table 3.4). These differences were still highly significant after the Bonferroni adjustment. The most dimorphic character, bill depth, had an average difference of 0.68 (\pm 0.5) mm between partners. In 92.4 % of cases, males had a deeper bill than did their female partners.

Table 3.4 Differences between male and female Short-tailed Shearwater within the same pair. Total pairs $n = 171$.

Characteristic	Mean difference (\pm s.d.)	% male larger (n)	Paired t	P
Head length (mm)	2.04 (\pm 2.8)	79.5 (136)	9.4	<0.001
Bill length (mm)	0.99 (\pm 1.6)	72.5 (124)	8.1	<0.001
Bill depth (mm)	0.68 (\pm 0.5)	92.4 (158)	17.2	<0.001
Wing length (mm)	3.33 (\pm 9.1)	67.8 (116)	4.7	<0.001
Tarsus length (mm)	0.86 (\pm 2.3)	64.9 (111)	4.9	<0.001
Body mass (g)	25.91 (\pm 88.1)	64.3 (110)	3.8	<0.001
PC1	<0.00 (\pm 1.4)	53.2 (91)	<0.01	>0.05

3.3.3 Tests for assortative mating

In pairs where both birds were measured, there was an opportunity to study assortative mating in their morphometric characters. A total of 171 pairs were used in the analysis. No significant correlation was found between partners in morphometric measurements (Table 3.5). Body mass and PC1 scores were not significantly correlated within-pairs (Table 3.5).

Table 3.5 Correlation analyses of morphometrics of Short-tailed Shearwater pairs. Total pairs $n = 171$.

	Head length	Bill length	Bill depth	Wing length	Tarsus length	Body mass	PC1
r	-0.069	0.106	0.090	-0.097	0.002	-0.016	0.016
P	0.37	0.17	0.24	0.20	0.98	0.83	0.83

3.4 Discussion

Over the three years of this study the linear body measurements of Short-tailed Shearwaters caught each year did not change significantly, with the exception of males' tarsus length. Despite the small size difference, this finding may have been due to the low sample size in 2008/09 or researcher bias. Body mass also differed in males across the three years. Female body mass did fluctuate between years, but not to a statistically significant extent. These observations suggest that annual variation occurs in the body condition of male shearwaters at the Furneaux Group colonies. Aspects of the breeding biology, behaviour, and body condition of seabirds can be an important indicator of marine food supply, and the observed trend may indicate annual fluctuations in food availability at distant shearwater feeding grounds during the breeding season (Weimerskirch and Cherel 1998; Cherel et al. 2005).

Male Short-tailed Shearwaters captured on Great Dog Island were, on average, significantly larger than females on all linear body measurements, body mass, and PC1 scores. These findings support previous studies of this species on Great Dog Island and across their geographical range (Meathrel et al. 1993a; Bull et al. 2005; Bradley and Meathrel 2006; Einoder et al. 2008). The differences between the sexes observed in this study have been reported in other studies of procellariids, for instance in Manx Shearwater (*P. puffinus*) (Brooke 1990), Hutton's Shearwater (*P. huttoni*) (Cuthbert and Davis 2002), Balearic Shearwater (*P. mauretanicus*) (Genovart et al. 2003), Pink-footed Shearwater (*P. creatopus*) (Guicking et al. 2004), Cory's Shearwater (*Calonectris diomedea*) (Lo Valvo 2001), Antarctic Petrel (*Thalassoica antarctica*) (Lorentsen and Rov 1994), and Gould's Petrel (*Pterodroma leucoptera*) (O'Dwyer et al. 2006b), although the degree of sexual dimorphism varies considerably between these species. The degree of sexual size dimorphism presented

in this study was between 1 and 7.5%. A similar range, namely 0.3 – 8.3%, was found for Balearic Shearwaters (Genovart et al. 2003). However, this range is small given the sexual dimorphism between Northern Giant Petrels (*Marconectes halli*), with males being 20 – 25% heavier and from 5 – 16% larger than females in linear measurements (González-Solís 2004).

Short-tailed Shearwaters could be sexed accurately in 84% of cases using bill depth and total head length in a DFA. Validation methods suggested a more realistic estimate of the success rate for the function of 83%. Thus, using the DFA on other shearwaters from this study colony I would expect to make an error in sexing of less than two in 10 times. This contradicts the findings of Meathrel et al. (1993a), who suggested that sex for this species cannot be predicted based on structural size.

I have not been able to apply other researchers' DFA derived models on adults used in this study. Nevertheless, the present findings suggest that there is some geographical variation within the species and reinforce the need for researchers to obtain sex models from locally caught birds (Weidinger and van Franeker 1998; Guicking et al. 2004). Geographic variation may reflect some kind of ecomorphological adaptation to different environmental conditions (Spear and Ainley 1998; Guicking et al. 2004).

The success rate achieved in this study for sexing Short-tailed Shearwaters lies between that reported for many shearwater species (>90%; Lo Valvo 2001; Genovart et al. 2003; Guicking et al. 2004; Thalmann et al. 2007) and for petrels (59-86%, Weidinger and van Franeker 1998; 73%, O'Dwyer et al. 2006). At a Short-tailed Shearwater colony in South Australia, 1,500 km to the west of Great Dog Island, Tasmania, Einoder et al. (2008) were able to predict sex 92% of the time, despite their low sample size. However, application of their sex model to another colony close by

reduced its accuracy to 70 – 80% (Einoder et al. 2008). Although the results of a DFA are sensitive to sample size and other statistical attributes (Morrison 1984), much of the variation in success rate is likely to result from variation in the relative degree of sexual size dimorphism (Chardine and Morris 1989).

The stepwise DFA used to determine the classification function chose bill depth, followed by total head length, indicating that bill depth was the better discriminator of sex. The value of bill depth in determining sex in procellariids has been reported previously (Lo Valvo 2001; Genovart et al. 2003; Einoder et al. 2008). Used alone, bill depth successfully sexed 82% of Short-tailed Shearwaters in the sample. However, given the reduction of success rate when bill depth alone was used, I recommend the use of both bill depth and total head length when sexing live Short-tailed Shearwaters in the Furneaux Group colonies. Sexual size dimorphism in bill morphology has been suggested as reflecting sex differences in foraging behaviour (González-Solís et al. 2000a,b; González-Solís 2004). However, it is not known whether a sex difference in foraging behaviour exists in Short-tailed Shearwaters.

In almost all Short-tailed Shearwater pairs observed in this study, the male was larger. Similar results have been obtained by Meathrel et al. (1993a) and Einoder et al (2008) for Short-tailed Shearwaters. Differences in relative size of certain body parts, such as bill depth, within a pair may be a more reliable indicator of sex. Predicting sex within-pairs was achieved with a higher accuracy rate than the DFA when bill depth of both birds was analysed. Within-pair comparisons have substantially improved the accuracy of determining sex in seabirds with monomorphic plumage such as Cape Petrels (*Daption capense*) (Weidinger and van Franeker 1998), Common Terns (*Sterna hirundo*), Arctic Terns (*S. paradisaea*) (Fletcher and Hamer 2003), and Brown Noddies (Chardine and Morris 1989).

Short-tailed Shearwaters from this colony showed no assortative mating according to body mass or linear body measurements. These results contrast with those of Bradley and Meathrel (2006) and Einoder et al. (2008) who found positive assortative mating for bill depth, tarsus length, and body size index. Despite the fact that assortative mating has been shown to occur in Brown Noddies (Chardine and Morris 1989) and Arctic Terns (Fletcher and Hamer 2003) it seems that Short-tailed Shearwaters mating does not occur as a result of similar morphological traits. A lack of assortative mating in Short-tailed Shearwaters based on size alone is perhaps not surprising given the structural similarity between males and females (the most dimorphic feature, bill depth, was only 7.5% larger in males). If assortative mating occurs in Short-tailed Shearwaters it therefore appears to be based on traits other than structural size. In this species, it has been suggested that assortative mating may be determined by age since first bred (Wooller et al. 1990; Bradley et al. 1995), which has been found for Northern Giant Petrels (González-Solís 2004).

In summary, sexual size dimorphism does occur in the Short-tailed Shearwater. The most dimorphic feature of the species is bill depth, and when combined with total head length, sex can be predicted with 84% accuracy using a DFA model. When applying a discriminant function analysis to other colonies of Short-tailed Shearwaters, I would recommend investigators use measurements of their specific population due to geographic variation within the species. Size differences are also reflected within-pairs. For pairs in which it is difficult allocating gender, within-pair comparison of bill depth should assist in determining sex. Assortative mating was not observed in this species, despite the findings of Bradley and Meathrel (2006) and Einoder et al. (2008). In future studies, where sexing is an important feature of the study, researchers should really invest the time into directly validating

sex. Finally, I recommend one observer perform all morphological measurements to eliminate inter-observer differences as the degree of dimorphism in Short-tailed Shearwaters is small.

CHAPTER 4: Effects of Investigator Disturbance on Hatching Success and Chick Size and Mass

4.1 Introduction

As indicated in Chapter 1, there have been long-held concerns about the impact of investigators in ecological studies of wildlife, particularly in studies of avian species (Götmark 1992; Carney and Sydeman 1999; Nisbet 2000; Phillips et al. 2003; Carey 2009). Nisbet (2000) first made the clear distinction between human or recreational disturbance and investigator disturbance, and thus provided a formal description of the implications of investigator effects. In behavioural, demographic, and ecological studies, researchers should aspire to unbiased observations when studying wildlife in order to observe individuals under natural conditions without altering those conditions. However, without experimental evidence that explores the effects of investigator disturbance it is difficult to determine the magnitude of that disturbance, consider strategies for avoiding it, or at least make appropriate adjustments to take it into account.

Many researchers have not assessed the effects that their activities might have had on birds' normal behaviour (Götmark 1992; Nisbet 2000). However, while some researchers have claimed that no disturbance effect occurred in their studies (Saffer et al. 2000a; O'Dwyer et al. 2006a), others indicate that researchers do have an impact (Weimerskirch et al. 2002; Blackmer et al. 2004). This observer effect has the potential to create biased results that, in turn, could compromise our understanding of a species' ecological and behavioural attributes (Serventy and Curry 1984).

Studies of investigator disturbance have been conducted on a wide range of avian taxa, particularly colonial nesting waterbirds such as gulls, terns, pelicans, cormorants, and penguins (for reviews see Carney and Sydeman 1999; Nisbet 2000).

There have been fewer experimental studies that quantify investigator disturbance of procellariiform seabirds (Carey 2009). The potential negative effects of investigator disturbance on birds include predation of eggs and young (Hockey and Hallinan 1981), desertion of nests (Giese 1996), reduction in fledging success (Pierce and Simons 1986; Whidden et al. 2007), physiological changes such as increased heart rates (Weimerskirch et al. 2002) and acute stress-induced levels of plasma corticosterone (Brewer et al. 2008). These outcomes have been attributed, among other things, to handling birds during research activities. Handling of adults and their young is necessary for some behavioural and ecological studies. Birds are handled to attach rings for individual recognition, to make morphological measurements, to acquire blood samples, or to attach tracking devices. Handling, even when conducted in a prompt and professional manner as required under current animal ethics permits, may trigger adverse outcomes, so it is important to determine the extent of handling that birds can tolerate before negative effects are observed.

In this chapter, the frequency of handling during the incubation period was used to quantify investigator disturbance on the length of incubation (average 53 days; Serventy 1967), hatching success, chick survival to pre-fledging, and chick body size and peak mass of Short-tailed Shearwaters (*Puffinus tenuirostris*). Anecdotal accounts of investigator disturbance affecting these seabirds provide some evidence that handling of adults during the incubation period can have a negative effect on hatching success (Allan 1962; Morse and Buchheister 1979; Warham 1990; Marks and Leasure 1992), but there is little published experimental evidence to support this — i.e., comparisons between control (not handled) and treatment (handled) groups. Handling of adults during the incubation period and subsequent effects of the survival and quality of their offspring has also received little experimental investigation

despite the possible compromised outcomes (Gangloff and Wilson 2004; Carey 2009). Based upon anecdotal accounts from previous studies, and evidence provided by Blackmer et al. (2004), I predicted that hatching success would be lower as the frequency of handling increased and that there would be a concomitant difference in pre-fledging chick survival and body size.

This study is the first to quantify the effects of investigator disturbance on any species of shearwater.

4.2 Methods

4.2.1 Field procedures

This research was conducted between November 2006 and March 2007 on Great Dog Island. Birds used in this study had experienced no previous handling by researchers except for 12 birds that had been banded as chicks 10 to 12 years previously as part of an investigation into parental attendance and chick provisioning patterns (Hamer et al. 1997). Thirty active burrows in each of four treatments (total $n = 120$) were chosen during daily inspections of approximately 300 burrows during the egg-laying period between 22 and 27 November 2006. An active burrow was defined as one with an incubating bird. All active burrows were located within 24 hrs of egg laying. Burrows were located in an area of 20 m \times 100 m to avoid confounding influences of microclimate and temporal bias. Each burrow was marked by a polyvinylchloride pole with a unique number and were clearly marked with coloured flagging tape for the duration of the project. Once an active burrow was found it was randomly allocated to one of four treatments of investigator disturbance. The disturbance experiment started as soon as the active burrows were found. Burrows were disturbed during daylight hours between 0730 and 1300 hrs throughout the investigation. All

burrows were inspected according to the time schedule of their respective treatment group: only once, at the beginning of the study (control); every day; every 3 days; or every 7 days (hereafter referred to as control, 1D, 3D, and 7D groups respectively). A maximum of two investigators were in the plot at any one time. Burrows were approached only if a disturbance event was imminent. This ensured that the minimally disturbed control group would be minimally affected because of visits to neighbouring burrows. Average burrow density of the study plot was 0.47 m^{-2} . However, the density of study burrows used in this study was 0.06 m^{-2} . The investigator disturbance ended once it was determined whether or not the egg had hatched, and the time between onset of incubation and hatching was recorded to the nearest day. Burrows were inspected for the presence of a chick 53 days after an egg was detected. If an egg was still present after 53 days from incubation, the burrow was checked daily until the fate of the egg could be determined (i.e., hatched or failed to hatch). Eggs that failed to hatch were classified as either rotten, predated or abandoned. If an egg was no longer present in a particular burrow during the investigation period the burrow was still inspected at the appropriate disturbance interval(s) to identify burrow use by non-breeding or failed birds.

4.2.2 Study groups and disturbance procedures

Pairs in the control group received the minimum amount of disturbance possible, whereas field procedures for the 1D, 3D, and 7D, treatment groups simulated investigator disturbance that might be experienced by incubating birds during routine monitoring in a scientific study where regular handling is required to obtain demographic or individual physiological parameters (Prince et al. 1981; Croxall and

Ricketts 1983; Johnstone and Davis 1990; Chaurand and Weimerskirch 1994; Booth et al. 2000).

4.2.2.1 Control group

If a burrow was allocated to the control group, the incubating bird and the egg were not removed from the burrow. Thus, only one member of a control pair received investigator contact and the other adult bird was not handled during the incubation period. After determining that a burrow was active by briefly feeling for the presence of an adult and an egg, it was left undisturbed for 53 days (the average length of the incubation period; Serventy 1967) until it was re-visited to determine hatching success. If an adult bird was present on the second visit, it was removed from the burrow and placed in a calico bag while the burrow was inspected for a chick. If a chick was found it was carefully removed (if it could be reached), weighed, and measured. Measurements taken for both adults and chicks are described in Chapter 2 Section 2.4.3.2. Chicks were weighed with a 300 (± 2) g Pesola scale and adult birds were weighed with a 1000 (± 10) g Pesola scale. Adults were banded with an Australian Bird and Bat Banding Schemes (ABBBS) band at this time. If an egg was present it was removed and inspected for any evidence of hatching (i.e., starring or pipping). The egg was then returned to the burrow along with the adult.

4.2.2.2 Daily treatment group

During the first visit to a burrow in the 1D treatment group the egg and the incubating bird were removed. To account for the influence of egg size on hatching success, eggs were measured with according to Chapter 2 Section 2.4.3.1. The body mass and morphometric measurements (head length, bill length, bill depth, wing and tarsus) of

the adult bird were also recorded as described for the control group. All adults encountered were banded with an ABBBS bands. The sex of the adult was also determined at this time by cloacal examination (Serventy 1956b) or later by a discriminant function analysis (Chapter 3). After handling, the egg and adult were returned to the burrow where they were left undisturbed until the following day, when the adult bird was removed from the burrow, the band number was checked, and its body mass was recorded. Morphometric measurements were not taken again, and handling took < 2 min. Once the presence of the egg was determined, the adult was returned to the burrow, thus completing the investigator disturbance until the following day. When the first incubation changeover occurred, 12 to 14 days into the incubation period, the partner was banded, weighed, and measured as described above. The frequency of handling continued daily thereafter. Because Procellariiformes frequently leave eggs unattended in nesting burrows (Matthews 1955; Warham 1990), cold and unattended eggs found at any time during the investigation were checked every day to determine whether the burrow had been completely abandoned or if a parent had returned to continue the incubation.

4.2.2.3 Three day and weekly treatment groups

For the remaining two treatment groups, procedures were the same as in the 1D treatment group initially, then burrows were disturbed every 3 or 7 days respectively during the incubation period. Once the average 53 day incubation had passed, burrows were inspected daily to ascertain hatching date and the size of the hatchling.

4.2.3 Chick survival, mass and size

Once hatching success and hatchling size were determined, the burrows in all 4 groups were left undisturbed for 9 weeks. Towards the end of March, young birds begin to explore outside their burrows (Serventy 1967). This behaviour increases the possibility that young chicks do not return to their natal burrows, usually because of predation. At this stage, chicks are approximately two-thirds grown and approach their peak body mass (Serventy 1967; Saffer et al. 2000*b*). Therefore, all treatment burrows that contained a chick in January 2007 were inspected in mid-March to ascertain chick survival and size. If a chick was present, it was removed, placed into a calico bag and weighed with Pesola a 2500 (\pm 20) g scale, and the measurements described above for adults were recorded. Chicks were banded with an ABBBS band and returned to their burrow. If a chick was not present it was assumed that it had perished since hatching.

4.2.4 Statistical analyses

Statistical analyses were performed using SPSS version 17.0 software package (SPSS Inc., Chicago, IL, December 2008). One-way ANOVAs were used to identify any differences in incubation length and egg size between control and treatment groups. To examine whether investigator disturbance influenced the probability that an egg would hatch, a multiple logistic regression model was used in which the explanatory variable was the frequency of disturbance (control, 1D, 3D and 7D) and the nominal dependent variable was hatched or failed to hatch. Next, a two-tailed *G*-test with William's correction factor was used to conduct pairwise comparisons of the number of eggs that hatched versus the number of eggs that failed to hatch among the four study groups (Sokal and Rohlf 1995). These six pairwise comparisons were corrected

for multiple comparisons using the Bonferroni method, and thus a result was considered significant when $P \leq 0.0083$ ($\alpha = 0.05/6$; Sokal and Rohlf 1995).

To examine whether chick mass and skeletal measurements varied across treatments, I first used ANOVA to identify any differences in chick body mass and body measurements between the four groups. Second, I used principal components analysis (PCA) to characterise variability in body dimensions within the total sample. The first principal component (PC1) comprised head length, bill length, bill depth, wing length and tarsus length, and was used as a single composite measure of body size (Rising and Somers 1989; Dytham 2003). Effects on body condition of chicks in each study group were investigated by using an ANCOVA model with body mass as the dependent variable, body size index (PC1) as a covariate, and treatment group as a fixed factor. Unless specified above, for all tests the significance level was $P \leq 0.05$ and descriptive statistics are presented as means \pm standard deviation (s.d.).

4.3 Results

4.3.1 Laying date and egg size

Egg laying began on the 22 November, and by 27 November 120 burrows had been allocated to the control or a treatment group. Mean egg laying date was 25 November, and there were no differences between the control and treatment groups ($F_{3,116} = 0.05$, $P = 0.9$). Thirty eggs from each of the three treatment groups were weighed and measured (1D, 3D, and 7D; total $n = 90$) and no differences were observed in any measured variable between groups (Table 4.1). However, egg mass tended to increase over the six days they were laid (Pearson correlation coefficient $r_{90} = 0.33$, $P = 0.001$). The mass and volume of the smallest egg was 67% of the largest.

Table 4.1 Mean (\pm s.d.) dimensions and masses of eggs laid in each treatment group by Short-tailed Shearwaters on Great Dog Island during 2006 – 07.

	Mean ($n = 90$)	Range ($n = 90$)	1D ($n = 30$)	3D ($n = 30$)	7D ($n = 30$)	$F_{2,89}$	P
Egg mass (g)	98.4 ± 7.4	82.0 – 120.0	99.2 ± 8.5	98.2 ± 7.4	97.9 ± 6.1	0.261	0.8
Length (mm)	71.7 ± 2.5	64.1 – 79.1	71.8 ± 2.5	71.0 ± 2.2	71.7 ± 2.5	2.286	0.1
Width (mm)	46.9 ± 1.4	43.5 – 51.0	46.8 ± 1.6	47.1 ± 1.4	46.9 ± 1.3	0.184	0.8
Estimated volume (cm ³)	80.7 ± 6.0	66.6 – 101.5	79.5 ± 6.8	81.3 ± 5.7	79.8 ± 6.0	0.493	0.6

4.3.2 Hatching success and incubation length

Overall hatching success was significantly lower the more often nests were disturbed (Wald $\chi^2 = 19.52$, $P < 0.001$, $n = 120$; Table 4.2). Pairwise comparisons revealed that the 1D and 3D treatment groups each had a significantly lower hatching rate than did the control group, whereas there were no differences in hatching success between 7D and control or 7D and 3D treatment groups (Table 4.3). Compared to the control group, investigator disturbance reduced hatching success by 39% in the 7D group, 61% in the 3D group, and 100% in the 1D group (Table 4.2).

Hatchling mass and size did not differ between groups (mass $F_{2,30} = 2.98$, $P = 0.06$; head length $F_{2,30} = 2.66$, $P = 0.08$; bill length $F_{2,30} = 0.38$, $P = 0.68$; bill depth $F_{2,30} = 0.03$, $P = 0.96$; wing length $F_{2,30} = 2.95$, $P = 0.07$; tarsus $F_{2,30} = 1.75$, $P = 0.19$).

All 120 burrows were monitored for the entire $53.5 (\pm 0.96, n = 38)$ day incubation period. The number of hatching checks needed to determine hatching success averaged $1.7 \pm 0.9 (n = 38)$ and differed slightly between groups (control: 1.3 ± 0.6 , 3D: 2 ± 0.5 , 7D: 2.1 ± 1.3 ; $F_{2,35} = 3.56, P = 0.04$). Duration of incubation differed significantly between treatment groups ($F_{2,35} = 4.60, P = 0.02$). *Post hoc* least significant difference testing revealed that the 7D group had a slightly, but significantly, longer incubation period ($54.1 \pm 1.3, n = 11$) than did controls ($53.2 \pm 0.5, n = 19$, mean difference $0.9 \pm 0.3, P = 0.01$) and pairs disturbed 3D ($53.1 \pm 0.3, n = 8$, mean difference $1.0 \pm 0.4, P = 0.02$). Because none of the 1D nests produced hatchlings, determining incubation length was irrelevant.

Although the causes of nest failure could not be identified in all cases, the primary cause of failure was nest abandonment by incubating parents. Of the 82 observed eggs that did not hatch, 75% failed because the parents permanently abandoned their nesting attempt. Sixty percent of egg abandonments occurred during the first half of the incubation period (Figure 4.1). Of eggs that failed to hatch, 6% were because they were either rotten or infertile. The fate of 6% of eggs in the control group could not be determined because of the interval between nest checks. Predation also accounted for some egg failures. Ten eggs were predated during the experiment (12% of eggs that did not hatch or 8% of all eggs monitored) by Blotched Blue-tongue Lizards (*Tiliqua nigrolutea*) and Australian Water Rats (*Hydromys chrysogaster*) (Carey 2010; Appendix 2). Predation occurred at all times of the incubation period and in all treatment groups.

The minimum number of disturbances sufficient to cause permanent egg abandonment was a single visit in the 1D treatment group (mean 14.1 ± 11.1 visits, range 1 - 44 visits). Temporary egg neglect was observed in all 1D burrows at some

stage during the incubation period. Temporary egg neglect in the 1D treatment group averaged 3.2 ± 2.4 days (range: 1 - 17 days). Only two 1D burrows (6.6%) were active after the 53 day incubation period had passed, and neither of the eggs in those burrows hatched.

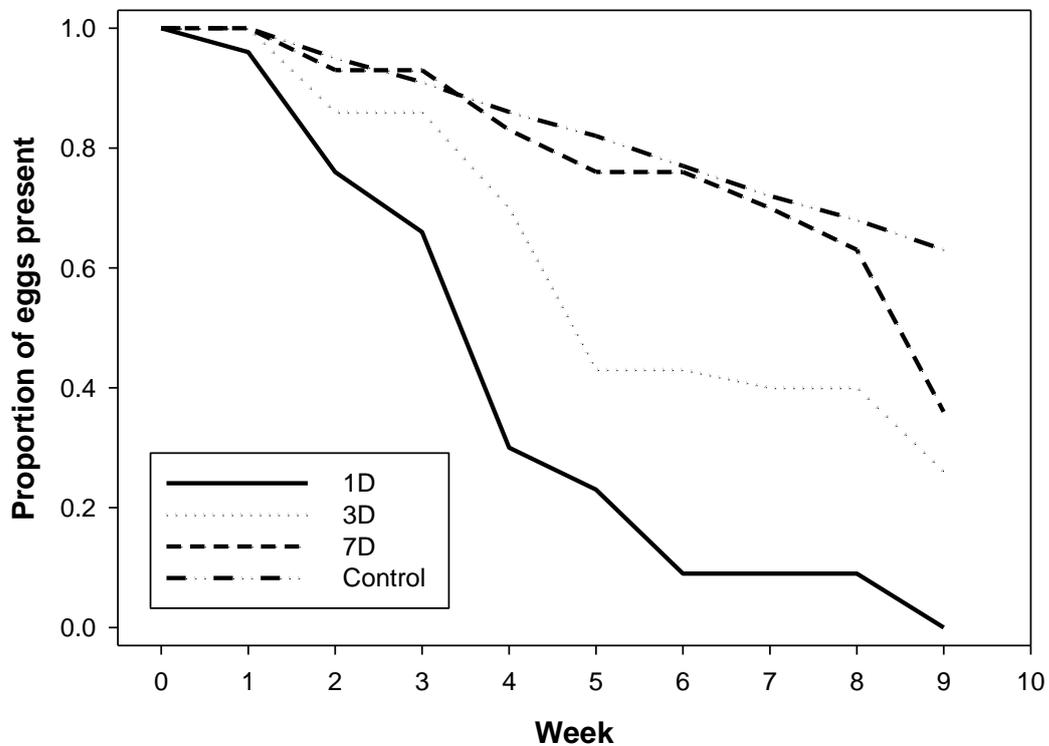
Table 4.2 Comparisons showing the differences in hatching success, fledging survival, and overall reproductive success in the four treatment groups. Numbers are indicated in parentheses.

Treatment (<i>n</i> = 30)	Hatching success	Fledging survival	Overall reproductive success
Control	63.3% (19)	57.8% (11)	36.6% (11)
1D	0.0% (0)	n.a.	0.0% (0)
3D	26.6% (8)	62.5% (5)	16.6% (5)
7D	36.6% (11)	63.6% (7)	23.3% (7)

Table 4.3 Pairwise comparisons using a *G*-test with William's correction factor of the number of eggs that hatched versus the number of eggs that failed to hatch among the four treatment groups. n.s. = not significant.

Treatment	1D	3D	7D
Control	$\chi^2 = 35.5$ $P < 0.001$	$\chi^2 = 8.35$ $P = 0.004$	$\chi^2 = 4.32$ $P = 0.038$, n.s.
1D	-	$\chi^2 = 12.33$ $P < 0.001$	$\chi^2 = 17.74$ $P < 0.001$
3D	-	-	$\chi^2 = 0.70$ $P = 0.404$, n.s.

Figure 4.1 Proportion of active Short-tailed Shearwater nests over time among the four treatment groups. Note: for the control group a constant rate of egg loss is assumed over the incubation period.



4.3.3 Chick survival, mass, and size

All chicks were measured on the same day, control chicks (mean 56.5 ± 1.7 days) were slightly but not significantly older than 3D and 7D chicks (3D mean 55.3 ± 1.1 days; 7D 55.4 ± 0.9 , $F_{2,35} = 2.85$, $P = 0.07$). Chick survival was not significantly influenced by handling adult birds during incubation (Wald $\chi^2 = 0.11$, $d.f. = 2$, $P =$

0.74, $n = 38$; Table 4.2). Analysis of chick body mass revealed significant differences between the three treatment groups ($F_{2,21} = 5.96$, $P = 0.009$) with control chicks being on average $252 (\pm 74.9)$ g heavier than 3D chicks and $138 (\pm 71.3)$ g heavier than 7D chicks (Fig 4.2). Control chicks had significantly greater bill depths and wing lengths than did the 3D and 7D treatment groups (Table 4.4). PC1 accounted for 55% ($\lambda = 2.78$) of the total variance explained by the components and four variables loaded heavily and positively on this PC (> 0.71). The exception was bill depth = 0.15). Despite control chicks being larger on some variables, there was no statistically significant difference in PC1 scores between treatment groups. However, the differences did come close to being statistically significant (Table 4.4). After controlling for body size, no significant effect of investigator disturbance on body mass was detected between the three groups (ANCOVA: $F_{2,20} = 2.28$, $P = 0.12$); however, when comparing the control and combined disturbed groups, control chicks tended to be heavier (i.e., 3D and 7D, $n = 12$) (ANCOVA: $F_{2,20} = 3.65$, $P = 0.07$).

Figure 4.2 Boxplot indicating the differences in chick peak body mass (g) between treatment groups where adults had received different levels of investigator disturbance during incubation on Great Dog Island in March 2007. The plot shows the median value as a thick bar (50th percentile), the interquartile range as the box (25th – 75th percentile) and the full range as the ‘whiskers’. Letters denote *post hoc* testing to distinguish significantly different means using the least significant difference test (Fisher’s LSD test).

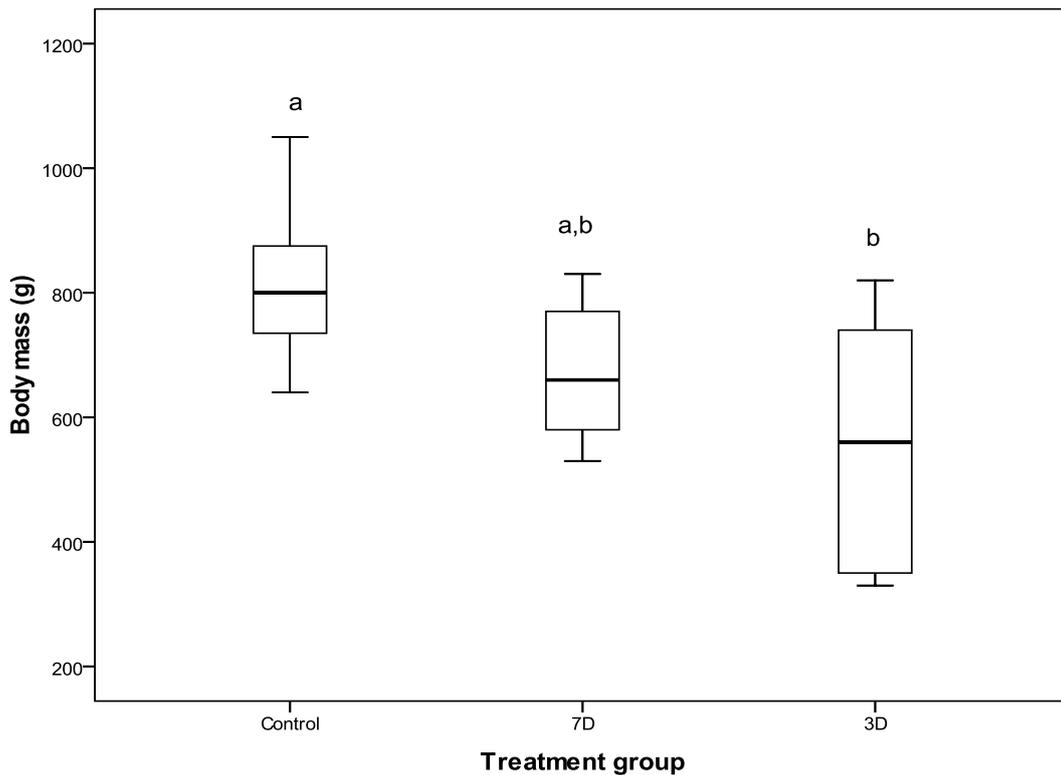


Table 4.4. Differences in body measurements between pre-fledging Short-tailed Shearwater chicks reared by parents that had received different levels of investigator disturbance during the incubation stage. Data presented are mean \pm s.d.

	Control (<i>n</i> = 11)	7D (<i>n</i> = 7)	3D (<i>n</i> = 6)	<i>F</i> _{2, 21}	<i>P</i>
Head length (mm)	81.05 \pm 2.3	79.64 \pm 1.5	77.85 \pm 5.2	2.02	0.15
Bill length (mm)	31.44 \pm 1.5	30.94 \pm 1.4	31.20 \pm 2.0	0.19	0.82
Bill depth (mm)	7.99 \pm 0.4	7.47 \pm 0.5	7.29 \pm 0.4	5.13	0.01
Wing length (mm)	161.81 \pm 13.7	148.57 \pm 10.4	132.83 \pm 25.9	5.85	0.01
Tarsus length (mm)	59.36 \pm 1.2	58.60 \pm 1.5	58.05 \pm 2.1	1.42	0.26
PC1 score	0.45 \pm 0.65	-0.15 \pm 0.4	-0.65 \pm 1.5	2.93	0.07

4.4 Discussion

In this study, handling adults daily and every third day significantly reduced the hatching success of Short-tailed Shearwaters. Weekly handling of incubating adults also reduced hatching success, but not significantly so compared with the control group. In response to investigator disturbance, Short-tailed Shearwaters reduced their parental effort by abandoning their eggs which is consistent with life history theory. Long-lived species, like the Short-tailed Shearwater, have a high probability of adult

survival, and reproduction in any one year represents a small fraction of an individual's lifetime reproduction (Lack 1954; 1968). Therefore, parents likely reduced their investment in the current breeding attempt as a means of increasing the probability of future survival and thus future breeding attempts (Stearns 1992). Egg desertion was the primary response to investigator disturbance. This was particularly evident in the daily handling group, where there was a 70% reduction in active nests after the first four weeks of incubation. Temporary egg neglect was observed in all daily burrows, and may have occurred in the control and other two treatment groups. If temporary egg neglect did occur, it may account for the longer incubation period for eggs in the weekly treatment group. Interestingly, in the most disturbed group (1D) two birds continued incubating their egg well past the expected hatching date. One possibility for this is that the egg neglect in 1D and 3D groups was so severe that the embryo died, but a few 3D and 7D embryos survived and developed more slowly which extended the incubation period. Recent evidence suggests that poor development conditions lead to a reduction in the growth of the embryo with consequences for the organism later in life (Gorman and Nager 2004). As a result of high levels of investigator disturbance in Tufted Puffin (*Fratercula cirrhata*) colonies, Pierce and Simons (1986) also found that birds had longer incubation periods.

Egg neglect resulting in extended incubation periods has been reported for a number of seabirds (Mathews 1955; Boersma and Wheelwright 1979; Warham 1990). Short-tailed Shearwater embryos are likely to be able to survive periods of temporary egg neglect. However, the periodic visits of investigators, combined with natural egg neglect, could exacerbate the effects on embryonic development that may have caused the embryo to die.

Handling, banding, and nest monitoring have occurred in a number of other studies on seabirds, although the frequency of handling that was associated with nest abandonment is not reported (Götmark 1992; Nisbet 2000). Results presented in this study may exaggerate the effects of investigators because naïve birds were used. Habituated birds might be less likely to abandon their nests (Burger and Gochfeld 1999). Yet these results are consistent with other observations of long-lived seabirds. For example, as a result of investigator disturbance studies have shown a reduced reproductive success in puffins (Rodway et al. 1996), albatross (Wheeler et al. 2009), storm-petrels (Blackmer et al. 2004), boobies (Burger and Gochfeld 1993), and cormorants (Ellison and Cleary 1978). In the only other study to quantify the effects of handling on the reproductive success of a procellariiform, Blackmer et al. (2004) found that handling incubating birds daily or weekly significantly reduced hatching success of Leach's Storm-petrels by 56% and 50%, respectively. It seems that many storm-petrels are particularly sensitive to investigator handling (Blackmer et al. 2004; Carey 2009). Boersma et al. (1980) found that daily handling of Fork-tailed Storm-petrels (*O. furcata*) caused a significant reduction in hatching success. In their study, hatching success was 58% in nests that were checked daily compared with 84% in nests that were checked only four times late in the incubation period. The same is true for Tristram's Storm-petrel (*O. tristrami*). Marks and Leasure (1992) found that these birds abandoned their nests when investigators were present and nest checks were made. In their study, of the 22 nests that failed during incubation 55% failed between the first and second visits, and 23% failed between the second and third visits; only 33% of eggs hatched, and overall breeding success rate was 18%. Serventy and Curry (1984) found that handling of Short-tailed Shearwaters over a 25 year period on Fisher Island, Tasmania, resulted in a decline of occupied breeding burrows by 71%.

The investigator disturbance contributed to an increase in burrow desertion, decreased breeding success, decreased recruitment of young birds, and delayed the start of some birds breeding. Their study implicated investigator disturbance in the long-term decline of this population and complements findings from other long-term studies (Ollason and Dunnet 1980; Blackmer et al. 2004).

It is possible that the results of this study are biased because handling commenced so early in incubation. It may not necessarily just be how frequent an adult is handled that is important, but the timing during incubation as well. There are physiological reasons why disturbance at the start of incubation might be more severe, as birds have yet to switch firmly to a regular incubation schedule and even a low level of stress during that critical period may trigger abandonment.

Although in the current study investigator handling of adults had an adverse effect on hatching success, it did not affect chick survival up to two thirds of the way through pre-fledging development. In fact, both disturbed treatment groups had a slightly higher survival rate than did birds in the control group. However, when taking into account overall reproductive success, the control treatment group recorded a 36% success rate which, on average, was 16% higher than in the disturbed (3D and 7D) treatment groups. Booth et al. (2000) handled Little Shearwaters (*P. assimillis haurakiensis*) every two days during the incubation period and did not find any effect relative to the normal chick survival rate. Overall, 29% of 'study burrows' were successful in fledging a chick, compared with 30% of burrows in the control group. Similarly, investigator handling of incubating Gould's Petrel (*Pterodroma leucoptera*) did not seem to produce any differences between chick growth and survivorship (O'Dwyer et al. 2006a). However, recent evidence suggests that poor development conditions can lead to a reduction in the growth of the embryo with consequences for

the organism later in life (Gorman and Nager 2004; Nilsson et al. 2008) and may explain the results from the present study, where investigator disturbance had a slight effect on body size in that chicks from treatment groups were structurally smaller. Furthermore, the more disturbance there was, the smaller the chicks tended to be. Body mass was also affected in chicks from treatment groups. Parent birds that were handled every third day produced significantly lighter chicks than were found in the control group. Harris and Wanless (1984) and Hatchwell (1989) reported growth rate and age at departure of Common Guillemot (*Uria aalge*) chicks were reduced by daily human disturbance. Hatchwell (1989) went on to propose that the effect of disturbance might be due to reduced provisioning of chicks by parents, increased energy demands for thermoregulation in the absence of brooding, and/or increased energy expenditure due to the stress of being handled. Reasons for a reduced body mass and body size between the treatment groups are unclear. Reasons for a reduced body mass between the treatment groups are unclear. Nevertheless, it seems that handling adults during the incubation could also have some sub-lethal effects affecting post-hatching offspring development. This finding supports other experimental studies on prenatal developmental conditions that indicate the importance of carry-over effects of the incubation stage on the next life-history stage and the importance of incubation as a component of reproductive costs and for nestling quality (Gorman and Nager 2004; Nilsson et al. 2008; Pérez et al. 2008). Recent evidence demonstrates that reproductive effort during egg formation and incubation can cause intra-individual and intra-generational trade-offs (Nager et al. 2000, 2001; Nilsson et al. 2008). Extent of incubation effort can have substantial effects on the potential fitness of the offspring (Gorman and Nager 2004). Carry-over effects on future life-history stages represent another cost that may influence parental

care decisions because the production of poor-quality offspring is costly both to the parents and to the offspring themselves (Gorman and Nager 2004).

An alternative explanation for the poor development of offspring is the role of increasing levels of stress hormones such as corticosterone in adults as a result of handling (Buttemer et al. 1991, Astheimer et al. 1992). In many vertebrate species, including amphibians, reptiles, and birds, corticosterone is a main glucocorticoid involved in regulation of fuel, immune reactions, and stress responses. Variations in stress-related hormones such as corticosterone in response to investigator or tourist disturbance has been researched across seabird taxa such as penguins (for a review see Walker et al. 2008), but very little information exists with regard to any procellariiform (Carey 2009; but see Navarro et al. 2008). An increase in circulating corticosterone levels may direct behaviour away from reproduction and toward activities such as feeding that promote self-maintenance (Astheimer et al. 1992). If this is the case, these birds would reduce both food delivery rates and meal sizes during the chick provisioning stage. For some highly pelagic species, whose chicks are fed infrequently, even a small reduction of food could have serious negative outcomes, particularly in the early stages of chick development. Any reduction in delivery rates or meal size would slow growth rates and/or peak fledgling mass. Several studies on shearwaters have shown that a higher fledging mass has a positive outcome for post-fledging survival and recruitment into the breeding population (Manx Shearwater *P. puffinus*: Perrins et al. 1973; Brooke 1990; Sooty Shearwater *P. griseus*: Sager and Horning 1998). This physiological mechanism is based on the assumption that corticosterone levels remain elevated throughout the chick rearing period despite no further disturbance. This may not be true and provides an avenue for further research. It is also possible that reduced post-hatching development may

be a consequence of disturbed parents being in poorer condition during chick rearing and therefore their chick develop less well. Unfortunately, the present data cannot distinguish between these possibilities.

In summary, this study demonstrates that daily and every three day handling of adults during incubation has a significant negative impact on Short-tailed Shearwater hatching success and chick structural size and body mass. It also suggests the vulnerability of birds that have had little or no experience with researchers.

Investigator disturbance that has a detrimental effect on the individual's reproductive success, colony distribution, or population could exacerbate declines of threatened species (Blackmer et al. 2004) and therefore knowledge of these effects is important in designing any research program. Therefore, researchers would be well advised to consider their impact on the intended study species. This would be of particular importance when small or threatened populations are involved, as a number of populations are already under threat from other sources such as invasive species, habitat loss, and long-line fishing. This information could then be used to advance conservation objectives. Future research on seabirds should explore the effects that researchers have on their study animals in the short-term, and existing studies might also benefit from these investigations. This might also help to correct, or at consider the possibility of, biased or misleading data in past studies. Only then can we be sure that researchers are truly recording a bird's 'natural behaviour'.

Chapter 5: **Effects of Investigator Disturbance on the Pair-bond and Nest-site Fidelity of Short-tailed Shearwaters**

5.1 **Introduction**

In the previous chapter, frequent investigator disturbance (i.e., handling adults during the incubation stage) was identified as being detrimental to the hatching success and chick body mass and size of Short-tailed Shearwaters (*Puffinus tenuirostris*). That study highlighted the damaging effects of handling adults in the short-term (i.e., in the year of disturbance) by reducing a bird's reproductive success. However, little is known about a bird's reproductive success in the long-term (i.e., subsequent breeding seasons) after studies have been completed or when researchers move on to another study, unaware of their impact (see Serventy and Curry 1984). Knowledge of the long-term impacts of investigator disturbance are equally important as short-term impacts because of their potential impact on reproduction, populations and the accurate assessment of demographic parameters (Rodway et al. 1996; Blackmer et al. 2004).

Quantifying the effects of investigator disturbance post-investigator disturbance has rarely been examined in any colonial nesting seabird (Gömark 1992), including procellariiform seabirds (Chapter 1; Carey 2009). No such studies exist on any *Puffinus* shearwater species. Studies attempting to quantify the effects of investigator disturbance on long-lived seabirds reveal mixed results. For example, the fledging success of Atlantic Puffins (*Fratercula arctica*) remained low for 1 year, but not 2 years, after investigator disturbance (Rodway et al. 1996). In contrast, for disturbed (i.e., weekly and daily) Leach's Storm-petrel (*Oceanodroma leucorhoa*) pairs whose membership was the same in both years of the study, hatching success the following breeding season returned to normal levels that were similar to the hatching

success of control pairs (Blackmer et al. 2004). However, investigator disturbance did reduce nest-site fidelity in the following breeding season. Fewer disturbed pairs re-used their original burrows in the following year than did control pairs. In addition, 60% of weekly and 33% of daily pairs had one or both partners desert the burrow, whereas only 10% of control burrows were unoccupied.

In Chapter 1, I identified the negative consequences that some long-term studies have on procellariiform reproductive success. These include a low return-to-nest rate, reduced breeding success, and change in nest site fidelity. The duration of these long-term studies could not be replicated in this study because it was beyond the temporal boundaries of doctoral research, but the pair-bond and nest site fidelity, as well as a pair's reproductive success, could be monitored one year after initial investigator disturbance. The aim of the research presented in this chapter is to assess the long-term effects of investigator disturbance in subsequent breeding seasons of the Short-tailed Shearwater. Specifically, in this study I determined the return rate of birds that were monitored in Chapter 4 and ascertained their pair-bond and nest site fidelity in 2007/08, one year after the initial handling occurrences. The birds' reproductive success was also monitored. I predicted that highly disturbed pairs would return in lower numbers compared to pairs that received fewer or no disturbances. I also predicted that divorce between pairs would be highest in pairs that were disturbed the most frequently.

5.2 Methods

5.2.1 Field procedures

Fieldwork was conducted between 22 November 2007 to 11 March 2008 on Great Dog Island. During the 2007/08 breeding season, each control, daily (1D), every third day (3D) and weekly (7D) burrow used in the 2006/07 disturbance experiment

(Chapter 4) was re-visited to determine if it was occupied or empty. Any banded birds found were identified and weighed with 1000 (± 10) g Pesola scales, but they were not measured. Eggs that could be reached were collected, weighed with Pesola 300 (± 2) g scales, and measured with Vernier callipers (± 0.02 mm) as previously described in Chapter 2. If there were any un-banded birds found in these burrows they were weighed, measured, and banded as previously described. All burrows were continually checked throughout the 16 day egg laying period for activity. All partners of active burrows were identified approximately two weeks later when incubation changeover had occurred.

All un-marked burrows within a 10 m radius of the disturbance experiment study site were also checked to determine if any birds had changed burrows from the previous year. Any new burrows that contained banded birds that had been studied in the 2006/07 disturbance experiment were marked with an individually marked PVC pole. The distance from the original burrow used the previous season was measured (m) using a 100 m measuring tape. After locating any previously banded birds used in the 2006/07 season, partners were identified at the next incubation changeover. Once the identities of both members of the pair were complete, burrows were left undisturbed for the average 53 day incubation period. After this time, all burrows were inspected to ascertain hatching success in mid-January (10 – 21 January) followed by fledging survival, body size, and mass on 11 March 2008.

5.2.2 Statistical analyses

To determine whether investigator disturbance in 2006/07 affected hatching success in 2007/08, a *G*-test with William's correction factor was used to compare the number of eggs that hatched versus the number of eggs that failed to hatch across the four

study groups. For this analysis, only pairs whose membership was the same in both years were used because individual and pair attributes (e.g., breeding experience, individual quality, egg size) can influence breeding success (Wooller et al. 1989, 1990, 1996; Bradley et al. 1990, 1991, 1995). Although not all control birds were banded at the end of the 2006/07 breeding season (and therefore could not determine if all birds found in burrows were the same in both years) pair membership was assumed not to have changed since Short-tailed Shearwaters exhibit high nest-site fidelity and pair-bond (Serventy 1967; Wooller et al. 1989, 1990, 1996). Another procellariiform, Leach's Storm-petrel, also typically exhibit very high nest-site fidelity (95%, Morse and Buccheister 1979).

5.3 Results

5.3.1 Return rate

Return rate for the disturbed treatment groups was low in 2007/08. For the treatment groups, 7 (23%), 9 (30%), and 13 (43%) (29 out of 90) males returned from the 1D, 3D, and 7D treatment groups, respectively. Thirty females returned from the three treatment groups, 10 1D (33%), 10 3D (33%) and 10 7D (33%) (30 out of 90). Of the 16 control birds that were banded at the end of the 2006/07 season, 75% returned in 2007/08: 71% males and 77% females. However, this number is likely to be an underestimate since only 26% of adults in the control group were banded. If I make the assumption that all birds found in control burrows were the same individuals used in the 2006/07 season (including banded birds mentioned above), then the return rate could be as high as 85%, with 26 (86%) males and 25 (83%) females. However, this may be an overestimation of the return rate because undoubtedly not all birds may

have returned and therefore the true number probably lies within the range from 75 to 85%.

Pairwise comparisons between the control and three treatment groups indicated no differences in the return rates of adults in the 2007/08 season (Table 5.1). If the birds found in the control burrows are included as birds that had returned from the previous season, there is a significant difference between the birds that returned in the control group and each of the three treatment groups (Table 5.1). No difference was detected between the return rates of male and female adults ($\chi^2 = 0.01$, *d.f.* = 1, *P* = 0.89, *n* = 240). However, some caution should be exercised regarding the interpretation of these results because not all control birds were banded in the 2006/07 season and the identification of some individuals was therefore problematic.

Table 5.1 Pairwise comparisons between the four treatment groups using a *G*-test with William's correction factor of the number of adults that returned the colony versus the number of adults that failed to return in 2007/08. Control pairs were assumed to be the same as the previous year.

Treatment	1D	3D	7D
Control	$\chi^2 = 41.96$ $P < 0.01$	$\chi^2 = 37.36$ $P < 0.01$	$\chi^2 = 23.75$ $P < 0.01$
1D	-	$\chi^2 = 0.15$ $P = 0.69$	$\chi^2 = 2.95$ $P = 0.08$
3D	-	-	$\chi^2 = 1.78$ $P = 0.18$

In 2007/08, a high proportion of control burrows were occupied at some stage during the incubation period compared with the three other disturbance groups and this difference was significant (Figure 5.1; $\chi^2 = 12.51$, *d.f.* = 3, $P < 0.01$). Significantly more of the control burrows (70%) subsequently had eggs laid in them compared to 12 (40%) in 1D burrows, and 10 (33%) in both the 3D and 7D burrows ($\chi^2 = 11.18$, *d.f.* = 3, $P = 0.01$). A relatively consistent number of burrows were occupied but never had eggs laid in them (10 to 16%), and no difference was detected between treatment groups ($\chi^2 = 0.78$, *d.f.* = 3, $P = 0.85$). Almost half (46%) of 7D burrows were empty in 2007/08 (i.e., a bird was never found in the burrow). The 1D and 3D treatment groups had a significantly higher proportion of empty burrows than did the control group (Figure 5.1; $\chi^2 = 10.50$, *d.f.* = 3, $P = 0.01$). The two treatment groups that received the highest disturbance in 2006/07 recorded a number of burrows

that had collapsed and became ‘no holes’ (i.e., the burrow had collapsed, an entrance could not be found, or there was no evidence of an attempt by shearwaters to dig the burrow out) in 2007/08 (i.e., five 1D (16%) and three 3D (10%)) but this difference was not significant ($\chi^2 = 4.8$, $d.f. = 3$, $P = 0.18$).

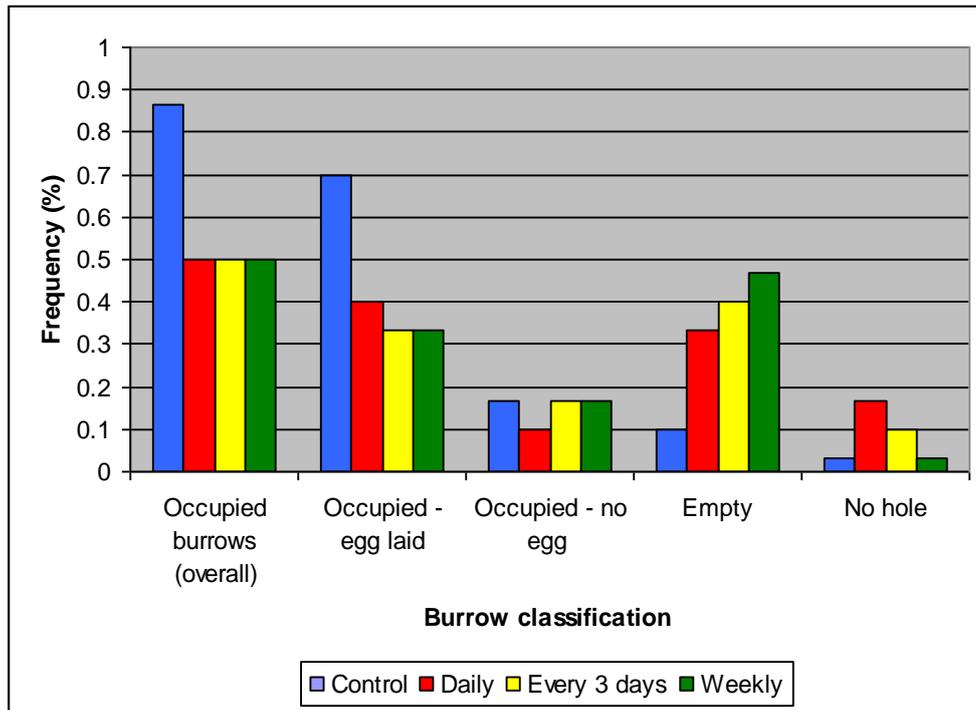


Figure 5.1 Histogram identifying the burrow classification in 2007/08, the year after the handling experiment (Chapter 4). For each treatment group $n = 30$.

5.3.2 Pair-bond and nest site fidelity

Investigator disturbance not only reduced hatching success in 2006/07, it also reduced nest-site fidelity in the following breeding season. Fewer disturbed (i.e., 1D, 3D, and 7D) pairs re-used their 2006/07 nesting burrows in 2007/08 than did control pairs (G_w $\chi^2 = 23.90$, $d.f. = 1$, $P < 0.01$, $n_{\text{control}} = 30$ pairs; $n_{\text{disturbed}} = 90$ pairs, Figure 5.2). In 2007/08, 86% of disturbed pairs had one or both partners desert the burrows that they had used in 2006/07, whereas only 30% of control burrows failed to contain an egg.

Of the 82 pairs that failed to hatch an egg in 2006/07, 83% subsequently deserted their burrows (i.e., did not re-use those burrows in 2007/08). Interestingly, of the 38 pairs that hatched an egg in 2006/07, 52% also deserted their burrows in 2007/08 and this difference between these two groups was significant ($\chi^2 = 12.17$, $d.f. = 1$, $P = 0.001$). Of the 24 pairs that were successful in raising a chick to pre-fledging in 2006/07, 58% subsequently deserted their burrows in 2007/08.

In 2007/08, 20 individuals from the disturbance treatment groups were located prospecting or breeding in the same general area as in 2006/07 but in different burrows and almost always with new partners. Only one instance was recorded where the same pair was found breeding but in a different burrow. Birds had moved an average distance of $3.02 (\pm 2.53)$ m (range: 1.32 – 12.67 m). There was no difference between the sexes in the distance they moved (males = $3.34 (\pm 3.56)$ m, range: 1.32 – 12.67 m, $n = 9$; females $2.77 (\pm 1.39)$ m, range: 1.85 – 6.55 m, $n = 11$, $t_{18} = 0.49$, $P = 0.63$).

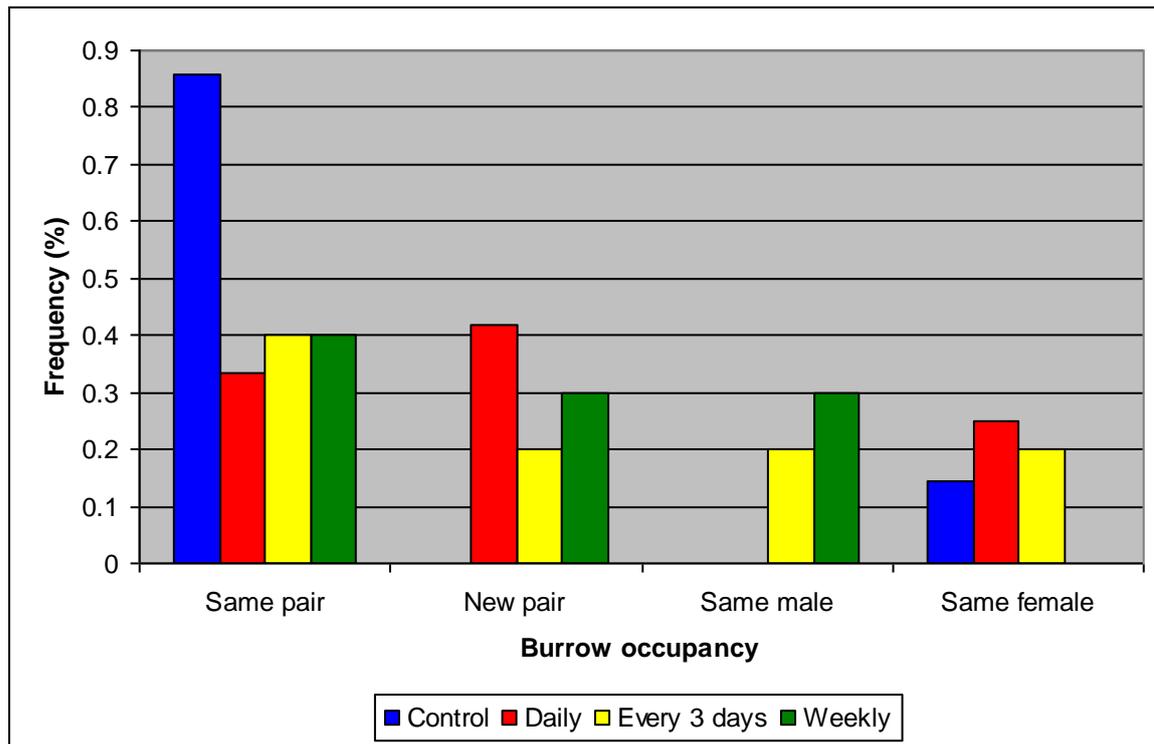


Figure 5.2 Histogram showing the nest-site fidelity of Short-tailed Shearwaters one year after investigator disturbance. Data represent burrows in which eggs were laid in 2007/08.

5.3.3 Reproductive success

5.3.3.1 Egg size

Egg size in 2007/08 did not differ between the four study groups (Table 5.2).

However, results might be limited by a small sample size (total $n = 24$). After all disturbed treatment group eggs were combined and again compared to the control group there were no significant differences on any measured variable (All $t_{22} < 0.98$, $P > 0.33$). Three control group eggs could not be reached, along with two 1D and one 7D egg. On average, eggs measured in the 3D treatment group were the heaviest and the widest and were the most voluminous.

Table 5.2 Mean (\pm s.d.) egg mass and dimensions of chicks laid in each treatment group in 2007/08.

	Mean (<i>n</i> = 24)	Range (<i>n</i> = 24)	Control (<i>n</i> = 15)	1D (<i>n</i> = 2)	3D (<i>n</i> = 4)	7D (<i>n</i> = 3)	<i>F</i> _{3, 20}	<i>P</i>
Egg mass (g)	89.6 \pm 6.5	76.0 – 101.0	88.7 \pm 7.6	87.0 \pm 1.4	93.0 \pm 5.4	91.3 \pm 1.5	0.58	0.6
Length (mm)	71.1 \pm 2.3	66.1 – 75.8	70.9 \pm 2.6	72.2 \pm 2.5	72.0 \pm 0.9	70.6 \pm 2.2	0.38	0.7
Width (mm)	46.6 \pm 1.3	44.0 – 48.0	46.4 \pm 1.5	46.3 \pm 0.9	47.2 \pm 1.3	47.2 \pm 0.9	0.51	0.6
Estimated volume (cm ³)	79.2 \pm 6.1	67.0 – 90.0	78.3 \pm 7.0	79.1 \pm 5.9	82.1 \pm 4.6	80.4 \pm 4.1	0.40	0.7

5.3.3.2 Hatching success

Hatching success between the two breeding season of 2006/07 and 2007/08 are difficult to compare because of the low return rate of adults and high divorce rate between pairs. Among the three disturbed treatment groups (i.e., 1D, 3D, and 7D), only 12 pairs laid an egg with same partner from 2006/07 but it was assumed that 18 pairs from the control group were identical pairs (see 5.2 Methods). In 2007/08, hatching success for the disturbed treatment groups combined was 33% (4 out of 12), while the control group recorded a noticeably higher hatching rate of 50% (9 out of 18). Between 2006/07 and 2007/08, 1D hatching success increased by 25%, remained the same for 3D at 25%, and decreased by 25% in the 7D treatment group. For the control group, hatching success remained moderately high in both years. However, it decreased from 66% in 2006/07 to 50% in 2007/08. For the 12 disturbed pairs, hatching success remained constant between 2006/07 and 2007/08 at 33%.

5.3.3.3 Chick survival, mass, and size

In 2007/08, chick survival from hatching to pre-fledging (mid-March) was high in the control group at 77%. This figure is an increase of 19% from the previous year.

Overall survival of disturbed chicks, on the other hand, fell by 50% in 2007/08.

The results concerning pre-fledging chick mass and size are difficult to interpret because of the low sample sizes (Table 5.3): Only one chick survived in the disturbed treatment groups compared to seven for the control group.

Overall reproductive success (i.e., number of fledged chicks from eggs laid) remained the same for the control group in both years, 38%. Disturbed pairs, however, fell from 33% in 2006/07 to 8% in 2007/08, a fall of 25%.

Table 5.3 Mean (\pm s.d.) body mass and morphometrics of pre-fledging Short-tailed Shearwater chicks in the control and disturbed (i.e., 1D, 3D, and 7D) treatment groups.

Treatment Group	Body mass (g)	Head length (mm)	Bill length (mm)	Bill depth (mm)	Wing length (mm)	Tarsus length (mm)
Control ($n = 7$)	521.4 \pm 135.5	77.91 \pm 2.0	31.43 \pm 2.1	7.73 \pm 0.3	135.00 \pm 15.4	57.76 \pm 1.7
Disturbed ($n = 1$)	670.0	76.80	29.00	8.44	131.00	57.62

5.4 Discussion

Remarkably little is known about the effects of investigator disturbance on avian reproductive success and nest-site fidelity in subsequent years. Results from this study suggest that Short-tailed Shearwaters are particularly sensitive to investigator disturbance in the short term (Chapter 4) and in the long term (this chapter), where the effects may be long-lasting. Among disturbed (i.e., daily, every third day, and weekly) Short-tailed Shearwaters, return rate to the colony was low, divorce was high, and reproductive success was suppressed in the second year (2007/08). In contrast, occupancy of control burrows was significantly higher than that for treatment groups, and 75% of banded adults returned to breed. Heavy rain during late 2007 may have also contributed to the failure of some pairs to hatch an egg. Quantifying this impact was difficult as burrows were not inspected until mid-January 2008. However, burrows that were inspected regularly during this time (burrows studied in Chapter 6) suggest that many adults abandoned their nesting attempts after the rain event because burrows became flooded. However, all of these observations are difficult to interpret because of the unexpectedly low sample size and only cautious interpretations are possible.

Investigator disturbance not only reduced return rate of adults, it also reduced nest-site fidelity. Investigator disturbance in 2006/07 caused 56% more disturbed pairs than control pairs to desert their burrows the following breeding season (2007/08). Since not all individuals belonging to the control group had been banded in 2006/07 (to minimise disturbance), I assumed that occupied control burrows in 2007/08 contained the same breeding partners in both years. If some of these occupied burrows in 2007/08 did contain different breeding partners than they had in 2006/07, the figures produced would have underestimated the proportion of control

burrows that deserted their 2006/07 burrow, causing the fidelity rates of the control group and the disturbed group to more similar. However, Short-tailed Shearwaters typically exhibit high nest fidelity (Serventy and Curry 1984) and is supported by the 75% return rate of banded control birds. Therefore, the estimated 70% of control pairs that re-used their 2006/07 burrows and laid an egg in 2007/08 is probably accurate, and hence disturbed pairs exhibited significantly lower nest-site fidelity than did control pairs.

The vast majority of birds that changed their burrow between the two seasons also changed their breeding partner. Only one pair in a changed burrow was found to be still breeding together. This pair, which was from the weekly disturbance group, successfully hatched a chick and raised it to the pre-fledging stage. Investigator disturbance that caused a bird to desert its burrow (and therefore its mate) may have been costly to lifetime reproductive success. Numerous studies on long-lived birds have demonstrated that indices of reproductive success improve as the duration of the pair bond increases (Wooller et al. 1989; Black 1996), including the present study species (Wooller et al. 1996). Additionally, mate change could delay reproduction, and procellariiform chicks that hatch late in the season often have lower survival rates than do early-hatched young (Richdale 1963; Harris 1979). Thus, investigator disturbance may have reduced the reproductive success of individuals that changed burrows and mates.

Short-tailed Shearwaters that deserted their 2006/07 burrows may have attempted to move away from the disturbance, as has been suggested for Kittiwake Gulls (*Rissa tridactyla*) (Sandvik and Barrett 2001), Ring-billed Gulls (Conover and Miller 1978), and Adélie Penguins (Reid 1968; Wilson et al. 1989). Failure to hatch an egg in 2006/07 may also have contributed to the decision to desert the burrow.

Approximately half of pairs that hatched their egg in 2006/07 subsequently deserted their 2006/07 burrows, whereas 83% of pairs that deserted their eggs in 2006/07 also deserted their burrows. It seems likely that whether birds changed burrows due to either investigator disturbance or reproductive failure, presumably they deserted their 2006/07 burrows in order to improve the likelihood of reproductive success in the future.

These results demonstrate quite clearly that investigator disturbance during incubation has powerful detrimental effects not only in the short term (Chapter 4) but also on return rates, nest-site fidelity, and reproductive success. However, the individuals studied in this research had received little or no investigator disturbance during their reproductive lifetimes, so reductions in return rates, pair-bond and nest-site fidelity that were observed are probably at the high end of the range. Long-lived birds such as procellariiforms have the potential to habituate to investigator disturbance within and across seasons (Burger and Gochfeld 1999; Nisbet 2000). Negative effects of disturbance might diminish as individuals gain additional exposure to research activities and/or procedures. However, this was not observed in a long-term study on Fisher Island, where over a 25 year period the population of Short-tailed Shearwater dramatically declined (Serventy and Curry 1984; Carey 2009; Chapter 1).

Although investigator disturbance has not been shown to reduce breeding performance in all seabirds studied (for a review see Nisbet 2000), several studies have obtained results that are similar to the present one (see reviews by Carney and Sydeman 1999, Nisbet 2000, and Carey 2009), suggesting that investigator disturbance may adversely affect a number of long-lived species, not just procellariid seabirds. Researchers studying long-lived seabirds should be encouraged to consider

both the short-term and long-term effects of investigator disturbance on reproduction, especially for naïve birds that have not previously experienced investigator contact.

Chapter 6: Incubation Routine and Body Mass Regulation in the Short-tailed Shearwater: A Case Study to Reduce the Impact of Handling in a Routine Scientific Study

6.1 Introduction

Life history theory predicts that investment in offspring is balanced against the cost associated with future reproduction (Stearns 1992). One way of assessing the potential cost of reproduction in birds is to monitor nest relief coordination and parental body mass (Drent and Dann 1980). During incubation, pelagic seabirds undergo large variations in their body mass as a result of concomitant fasting (Prince et al. 1981; Chaurand and Weimerskirch 1994; Tveraa et al. 1997). Parent birds must coordinate their incubation shifts with foraging trips at sea to ensure constant warming of the embryo and protection of the egg from predation (Fleet 1972; Grant et al. 1981; Booth et al. 1996; Carey 2010). A bird must spend sufficient time at sea to replenish its body reserves to cope with the period of fasting during its subsequent incubation spell (Johnstone and Davis 1990). However, if a partner spends too much time at sea, its mate may be forced to desert the egg as its own energy reserves become critically depleted (Chaurand and Weimerskirch 1994; Tveraa et al. 1997). As a consequence, the rate of breeding failure is high during this period (Johnstone and Davis 1990).

Procellariiformes typically have extended incubation periods, with long incubation shifts (Grant and Whittow 1983; Warham 1990). This is due, in part, to the large, heavy eggs and vast distances travelled to acquire sufficient food (Warham 1990; Weimerskirch and Cherel 1998; Cherel et al. 2005). Short-tailed Shearwaters (*Puffinus tenuirostris*) exhibit four long incubations shifts, alternating between both parents, spanning a total

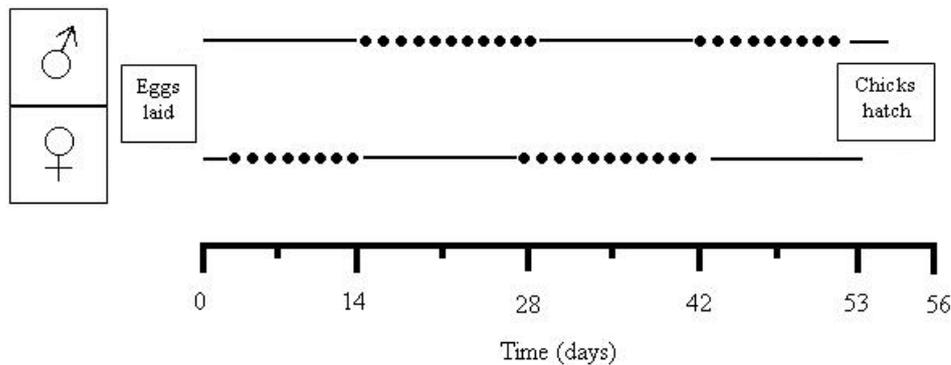


Figure 6.1 Diagrammatic representation of the incubation schedule of Short-tailed Shearwaters (*c.f.* Serventy 1967). Pairs usually perform four (but sometimes up to six) incubation shifts in order to hatch the egg. The solid black lines indicate the time spent on the nest. The filled circles indicate the time spent at sea. Labelled boxes show when eggs are laid and when chicks hatch.

incubation period of 53 days (Serventy 1967; Figure 6.1). A single egg is laid, and if breeding fails, the egg is not replaced. The male begins incubation while the female returns to sea to forage (Serventy 1967). Thus the first and third incubation shifts are commonly undertaken by the male, and the second and fourth shifts by the female. Each incubation shift lasts about 10 to 14 days (Serventy 1967).

When food resources are difficult to acquire, Procellariiformes may be forced to increase the length of an incubation shift while their partner is at sea (Chaurand and Weimerskirch 1994; Tveraa et al. 1997). This is achieved at the cost of the incubating parent's body condition, and that in turn has consequences for breeding success. For example, Antarctic Petrels (*Thalassoica antarctica*) can lose 20% of their body mass in one 2 week incubation shift, and adults with lower body condition spend more time foraging at sea which increases nest desertion rates (Lorentsen and Røv 1995; Tveraa

et al. 1997). Similarly, if its partner has not returned to take over incubation, the Blue Petrel (*Halobaena caerulea*) will abandon a nest when its body condition falls below a set mass threshold (Chaurand and Weimerskirch 1994). Clearly, incubation places a considerable demand on petrels to manage their own energy reserves, and they may therefore need to regulate their body mass closely. However, the role of body mass in the birds' behaviour during incubation remains unknown for most shearwater (*Puffinus*) species.

For Short-tailed Shearwaters, little is known about the incubation routine for the complete incubation period (see Serventy 1967; Serventy et al. 1971). In addition, little information is available about the relationships of body mass with incubation schedule, egg desertions, or time spent at sea. Therefore, the aims of this study were to determine the incubation routine of Short-tailed Shearwaters and to investigate the importance of body mass during incubation. In this study, I tested the hypothesis that body mass at the end of an incubation shift would determine the subsequent length of a foraging trip and the body mass upon return to the colony. Adults with lower body mass would be expected to have shorter incubation shifts and longer foraging bouts at sea. The occurrence of egg neglect in relation to body mass was also investigated. I predicted that adults that were not relieved by their partners would desert their eggs at a lower body mass than would adults that were relieved by their partner. It was expected that neglected eggs were less likely to hatch, thereby demonstrating the importance of body mass for effective parental care in this long-lived pelagic seabird.

In previous studies, researchers have weighed and/or inspected burrows every day or every second day to obtain their data (Johnstone and Davis 1990; Chaurand and Weimerskirch 1994). However, handling incubating adults daily or every second day may be considered excessive, and a study of this nature would require only

periodic handling at the start and end of an incubation shift. This would lead to a reduction in the number of times a bird is handled and possibly reduce the effects of a researcher's activities. In the previous two chapters, Chapters 4 and 5, I have demonstrated the negative effects of investigator disturbance on Short-tailed Shearwater reproductive success. Handling birds once a day and every third day significantly reduced hatching success as well as chick mass and size. Investigator disturbance also affected subsequent return rates of breeding adults. This chapter uses the knowledge acquired from Chapters 4 and 5 to determine an appropriate handling frequency to reduce the impact of investigator disturbance. In this chapter I again test the effects of handling incubating birds on hatching success, chick size, and survival in the short term, and pair-bond and nest-site fidelity in the long-term, and I document the incubation routine and body mass regulation. I predicted that birds that were handled once at the start and end of an incubation shift would have greater reproductive success than would birds used in previous chapters 4 and 5.

6.2 Methods

6.2.1 Field procedures

This research was conducted on Great Dog Island, between 25 November 2007 and 21 January 2008. Because the peak laying period is between 25 and 29 November (Serventy 1967; Meathrel et al. 1993a), burrows were initially inspected during that time. Sixty active burrows were marked with a polyvinylchloride pole, and a unique number was assigned to each site for the duration of the project. An active burrow was defined as one that contained an adult bird with an egg. When active burrows were encountered, the adults were removed by hand, and each was placed in a calico bag, weighed, and measured as described in Chapter 2. Adults were banded with an

Australian Bird and Bat Banding Scheme (ABBBS) band. Birds handled during egg laying were sexed by cloacal examination (Serventy 1956; Boersma and Davies 1987) or by a discriminant function analysis (see Chapter 3).

Arrivals and departures of birds were detected by placement of fine sticks at the entrance of each burrow. To minimise handling of birds and reduce the adverse effects of investigator disturbance (see Chapter 4 and 5), birds were weighed once at arrival (Day 1), and again at days 10, 12, and 14. If the burrow was still occupied by the same bird after Day 14, that bird was weighed daily until its partner returned. During non-weighing days burrow entrances were closely monitored (but not inspected) for the anticipated changeover. This sampling regime continued throughout the incubation period until all eggs hatched or failed. If a burrow was found empty or to contain a cold egg, it was inspected every day until an adult bird returned to continue the incubation (defined as egg neglect), the egg was predated, or the burrow was permanently abandoned. Once eggs hatched, burrows were not inspected again until March 2008. At that time, all burrows were inspected for pre-fledging chicks. If one was found it was removed from the burrow, weighed, and measured as described in Chapter 2.

In the following breeding season, 2008/09, all burrows were inspected for breeding adults and eggs at egg laying. Once the content of the burrows was ascertained, the burrow was left un-disturbed until mid-January 2009 to assess hatching success, and again in mid-March to determine chick survival, mass, and size (following the procedures outlined in Chapters 4 and 5).

6.2.2 Statistical analyses

Statistical analyses were performed using SPSS version 17.0 (SPSS Inc., Chicago, IL, December 2008). Pearson's correlation coefficients were used to test for associations between variables, and either Student's *t*-tests (both independent and paired, as appropriate) or analyses of variance (ANOVAs) were used to identify any group differences. Where the assumptions of these tests were not met, the non-parametric equivalents were used. The chi-square test was used to determine whether the proportion of temporary egg neglect varied during incubation. The significance criterion for all tests was set at < 0.05 . All data are presented as means \pm standard deviation (s.d.).

To determine whether investigator disturbance in 2007/08 affected hatching success in 2008/09, I performed the same statistical analyses as described in Chapter 5. For these analyses, I used a *G*-test (Sokal and Rohlf 1995) to compare treatment groups in terms of the number of eggs that hatched versus the number of eggs that did not hatch in 2008/09. I used 14 experimental and seven control pairs whose membership was the same in both years of the study. When analysing the data I excluded individuals that changed partners between 2007/08 and 2008/09 because individual or pair attributes (e.g., age, breeding experience, individual or burrow quality) can influence hatching success (Black 1996). Differences between linear measurements of eggs and chicks were tested with Student's *t*-test. The sequential Bonferroni adjustment was needed as multiple measures of the same individual were used; as a result, the critical value of $P = 0.008$ (see Sokal and Rohlf 1995).

6.3 Results

6.3.1 Incubation schedule

During the pre-egg laying stage it was uncommon (16.6%) to find both adults in the burrow, and once the egg was laid only a single bird was ever found. The main incubation shifts of adults ranged between 9 to 17 days over the $52 (\pm 1.9, n = 13)$ day incubation period, except for a short first shift by the female after egg laying and an occasional sixth shift undertaken by the male bird at the end of the incubation period (Table 6.1) that, if it occurred, completed the incubation until the egg hatched. Incubation changeover always occurred at night, and the relieved partner returned to sea the same night.

In total, males spent more time on the egg than did their female partners ($t_{24} = 3.62, P < 0.01$). Males averaged a total of $26 (\pm 1.7)$ days on the egg, and females $23.7 (\pm 1.6)$ days (52% and 48% respectively). During the first half of the incubation period, females had a significantly longer shift than did males ($t_{81} = 4.4, P < 0.01$, Table 6.1). This was not the case in the latter half of the incubation period, however, when the opposite occurred. Again, this difference was significant ($t_{37} = 5.1, P < 0.01$, Table 6.1). The time spent incubating the egg increased significantly for males in the fourth shift relative to the second shift ($t_{69} = 6.0, P < 0.01$, Table 6.1), while the total time incubating decreased significantly for females between the third and fifth shifts ($t_{49} = 3.9, P < 0.01$, Table 6.1). Individual males incubated for longer periods on the fourth shift than on the second shift (Wilcoxon signed rank test, $T = 3.5, P < 0.01, n = 24$), whereas individual females did not change their shift length between the third and fourth shifts (Wilcoxon signed rank test, $T = 1.8$, not significant [hereafter n.s.], $n = 13$).

During the first half of incubation, body mass of both male and female birds at the start of the shift was associated with the length of that incubation period (for males, $r_{48} = 0.31$, $P = 0.03$; for females, $r_{45} = 0.87$, $P < 0.01$). This association was not observed in the second half of the incubation period in either sex (for males, $r_{25} = 0.31$, $P = 0.12$; for females, $r_{12} = -0.50$, $P = 0.09$). Data combined over the incubation period revealed that body mass at the start of the incubation period was positively correlated with length of incubation both for males ($r_{73} = 0.64$, $P < 0.01$) and for females ($r_{57} = 0.72$, $P < 0.01$). Overall, the greater the body mass of an adult, the longer the incubation spell was likely to be ($r_{130} = 0.63$, $P < 0.01$).

Table 6.1 Mean (\pm s.d.) duration of incubation shifts, mass at the start and end of shift, mass at desertion and the proportion of shifts with desertions in Short-tailed Shearwaters. Sample size (n) in parentheses. F = female, M = male.

Shift	Sex	Duration (days)	Mass at start of shift (g)	Mass when relieved (g)	Mass at desertion (g)	% of desertions
First	F	1.7 \pm 1.3 (21)	-	530.0 \pm 28.9 (16)	523.3 \pm 33.8 (6)	27% (22)
Second	M	12.1 \pm 1.4 (46)	616.1 \pm 45.8 (57)	522.0 \pm 33.6 (35)	514.2 \pm 38.0 (12)	25% (47)
Third	F	13.6 \pm 1.6 (37)	671.7 \pm 36.5 (47)	530.0 \pm 27.1 (31)	532.9 \pm 36.8 (7)	18% (38)
Fourth	M	14.3 \pm 1.5 (25)	732.6 \pm 50.8 (39)	560.0 \pm 31.4 (15)	546.4 \pm 29.7 (11)	42% (26)
Fifth	F	11.5 \pm 1.9 (14)	711.3 \pm 49.6 (31)	600.0 \pm 70.7 (2)	562.0 \pm 43.8 (5)	71% (7)
Sixth	M	2.0 \pm 1.7 (3)	745.0 \pm 68.1 (4)	-	-	-

6.3.2 Body mass changes

With no food delivery by partners observed during the incubation period, incubating birds inevitably lost body mass as a result of complete fasting within the burrow. The average decrease in body mass was $11.1 (\pm 2.9) \text{ g day}^{-1}$ (range $5.0 - 17.5 \text{ g day}^{-1}$, $n = 119$), which represented a daily loss of 1.6% from the initial body mass (range 0.7 – 2.57%, $n = 119$). Adults lost on average 20.1% (± 6.6) of body mass during an incubation shift. Incubating females lost slightly more mass during an incubation shift than did males (females 21.3 (± 4.1) %, $n = 55$; males 19.2% (± 6.5), $n = 81$; Mann-Whitney test, $z = 2.00$, $P = 0.04$). The greatest body mass lost by an individual female was 32.8% during an incubation shift; the maximum that an individual male lost during an incubation shift was 33.3%.

The total body mass lost was closely related to the number of days spent incubating ($r_{119} = 0.70$, $P < 0.01$). The total mass lost during the first half of the incubation period was significantly less for the males (males $101.8 (\pm 35.6)$ grams, $n = 45$; females $144.0 (\pm 28.3)$ g, $n = 38$, $t_{81} = 5.9$, $P < 0.01$). This was reflected in the daily mass loss of males and females during the first half of the incubation period (respectively, $8.8 (\pm 2.5) \text{ g day}^{-1}$, $n = 45$, and $11.3 (\pm 1.8) \text{ g day}^{-1}$, $n = 38$, Mann-Whitney test, $z = 4.7$, $P < 0.01$). However, during the second half of the incubation period, total mass loss was significantly higher for males than it was for females (respectively, $188.5 (\pm 36.4)$ g, $n = 26$ and $148.0 (\pm 36.5)$ g, $n = 10$, $t_{34} = 3.0$, $P < 0.01$). However, the average daily mass lost was similar for both sexes during the second half of the incubation period (males $13.7 (\pm 2.2) \text{ g day}^{-1}$, $n = 26$ and females $13.8 (\pm 1.6) \text{ g day}^{-1}$, $n = 10$, $t_{34} = 0.8$, n.s.).

The average body mass of males and females at the start of an incubation shift significantly increased between shifts ($t_{94} = 11.7$, $P < 0.01$ and $t_{76} = 4.1$, $P < 0.01$

respectively, Table 6.1), while the average mass at the end of an incubation shift when relieved by their partners also increased for males but not for females (respectively, $t_{63} = 2.5$, $P = 0.01$ and Mann-Whitney test, $z = 1.7$, $P = 0.09$, n.s., Table 6.1). Individual males and females were heavier when they started the fourth and fifth shifts than when they started the second and third shifts (Wilcoxon signed rank test, males $n = 38$, $z = 5.1$, $P < 0.01$ and females, $n = 29$, $z = 3.7$, $P < 0.01$). Individual males and females were also heavier when they ended their fourth and fifth shifts than when they had been relieved on their second and third shifts respectively (Wilcoxon signed rank test, males, $n = 24$, $T = 3.4$, $P < 0.01$ and females, $n = 13$, $T = 2.8$, $P < 0.01$).

6.3.3 Egg neglect

Temporary egg neglect occurred in 93% of burrows studied in the colony. The proportion of temporary egg desertion varied significantly during incubation ($\chi^2_4 = 16.4$, $P < 0.01$), being highest at the end of the incubation period (Table 6.1). An average of 1.41 (± 0.91) periods of egg neglect (range 0-4 periods) was observed in the burrows during the incubation period. There was significantly less egg neglect in burrows where the chick hatched than in unsuccessful burrows (respectively, 0.54 (± 0.52) periods, range 0 – 1, $n = 13$ and 1.65 (± 0.85) periods, range 0 – 4, $n = 36$, $t_{57} = 4.5$, $P < 0.01$). The observed duration of egg neglect was also significantly less in successful than in unsuccessful burrows (respectively, 0.58 (± 0.5) days, $n = 12$ and 2.6 (± 2.8) days, $n = 27$, Mann-Whitney test, $z = 3.6$, $P < 0.01$, $n = 39$).

Birds that deserted the egg did so after incubating periods that ranged from 1 to 16 days. Body mass did not change over the incubation period for females that deserted their nests ($F_{2,15} = 1.5$, n.s., Table 6.1), but body mass at desertion was significantly higher in the fourth shift than in the second shift for males ($F_{1,21} = 5.0$, $P = 0.03$, Table 6.1). For both males and females, no significant differences were

detected between the body mass of birds that deserted a nest and the body mass of birds when they were relieved having remained on the nest (males 529.6 (37.4) g, $n = 23$; 533.4 (± 37.1) g, $n = 50$ $t_{71} = 0.41$, n.s. respectively; and females 537.8 (± 39.0) g, $n = 18$; 532.9 (± 32.0) g, $n = 49$, $t_{65} = 0.53$, n.s. respectively; Table 6.1). For birds that deserted nests, there was no significant difference in the body mass at desertion between males and females (males 529.6 (± 37.4) g, $n = 23$ and females 537.8 (± 39.0) g, $n = 18$, $t_{39} = 0.69$, n.s., Table 6.1).

6.3.4 Return from sea

Adults returned to the burrow after varying amounts of time away at sea (range 11 - 28 days, Table 6.2). Males and females spent similar lengths of time foraging at sea in both halves of the incubation period ($t_{51} = 0.59$, n.s. and $t_{30} = 0.74$, n.s., respectively, Table 6.2). The time spent at sea by males was similar for their two foraging trips during the incubation period; however, females significantly increased their time at sea during their second trip (males $t_{40} = 0.74$, n.s.; females $t_{41} = 2.5$, $P = 0.01$, Table 6.2).

While at sea, foraging birds increased in body mass ranging from 1 - 19 g day⁻¹ (mean 12.2 (± 4.0) g day⁻¹, $n = 85$). Males gained significantly more body mass than did females (206.9 (± 57.7) g, $n = 42$ and 168.1 (± 52.3) g, $n = 43$ respectively; $t_{83} = 3.25$, $P < 0.01$, Table 6.2). Thus, while at sea males' average daily mass gain was higher than that of females (13.8 (± 4.1) g day⁻¹, $n = 42$ and 10.6 (± 3.3) g day⁻¹, $n = 43$ respectively; $t_{83} = 4.02$, $P < 0.01$, respectively, Table 6.2). For male birds there was no difference in average daily mass gain between their two stays at sea ($t_{40} = 1.0$, n.s., Table 6.2). Female birds, however, significantly increased their average daily mass gain during foraging between the first and third stays at sea ($t_{41} = 3.2$, $P < 0.01$, Table 6.2).

Table 6.2 Mean (\pm s.d.) duration, mass gain, and daily mass gain of stays at sea in Short-tailed Shearwaters.

Stay at sea	Sex	<i>n</i>	Duration (days)	Mass gain (g)	Daily mass gain (g/day)
First	F	15	15.0 \pm 2.2	124.7 \pm 42.5	8.6 \pm 3.2
Second	M	38	15.5 \pm 2.5	210.5 \pm 58.1	14.0 \pm 4.0
Third	F	28	16.7 \pm 2.0	191.4 \pm 41.3	11.7 \pm 2.9
Fourth	M	4	15.0 \pm 2.7	172.5 \pm 45.7	11.9 \pm 4.3

Overall, when birds left the nest to return to sea, their body mass at departure was positively related to the subsequent time spent foraging ($r_{82} = 0.22$, $P < 0.05$, Figure 2a). There was no relationship between body mass at the end of an incubation period and body mass upon their next return from sea after foraging ($r_{82} = 0.21$, n.s., Figure 2b). The mass when birds left the nest to return to sea was inversely related to the mass gained at sea ($r_{82} = -0.37$, $P < 0.01$, Figure 2c).

When data for both sexes were combined, the duration of a shift and the total mass an incubating bird lost were not related to the subsequent duration at sea, mass on return, or the mass gained at sea (Table 6.4). However, there were differences between the sexes. For females only, the duration of the incubation shift was inversely related to the duration of time away at sea ($r_{28} = -0.37$, $P = 0.05$). For males only, the duration of a shift was significantly related to the mass on return from sea ($r_{41} = -0.35$, $P = 0.02$) but not by females ($r_{28} = -0.23$, n.s.). The total duration of a shift in males was negatively related to the total mass gained at sea ($r_{41} = -0.36$, $P = 0.02$). However, in females there was a significantly positive relationship between the duration of an incubation shift and the mass gained while at sea ($r_{28} = 0.49$, $P < 0.01$).

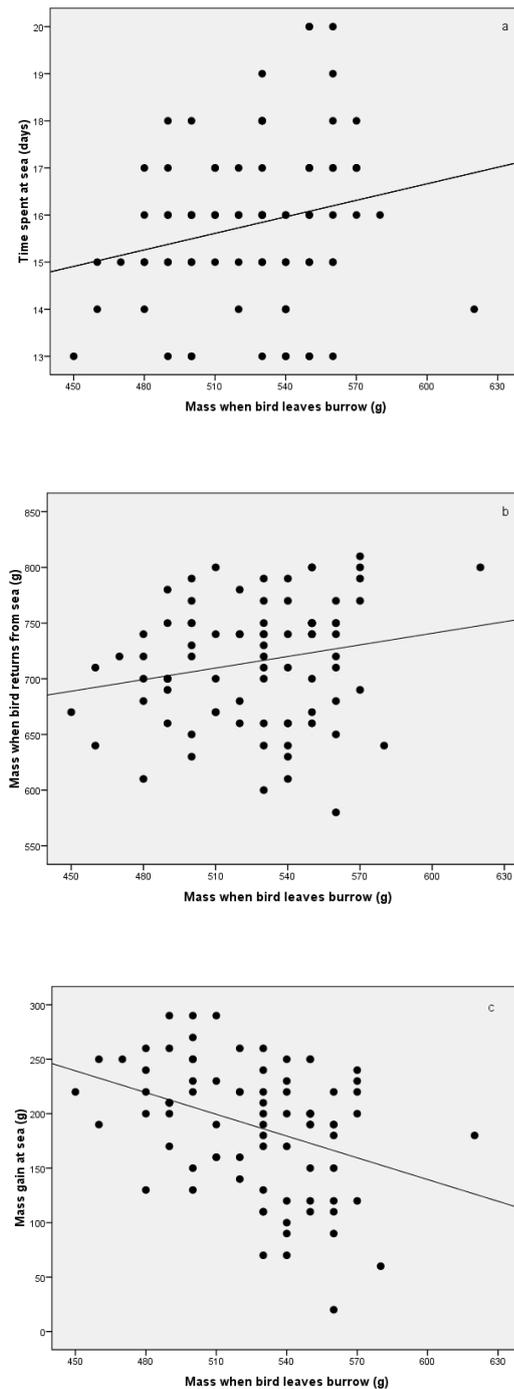


Figure 6.2 The relationship between the body mass of Short-tailed Shearwaters leaving their burrow after an incubation shift and (a) the duration of the foraging trip ($y = 0.0117x + 9.6456$; $R^2 = 0.04$), (b) the mass when the bird returns to the nest ($y = 0.3466x + 532.83$; $R^2 = 0.04$), and (c) the mass gain at sea ($y = -0.06653x + 538.83$; $R^2 = 0.14$).

Table 6.3 The relationship between duration of incubation period and body mass loss during that time, and the duration and mass gain during the foraging trip at sea in Short-tailed Shearwaters. Values shown are Pearson correlation coefficients (r). n.s. = not significant.

	Duration of stay at sea	Mass on return from the sea	Mass gain at sea
Duration of shift	0.05 n.s.	-0.19 n.s.	-0.15 n.s.
Total mass loss	0.01 n.s.	-0.17 n.s.	-0.20 n.s.

The total mass lost during an incubation period was not significantly related to the duration of stay at sea for either males or females ($r_{41} = -0.14$, n.s; $r_{28} = -0.16$, n.s respectively) or the mass on return from sea ($r_{41} = -0.20$, n.s; $r_{28} = 0.09$, n.s). For males, there was a negative relationship between total body mass lost during the incubation shift and total mass gained while foraging ($r_{41} = -0.32$, $P = 0.04$). The relationship was reversed in females, where there was a significant positive relationship between total mass lost while incubating and total mass gained while foraging at sea ($r_{28} = 0.41$, $P = 0.02$).

6.3.5 Reproductive success

6.3.5.1 Egg size

All of the experimental eggs could be reached during initial inspection but two, or 9.5%, of control eggs could not be reached. Of the eggs that could be retrieved from burrows, egg size was similar on all variables between experimental and control groups (Table 6.5).

Table 6.4 Mean (\pm s.d.) mass and size of Short-tailed Shearwater eggs used in the incubation routine and body mass regulation experiment.

Group	Experimental (n = 60)	Control (n = 19)	t_{77}	P
Egg mass (g)	88.5 (\pm 6.9)	89.5 (\pm 7.3)	0.57	0.56
Egg length (mm)	71.4 (\pm 2.5)	70.8 (\pm 2.5)	0.93	0.35
Egg width (mm)	46.6 (\pm 2.0)	46.7 (\pm 1.5)	0.13	0.89
Egg volume (cm ³)	79.4 (\pm 7.7)	78.9 (\pm 6.5)	0.26	0.79

6.3.5.2 Hatching success

Hatching success in the experimental group was low compared to the control group, and the difference was significant (experimental 21.7%, $n = 60$; control 57.1%, $n = 19$, $G_W = 8.7$, $P < 0.01$). Again, there was some difficulty in reaching hatchlings, but 53.8% of experimental and 16.6% of control hatchlings were retrieved and measured. There were no significant differences between the two groups in hatching mass or skeletal measurements (Table 6.6).

Table 6.5 Mean (\pm s.d.) mass and skeletal measurements of Short-tailed Shearwater hatchlings.

Group	Experimental ($n = 7$)	Control ($n = 2$)	t_7	P
Mass (g)	87.1 (\pm 20.3)	84.0 (\pm 28.3)	0.18	0.86
Head length (mm)	45.4 (\pm 1.1)	45.7 (\pm 2.6)	0.26	0.80
Bill length (mm)	21.5 (\pm 5.0)	18.1 (\pm 0.1)	0.92	0.38
Bill depth (mm)	6.4 (\pm 0.5)	6.1 (\pm 0.3)	0.77	0.46
Wing length (mm)	30.2 (\pm 1.3)	31.0 (\pm 2.8)	0.53	0.61
Tarsus (mm)	26.2 (\pm 1.5)	27.1 (\pm 2.2)	0.72	0.50

6.3.5.3 Chick survival, mass and size

Chick survival from hatching to pre-fledging was exceptionally high for both groups. No difference in chick survival rate could be found (experimental 84.6%, $n = 13$; control 83.3%, $n = 12$, $G_W = 0.008$, $P = 0.93$). There were no significant differences in mean mass or skeletal measurements of pre-fledge chicks raised by adults subject to the incubation routine experiment and those raised by control birds (Table 6.7).

Overall, there was a significant difference in the reproductive success of the two groups. Pairs used in the incubation routine experiment recorded 18.3% breeding success and control pairs 47.6% success ($G_W = 6.47$, $d.f. = 1$, $P = 0.01$).

Table 6.6 Mean (\pm s.d.) body mass and measurements between pre-fledging Short-tailed Shearwater chicks reared by pairs used in the incubation routine experiment and control parents.

Group	Experimental ($n = 11$)	Control ($n = 9$)	t_{18}	P
Mass (g)	600.9 (± 116.4)	532.2 (± 155.7)	1.13	0.27
Head length (mm)	78.8 (± 2.8)	78.0 (± 1.9)	0.75	0.46
Bill length (mm)	30.7 (± 1.1)	31.4 (± 1.8)	1.05	0.30
Bill depth (mm)	7.7 (± 0.4)	7.6 (± 0.4)	0.47	0.64
Wing length (mm)	142.1 (± 10.3)	131.3 (± 16.4)	1.80	0.08
Tarsus length (mm)	58.5 (± 1.3)	58.0 (± 1.6)	0.86	0.39

6.3.6 Recapture rate after 12 months

In 2008/09, the recapture rate was 31.5% (51 of the 162 birds that had been banded were re-caught). The return rate was slightly lower for experimental birds than for control birds, but this difference was not significant (experimental = 27.5%, $n = 120$; control = 42.9%, $n = 42$, $G_w = 3.29$, $d.f. = 1$, $P = 0.07$). There was a significant difference between the return rates of experimental males and control male birds. In this instance, experimental males returned at a lower rate than did the control male birds (experimental = 26.7%, $n = 60$; control = 52.4%, $n = 21$; $G_w = 4.46$, $d.f. = 1$, $P = 0.03$). Experimental females, however, returned at a similar rate to control females (experimental = 28.3%, $n = 60$; control = 33.3%; $G_w = 0.18$, $d.f. = 1$, $P = 0.66$).

In 2008/09, three burrows from the experimental group could not be found because their PVC marker had disappeared. These three burrows were therefore excluded from any further analyses. In 2008/09, there was a high incidence of collapsed or empty burrows in both experimental and control groups (Figure 6.3). A small proportion of burrows were, at some stage through the incubation period, occupied by individuals or in some cases pairs, but an egg was never found in those burrows. The majority of burrows used by control pairs in 2007/08, were again used in 2008/09 (52%) but only 32% of experimental burrows were used the following season (Figure 6.3).

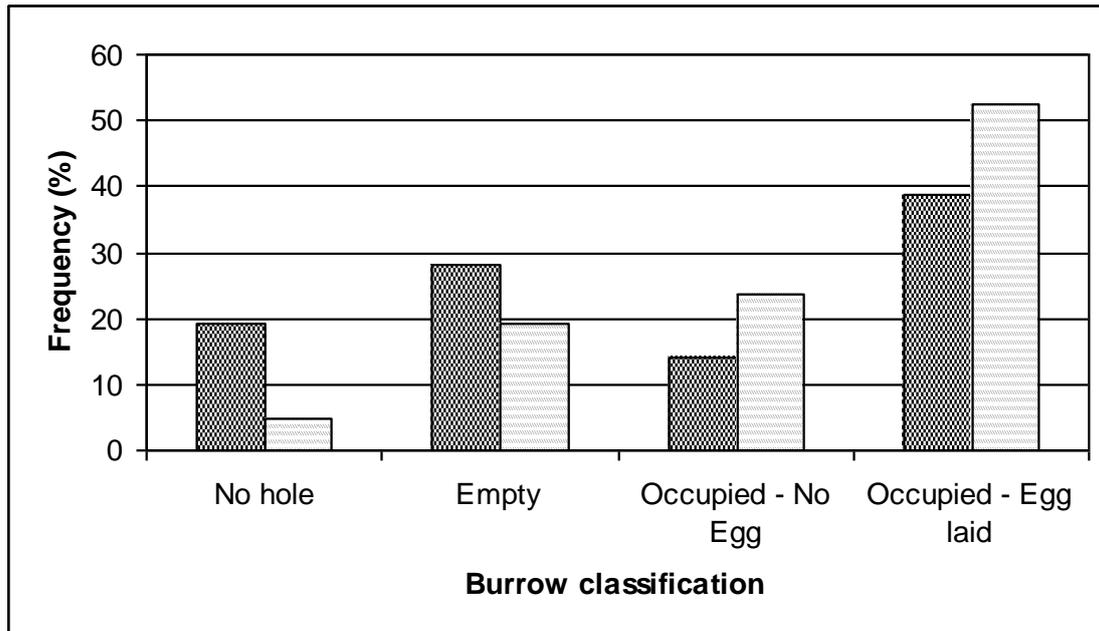


Figure 6.3 Bar graph showing the frequency of burrow use in the year after the incubation routine experiment. Checker bar = experimental, diagonal dash = control.

6.3.7 Pair-bond and nest site fidelity

Fewer experimental pairs re-used their 2007/08 nesting burrows in 2008/09 than did control pairs, but this difference was not significant (experimental = 22.8%, $n = 57$; control = 33.3%, $n = 21$; $G_w = 0.86$, $d.f. = 1$, $P = 0.35$; Figure 6.3). Of the 57 experimental burrows that were found, 62% of pairs had one or both partners desert the burrows that they had used in 2007/08, whereas 48% of control burrows were subsequently unoccupied by the same pair.

In burrows where eggs were laid, the majority were occupied by the same pair as had used the burrow in the previous year (Figure 6.4). A small proportion of burrows were used by divorcees with a new partner (experimental = 18%, $n = 22$; control = 18%, $n = 11$), while other burrows were occupied by new pairs (experimental = 18%, $n = 22$; control = 18%, $n = 11$) (Figure 6.4).

In 2008/09, no birds banded as part of this study were found breeding in different burrows in 2007/08. If these birds did return they were breeding outside the 10 m radius search area. However, birds may have returned but were not found during the routine burrow searches because they departed before a nest inspection took place. This is a possibility, as some burrows that were classified as ‘empty’ were occasionally found with either fresh diggings or shearwater footprints outside the burrow. It was difficult to determine whether these signs of activity were from 2007/08 birds returning to their burrows, prospectors, or failed breeders.

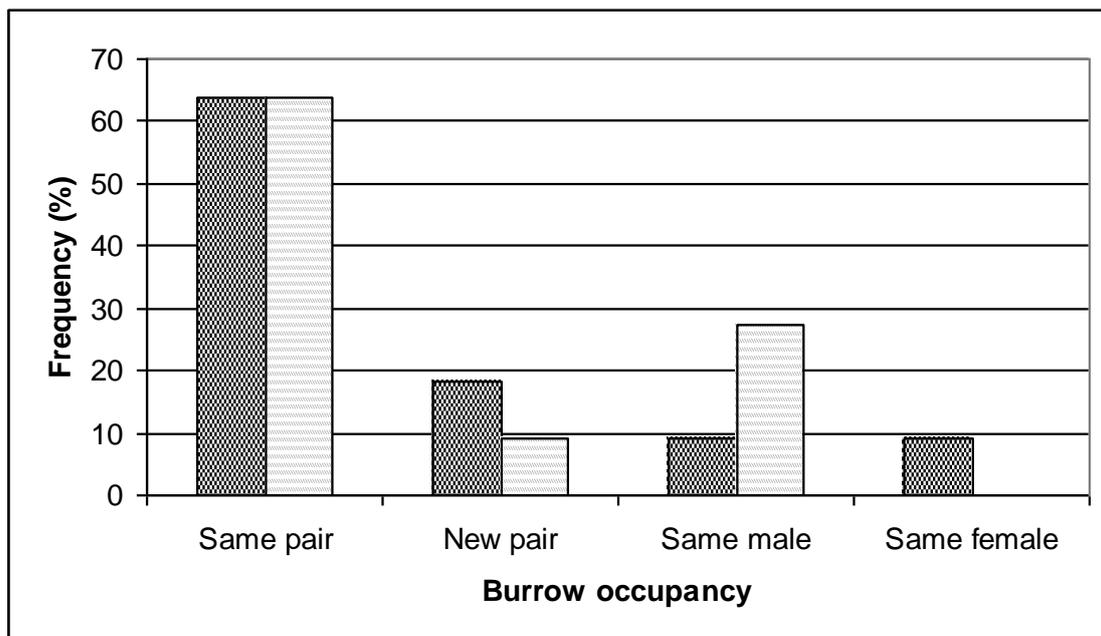


Figure 6.4 Bar graph showing the nest site fidelity in burrows where eggs were laid used in the incubation routine experiment (07/08) and the subsequent year (08/09). Checker bar = experimental, diagonal dash = control.

6.3.8 Reproductive success post-disturbance

6.3.8.1 Egg size

Apart from egg length, egg size in 2008/09 between the experimental and control groups did not differ (Table 6.8). On average, experimental eggs were slightly heavier and longer compared to control eggs. However, control eggs were marginally wider.

Pair-wise comparisons between the experimental and control groups in both breeding seasons indicated that experimental eggs neither increased nor decreased in either mass or size (Table 6.9). Control eggs were significantly lighter in 2008/09, but no differences in egg size between the seasons were detected (Table 6.9).

Table 6.7 Mean (\pm s.d.) egg size of pairs in 2008/09.

Treatment	Experimental <i>n</i> = 14	Control <i>n</i> = 6	<i>t</i> ₁₈	<i>P</i>
Egg mass (g)	89.4 (\pm 7.6)	86.3 (\pm 6.7)	0.85	0.40
Egg length (mm)	71.5 (\pm 2.1)	69.3 (\pm 2.1)	2.09	0.05
Egg width (mm)	46.9 (\pm 1.9)	47.0 (\pm 1.1)	0.15	0.87

Table 6.8 Pair-wise comparisons of the eggs laid in 2007/08 and 2008/09 in experimental and control burrows.

Treatment	Variable	2007/08	2008/09	Paired <i>t</i>	<i>P</i>
Experimental <i>n</i> = 14	Egg mass (g)	88.7 (± 8.2)	89.4 (± 7.6)	-0.50	0.62
	Egg length (mm)	71.2 (± 2.6)	71.5 (± 2.0)	-0.36	0.72
	Egg width (mm)	46.9 (± 2.1)	46.9 (± 1.9)	-0.06	0.95
Control <i>n</i> = 6	Egg mass (g)	90.0 (± 9.0)	86.3 (± 6.7)	3.12	0.02
	Egg length (mm)	69.4 (± 2.8)	69.3 (± 2.1)	0.10	0.91
	Egg width (mm)	47.2 (± 1.6)	47.0 (± 1.1)	0.61	0.56

6.3.8.2 Hatching success

The negative effect of investigator disturbance on hatching success that was evident in 2007/08 did not persist in the subsequent breeding season. In 2008/09, the hatching success of pairs whose membership was the same in both years did not differ among treatment groups ($G_w = 1.13$, $d.f. = 1$, $P = 0.61$). Hatching success increased from 28.5% to 64.3% in the experimental pairs. In contrast, the hatching success of the control pairs was high in both years of the study: 85% in 2007/08 and 85% in 2008/09.

6.3.8.3 Chick survival, mass and size

Chick survival from hatching to pre-fledging was high for both treatment groups. No difference in chick survival rate could be found (experimental 55.6%, $n = 9$; control 83.3%, $n = 6$, $G_w = 1.32$, $P = 0.25$). Analyses revealed no significant differences in mean mass or skeletal measurements of pre-fledge chicks raised by adults in the experimental group versus those raised by control birds (Table 6.10).

Pairs in the experimental group had an overall breeding success rate of 33.3%, and control pairs 71.4%, in 2008/09.

Table 6.9 Mean (\pm s.d.) body mass and measurements between pre-fledging Short-tailed Shearwater chicks reared by pairs used in the incubation routine experiment and control parents in 2008/09.

Variable	Experimental (<i>n</i> = 5)	Control (<i>n</i> = 5)	<i>t</i> ₈	<i>P</i>
Mass (g)	546.0 (\pm 117.3)	500.0 (\pm 106.5)	0.64	0.53
Head length (mm)	77.4 (\pm 3.5)	78.6 (\pm 1.6)	0.65	0.53
Bill length (mm)	32.0 (\pm 1.0)	31.4 (\pm 1.3)	0.81	0.43
Bill depth (mm)	7.7 (\pm 0.4)	7.5 (\pm 0.3)	0.48	0.64
Wing length (mm)	143.8 (\pm 9.9)	147.0 (\pm 10.7)	0.48	0.63
Tarsus length (mm)	56.8 (\pm 1.4)	58.3 (\pm 1.0)	1.87	0.09

6.4 Discussion

6.4.1 The effects of handling

Results from this experimental study have shown that investigator handling at the start and end of an incubation shift can significantly affect hatching success of Short-tailed Shearwaters. These effects did not, however, carry over into the next life history stage and affect chick survival, mass, or size — which is in contrast to the results of Chapter 4. In the following year, no further effects were found on a bird's return rate, pair bond, or nest site fidelity, thus differing from the results recorded in Chapter 5. These observations suggest that the frequency of handling employed in this study

reduced the overall effect of investigator disturbance, except for hatching success. This study again demonstrates how sensitive to investigator handling some Short-tailed Shearwaters are during the incubation period. This can be further demonstrated by the increase in hatching success in 2008/09 from 28.5% to 64.3%. Minor modification of these handling methods, for example, weighing incubation adults only twice in each incubation shift, may continue to reduce the impact of investigators. A larger sample size and replication across colonies and islands would also provide an indication of the robustness of the findings from the present study. This study demonstrates the trade-off between collecting accurate, useful data and the possibilities of biasing the results.

Studies that investigate questions regarding life history and the costs of incubation rarely report the effect that investigators have on study birds (see Chaurand and Weimerskirch 1994). However, understanding investigator disturbance may aid in the interpretation of subsequent results and certainly explain a reduction in sample size throughout the incubation period. Future studies that address similar questions on incubation routine and body mass regulation may require several pilot studies before the main project starts to determine an appropriate handling regime that each species can tolerate. This will demand a detailed knowledge of a species' biology and incubation behaviour. Subsequent results from this study (section 6.4.2) may be interpreted with some caution as data may have been slightly biased. Only continued investigation with a variety of handling procedures will resolve this problem.

6.4.2 Incubation routine and body mass regulation

Cooperation in reproduction decision making can only evolve if pairs can find optimal solutions that promote both survival and reproduction. The results of this study show that body mass during the incubation period plays an important role in Short-tailed Shearwater reproductive behaviour, confirming the fundamental importance of body mass regulation in this species. These birds began their incubation shifts with a high body mass that inevitably declined during the shift because they neither ate nor drank at that time. During incubation, these birds lost an average 1.6% of their initial body mass per day, culminating in an average 20% reduction of their body mass over an incubation shift. Some individual birds demonstrated an ability to extend their incubation shift if their partner did not return from sea. In such cases, the incubating bird was able to lose up to a third of its body mass. This adaptation may help to buffer the late return of a partner if food resources are inadequate or foraging is difficult. Body mass at the start of an incubation shift was evidently important in regulating the length of that particular shift. It seems logical that a higher commencing body mass permits a longer incubation shift. Individuals that began their incubation shift at a low body mass might not be able to remain on the egg until their partner returned from sea, and could have to abandon the egg for their own welfare and thus for the sake of future reproductive output. The body mass at nest abandonment was similar to mass when a bird was relieved by its partner. This suggests that relief by partners is timed to occur just before the point of abandonment and perhaps explains why periods of egg neglect are short, particularly for birds that breed successfully. The lack of a precise mass threshold at egg abandonment may be difficult to determine in this species given the variability in size of birds, but the

results of this study suggest that birds are not prepared to stay any later than when they reach a body mass at which they would expect to be relieved.

The results of this study reveal that Short-tailed Shearwaters regained their lost body mass when they returned to sea at a more rapid rate than they had lost it. Time spent at sea was approximately 15 days, and birds gained an average of 12 g day⁻¹. Females' body mass gain was greater during their second foraging trip but remained the same for male birds on both foraging trips. Males gained a greater amount of mass than did females, however, and there were no differences in the average daily mass gains between their two foraging trips.

The differences observed between the body mass gain between males and females may reflect sex-specific foraging ranges in this species. That appears to be the case for giant petrels (*Macronectes* spp.) (González-Solís et al. 2000a,b, 2008; Quintana et al. 2010). Alternatively, females may have had difficulty locating food during their first stay at sea as their daily mass gain was lower at that time. During their second trip to sea, an increase in body mass may have resulted from an increase in food availability in the Southern Ocean. At this time, zooplankton volume increases in the sub-Antarctic (Knox 1984; Atkinson and Peck 1988; Reid et al. 2005). Time spent at sea was significantly related to a bird's body mass when it left its burrow. This indicates that birds were required to achieve a body mass that would be sufficiently high to cope with their next incubation shift. During incubation, the time individuals have available for foraging is constrained by their partner's ability to remain on the egg. An extended foraging trip does not necessarily increase the probability of successful foraging (Chaurand and Weimerskirch 1994). It does, however, increase the probability of nest desertion by the incubating bird. Some Short-tailed Shearwaters were observed to have a foraging trip of up to 28 days, but

time spent at sea was not related to mass upon return or mass gained while at sea. This could have occurred because they had difficulty foraging effectively. This observation may also support the theory of a threshold in return mass which proposes that the individual will forage to achieve a threshold that will be dependent both on time spent and the quality of the bird.

Birds that had difficulty gaining body mass could have been young breeders or inexperienced birds. A bird's age and experience are variables known to affect the breeding success of a wide range of birds, including procellariids such as Manx Shearwater (Brooke 1978) and the Northern Fulmar (*Fulmarus glacialis*) (Ollason and Dunnet 1978). These variables may, in turn, be positively correlated with body mass or condition (Sæther 1990; Weimerskirch 1992, 1995; Lecomte et al. 2010). In essence, the ability of birds to gain body mass across the incubation period may be directly related to them being more efficient foragers. This explanation has been put forward for the Antarctic Fulmar (*Fulmarus glacialoides*) (Weimerskirch 1990). Overall, the duration of an incubation shift and the total amount a bird lost during that incubation shift were not related either to how long the bird stayed at sea or to body mass on return from foraging. The association between a bird's mass when it left the nest and the trip duration at sea and the mass gain is reasonable, as a set mass threshold can be achieved more rapidly if the mass of the bird is already high (Chaurand and Weimerskirch 1994). Thus, if birds reach their desired body mass quickly (from successful foraging) they can return more quickly to land and relieve their mate. If foraging is difficult, they spend a prolonged amount of time at sea to acquire their desired body mass at the risk of their partner abandoning the nest as a result of limited energy reserves.

The incubation routine of Short-tailed Shearwaters had been studied previously, but to only a small extent (Serventy 1967). No detailed work has been published, and this is the first comprehensive study of its kind. The results reveal that incubation shifts average 11 to 14 days, but are different between the sexes. Male birds spent more time incubating than did females, and this is in accord with findings from other studies of procellariiforms (Jouventin et al. 1985; Warham 1990). Male birds in the present research were on average 3% larger than their female partners (see Chapter 3), and there may therefore be different energy budgets for the two sexes that create a potential for differential parental effort (Clutton-Brock 1991). This could explain why males averaged a total of 26 incubation days compared with the females' 23.7 days (52% and 48% of the average total incubation period respectively). These results do, however, contrast with those of Fisher (1971) who found that noticeable differences in incubation shifts occurred during the early stages of the incubation period, but that birds adjusted their shifts later so that the total time spent by each sex was similar.

The degree of intermittent incubation behaviour has not been studied in Short-tailed Shearwaters, but this study revealed that egg neglect was common. Warham (1990) has suggested that eggs may be neglected at any stage of the incubation cycle, but perhaps more at the start when there has been little investment in the breeding attempt, and less so as the point of hatching approaches. This particular pattern was not observed in this study, possibly because changeovers between parents were sometimes delayed to ensure that the on-duty bird had adequate food for the chick. Imber (1976) noted a higher frequency of changeovers three days before hatching in Grey-faced Petrels (*Pterodroma macroptera*), and suggested that the duration of the last incubation shift was precisely timed to ensure a changeover at 55 days, the peak

time of hatching. The advantage to a pelagic species that is dependent on synchronised breeding shifts is that an uncovered egg does not necessarily result in instant breeding failure even if it does decrease the probability of hatching success (Boersma and Wheelwright 1979). This situation permits adults that have not achieved their desired body mass to persist with foraging without certain breeding failure. Warham (1990) also suggested that the resistance to egg chilling may be a major adaptation to pelagic foraging that allows the parent birds to nest far from their main food source.

Results from this study demonstrate that body mass during incubation plays an important role in Short-tailed Shearwater reproductive behaviour, enabling adults to regulate the trade-off between risks of breeding failure and risks of adult mortality. Subsequent research might reveal whether these results are consistent across different years, colonies, and age of birds and their breeding experience. Further research in which data are collected over a number of years is needed to identify sex-specific foraging locations of this species and to investigate the effects that age and experience have on individual body mass and body condition.

Chapter 7: Trans-equatorial Migration of Short-tailed Shearwaters Using a New Method for the Long-term Attachment of Global Location Sensor Data-Loggers

7.1 Introduction

With a growing interest in seabird ecology and at-sea behaviour, and because of improvements to remote sensing devices (for a review see Burger and Shaffer 2008), there has been a considerable increase in tracking studies in recent years. In the past, most studies have been fairly short in their duration (only weeks or months), but recent advances in global location-sensing (GLS) loggers, or geologgers, have facilitated longer deployments (12–18 months) (Afanasyev 2004; Croxall et al. 2005; Phillips et al. 2006). These technological advances have expanded our knowledge of the ecology and behaviour of procellariiform seabirds considerably, particularly with regard to migration patterns and distant foraging locations, non-breeding distribution, and the overlap of their range with long-line fisheries (Igual et al. 2005; Phillips et al. 2006, 2007; Shaffer et al. 2006, 2009; Phalan et al. 2007; Guilford et al. 2009; Catry et al. 2009). This information is invaluable for conservation efforts.

While there are clear benefits from tracking seabirds, concern has been raised about the effect of the devices themselves on the reproductive and foraging behaviour of the birds as the extra weight of the data-logger, as well as the method and location of attachment, may affect flight, diving, and foraging ability (Wilson et al. 1986; Söhle et al. 2000; Phillips et al. 2003; Söhle 2003; Igual et al. 2005; Carey 2009; also see Chapter 1), particularly if the tracking device is greater than 3% of a bird's total body mass (Phillips et al. 2003). Recently, leg-mounted GLS devices have been deployed on a variety of procellariiform seabirds such as Grey-headed Albatrosses (*Thalassarche chrystostoma*) (Croxall et al. 2005), White-chinned Petrels (*Procellaria*

aequinoctialis) (Phillips et al. 2006), Sooty Shearwaters (*Puffinus griseus*) (Shaffer et al. 2006, 2009), Manx Shearwaters (*P. puffinus*) (Guilford et al. 2009), Streaked Shearwaters (*Calonectris leucomelas*) (Takahashi et al. 2008; Yamamoto et al. 2008), and Cory's Shearwaters (*C. diomedea*) (Iguar et al. 2005; González-Solís et al. 2007). Such deployment has occurred for up to 18 months with little apparent effect on feeding ecology or demographic parameters. However, in some cases there were low return rates (Table 7.1). In the research indicating this, light-level geolocators were attached to plastic or Darvic bands placed on the bird's leg. The advantages of Darvic bands are their weight, ease of attachment, and relatively long durability with little reported effects on the bird's tarsus. However, one of the distinguishing features of shearwater morphology is these birds' laterally compressed (streamlined) tarsometatarsi (hereafter tarsus), which are believed to lessen resistance to water while pursuing prey (Wood 1993). Unless modified to fit the shearwater tarsus, attachment of a round Darvic band to a compressed tarsus may be hazardous to the bird as any movement over the toes or rotating around the tarsus could cause injury. In addition, using a round Darvic band increases the risk of shading of the light sensor if the sensor faces inward towards the bird because that can affect the quality of light data (Afanasyev 2004). Darvic bands can be reshaped by heating them, then moulding them to fit the shape of the tarsus (Scott Shaffer pers. comm.). However, this can make the plastic band friable (David Drynan, Australian Bird and Bat Banding Scheme (ABBBS), pers. comm.) and thus could lead to the loss of some devices.

The migratory movements of small Southern Hemisphere breeding seabirds remain largely unknown, despite their status as top order marine predators and indicators of ocean health (Shaffer et al. 2006). One of these birds, the Short-tailed Shearwater (*Puffinus tenuirostris*) is a small procellariiform (≈ 500 g) with an

Table 7.1 Comparison of mean total weight of band and geollogger, length of deployments, and rates of return of procellariform GLS studies. NR, not reported

Species	<i>n</i>	Mean total weight band + geollogger	% of bodyweight	Length of deployment of geollogger	Rates of return (%)	Source
White-chinned Petrel (<i>Procellaria aequinoctialis</i>)	35	10.5 g	<1%	Mean 366 days (range 226–664 days)	31%	Phillips et al. (2006)
Sooty Shearwater (<i>Puffinis griseus</i>)	33	11 g	1.40%	Mean 262 ± 23 days (s.e.)	60%	Shaffer et al. (2006), Adams et al. (2009)
	28	6 g	<1.5%	0–30 days	100%	Shaffer et al. (2009)
Short-tailed Shearwater (<i>P. tenuirostris</i>)	27	5.4 g	0.6 – 1.2%	1 year	74%	This study
	40	12 g	1.5–2%	1 year	60–65%	Igual et al. (2005)
Cory’s Shearwater (<i>Calonectris diomedea</i>)	52	10 g	NR	1 year	42%	González-Solís et al. (2007)
Streaked Shearwater (<i>C. leucomelas</i>)	11	7 g	1.30%	290 days	36%	Takahashi et al. (2008)
	48	7 g	1.2–1.5%	1 year	79.2%	Yamamoto et al. (2008)
Manx Shearwater (<i>P. puffinus</i>)	12	2.5 g	NR (0.6% for a 400-g adult)	11 months	100%	Guilford et al. (2009)
Cook’s Petrel (<i>Pterodroma cookii</i>)	10	3 g	1.5%	14 days (<i>n</i> = 8 birds), 1 year (<i>n</i> = 2)	80% (after 2 weeks)	Rayner et al. (2008)

estimated global breeding population of 23 million birds (Skira 1991). Observations of migrating Short-tailed Shearwaters suggest that the population conducts a trans-equatorial flight across the Pacific Ocean. Early results from banding studies and museum collections implied a broad ‘figure-of-eight’ movement across the Pacific Ocean (Serventy 1953, 1956, 1957, 1961). More recent oceanic transects suggest that birds migrate in broad fronts in the western and central Pacific (Maruyama et al. 1986). Knowledge of these birds’ presence in the Southern Ocean was not confirmed until 1981, and it was further substantiated with brief satellite telemetry and stable isotope studies (Klomp and Schultz 2000; Cherel et al. 2005; Einoder et al 2011). In essence, non-breeding birds are believed to leave the colonies early in March (Serventy 1967), followed by breeding adults in April and May (Marchant and Higgins 1990), and then followed by fledglings. Migration is thought to be short — approximately 4 to 6 weeks for birds to reach the eastern part of the Bering Sea and Chukchi Sea (Marchant and Higgins 1990). It has been suggested that the return journey commences at the beginning of September through the western sector of the Pacific, although there is evidence that shearwaters pass through the Gulf of Alaska to waters off California before heading south to Australia. Whichever path is used, the first birds are seen back at their nesting islands from early September onwards, with landfall occurring in late September (Marshall and Serventy 1956; Robertson 1957; Serventy 1967; Skira 1991).

Until now, there was little information on the exact timing, speed, and flight paths for migrating Short-tailed Shearwater, a species that is a major consumer of oceanic resources (Hunt et al. 2002; Ito 2002). Nor was information available about individual variation in wintering site and at-sea behaviour. In this chapter, I first describe the development of a modified band used for long-term attachment of

geolocators to Short-tailed Shearwaters. The aim was to produce a modified band that would satisfactorily fit a shearwater's compressed tarsus, was of low mass and low resistance, and had longevity in relation to the environment in which it would need to perform, thus maximising retrieval rates. In this chapter I also provide the first comprehensive information about the migratory journey and wintering habitats of Short-tailed Shearwaters by using global location sensors (GLS loggers).

7.2 Materials and Methods

7.2.1 Development of bands

After reviewing the attachment methods from several shearwater and petrel GLS tracking studies (Iguar et al. 2005; Phillips et al. 2006; Shaffer et al. 2006; González-Solís et al. 2007; Rayner et al. 2008; Takahashi et al. 2008), I developed a band similar in size and shape to that of the ABBBS size-16 shearwater band. ABBBS stainless steel bands had been designed specifically to match the shape of the legs of shearwaters (Lowe 1989) by being compressed laterally. This feature was important to ensure that the band did not rotate while attached to the leg, thereby, as required by the project's research permits, reducing the potential to cause abrasion. After trialling stainless steel bands as a possibility, I found it too difficult to 'close' the band on artificial shearwater legs. Instead, marine grade aluminium was chosen. Aluminium is lightweight and malleable, and thus possesses two of the qualities needed for the new band to be functional. Using measurements of size-16 shearwater bands as a guide (diameter 10.5×4.3 mm, length (height) 7 mm; ABBBS), these new bands were cut to size and tested in the laboratory on several artificial legs. As a result, the bands were made longer (25 mm) to assist with mounting and stabilising the logger. The internal diameter of the closed band was also made slightly wider (11×6 mm) to ensure that there was no rubbing on the tarsus. Three 2-mm holes were drilled on

either side of the band to allow sand and other debris to flush once the bird returned to sea (Fig. 7.1a). The edges of the band and the cable-tie holes were smoothed with a fine-tooth file to further reduce the risk of abrasion.

Next, a means of attaching the geollogger to the band was assessed. I found from other studies that one of the most commonly-cited ways to attach the geollogger to the plastic Darvic bands was to use weather resistant, nylon cable-ties. I trialled a 2.3-mm wide UV-resistant cable-tie (from RS Components Ltd, <http://www.rsaustralia.com>). In order to attach the geollogger to the aluminium band, two 2.2-mm holes were drilled 7 mm apart into the flat side of the band. One cable-tie was then fed through the holes ready for attachment of the geollogger (Fig. 7.1a). Mean total mass of the band, including cable-tie, was 3.6 g (± 0.02 s.e.m., $n = 62$). All means are given \pm standard error of the mean.

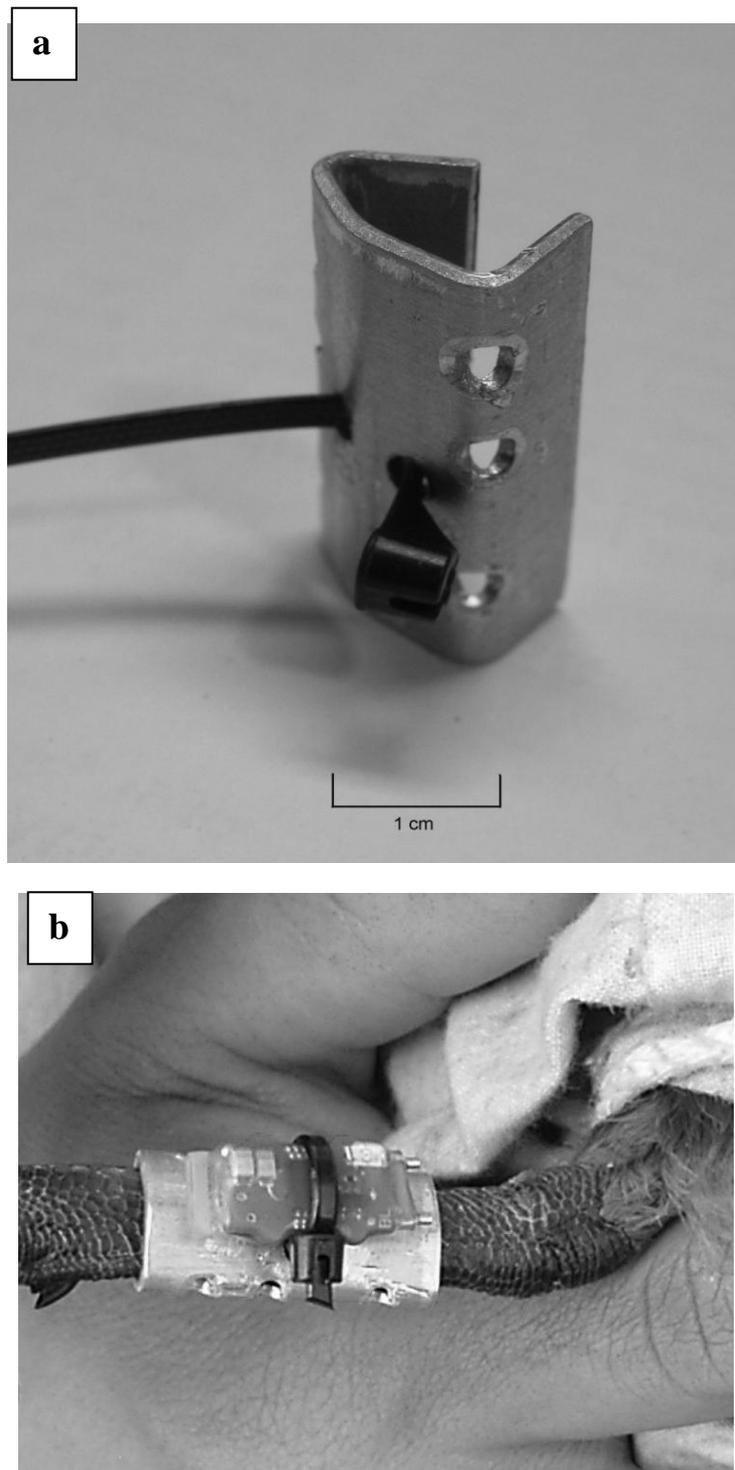


Figure 7.1 Photographs of (a) a modified band ready for deployment on a shearwater (note the cable-tie has already been attached) and (b) band with geollogger attached on the tarsus of a Short-tailed Shearwater. The trailing end of the cable-tie has been removed.

7.2.2 Field testing and deployment

Several fully constructed bands were again tested on artificial Short-tailed Shearwater legs before deployment. This allowed the bander (MJC) to practise closing the band and attaching the geolocator to the band. It also helped to ensure that there was no rubbing between the leg and the band. In all cases the band moved freely up and down the artificial leg and could not rotate around the leg.

During December 2007, 27 geolocator loggers were attached to adult Short-tailed Shearwaters (13 males, 14 females) breeding on Great Dog Island. Each adult was removed from its burrow by hand and placed in a calico bag. The birds were then weighed with Pesola scales (1000 ± 10 g) and measured. All birds had been previously banded with ABBBS bands as part of a long-term study on recruitment (Meathrel and Carey 2007). Each new band was placed on the bird's left leg. First, the band was closed around the tarsus with the UV cable-tie already threaded through the two holes. Then the geolocator (MK13, British Antarctic Survey, Cambridge, UK), embedded in transparent resin and weighing 1.8 g, was placed in position on the band and the cable-tie tightened around the geolocator. Pre-attachment of the geolocator was not possible as it would interfere with the band being closed around the tarsus. A cable-tie tool (RS Components Ltd) was used to tighten the tie further, and the trailing end of the cable-tie was removed at the clasp with pliers (Fig. 7.1*b*). This procedure took approximately 5 minutes. Finally, the band was checked to ensure that it could move up and down the tarsus freely. In all cases the band did move freely and showed no signs of likely abrasion. The bird was then placed back in its burrow.

Total mass of the band plus the mass of the geolocator was 5.4 g (± 0.02 , $n = 27$) and represented a range of 0.7–1% of adult body mass and 1.3% of the lightest

body mass previously measured (410 ± 10 g, adult female, 24 September 1989) (C. E. Meathrel, unpubl. data). These figures are comparable to weights of geologgers used in other studies of procellariiform seabirds (Table 7.1) and fall well below the recommended 3% additional weight for flying seabirds (Phillips et al. 2003).

7.2.3 Assessing short-term impacts

In this study, birds were left for 2 to 3 weeks after attachment of the band before they were re-caught and assessed for any injuries. Only male birds were handled during this time because female birds are more susceptible to abandonment of the nest if handled (Warham 1990). Males had just returned from sea and were beginning their second incubation shift. Birds were caught by hand, weighed with a Pesola scale and assessed for any abrasion or discolouration where the geologger was attached. For a comparison, 20 birds without geologgers within the same colony were also caught and weighed to assess any short-term effects on body mass.

7.2.4 Recovery and removal of geologgers

During the subsequent breeding season, in November and December 2008, marked burrows from the previous season were inspected during laying and early incubation. Burrows within a 10-m radius of these marked burrows were also inspected in case adults had moved burrows. A 10-m radius was chosen as a search area because adult Short-tailed Shearwaters have strong fidelity to their nesting site and rarely move more than 3 m from their original burrow (Serventy and Curry 1984; Skira 1991; also see Chapter 5).

The adults that had returned were first placed into a calico bag. They were then weighed and the geologger was removed. To remove the bands, first the UV

cable-tie was cut and the geollogger was removed. Then two sets of circlip pliers were inserted either end of the band gripping its two butt-ends. Pressure was carefully applied to prise open the band until the circlip pliers could be inserted between the butt-ends of the band. Once this was achieved, pressure was applied which opened the band and it was then removed. This procedure took less than 7 minutes and was achieved by two people — one to hold and steady the bird, the other to remove the band.

All birds were then assessed for injury, if any, caused by the band or its subsequent removal. Geollogger-bands were examined for growth of goose barnacles (*Lepas* spp.) noted by Phillips et al. (2007), and for other marine organisms. Since Short-tailed Shearwaters are burrow nesting, bands were also examined for evidence of abrasion caused by digging.

To determine any effects of the band on the body mass of equipped adults after they had returned to the burrow, an additional 20 birds without geologgers were weighed for comparison purposes. In addition, in order to determine the effects of the bands on rates of adult returns, 40 birds that were banded, were used as an extra control group. These adults were a part of the same colony and had been banded in November and December 2007. They had been handled only once at laying or early incubation. Their burrows and a 10-m radius were again inspected in November and December 2008.

7.2.5 GLS data analysis

The British Antarctic Survey geollogger measures light levels every 60 seconds, and a maximum value over each 10 minute recording interval was logged. Light data were processed with ‘TransEdit’ and ‘BirdTracker’ software developed by the British

Antarctic Survey. Sunrise and sunset times were identified based on light curve thresholds, with longitude calculated from time of local midday relative to Greenwich Mean Time, and latitude was calculated from day length, thus providing two locations per day (Phillips et al. 2004). During processing, locations derived from light curves with obvious interruptions around sunset and sunrise were identified and later excluded if appropriate, following the procedure of Phillips et al. (2004). During processing, location estimates were filtered for unrealistic travel rates using a speed filter (McConnell et al. 1992) with a threshold speed of 50 km h⁻¹ (Spear and Ainley 1997). Locations were inaccurate around the equinoxes when it is impossible to estimate latitude directly from daylight length (Phillips et al. 2004). Based on concurrent deployment of GLS loggers and satellite tags on Black-browed Albatrosses (*Thalassarche melanophrys*), locations were considered to have a mean accuracy \pm s.d. of around 186 \pm 114 km (Phillips et al. 2004).

In total, 93% of locations were retained after filtering. Track lines for each bird were created from the remaining locations using a curvilinear interpolation scheme (hermite spline; Tremblay et al. 2006) at 10 minute intervals. Total distance travelled and maximum distance from the colony (or range), were estimated from each interpolated track.

Utilisation distribution (UD) kernels were calculated from all locations to characterise the wintering distribution and patterns of habitat use by non-breeding shearwaters. UD kernels were calculated using the Iknos Kernel program (Y. Tremblay, unpublished) developed in MatLab, with a grid size of 80 km. A minimum of two individual birds within a grid cell were required to be counted, and each cell was normalised for bird effort by dividing each cell by the number of birds contributing to all the locations within a grid cell (BirdLife International 2004b).

Spatial area was calculated for kernels after subtracting the area of each major land mass that overlapped with a UD kernel.

7.2.5.1 Habitat analyses

To examine the habitat characteristics where Short-tailed Shearwater travelled to and remained for the boreal winter, we used GLS-derived location data and complementary remotely sensed data. Remotely sensed data were obtained from time series of environmental data at <http://coastwatch.pfel.noaa.gov/> (see this website for metadata on satellite sensors and parameters). These data sets included science quality products for primary productivity (PP) estimated using methods described in Behrenfeld and Falkowski (1997) with resolution of 0.1°, Sea Surface Temperature (SST) which was a multiple-satellite blended product with resolution of 0.1° (see Powell et al. 2008 for details on specific SST datasets), and 3-day average surface wind vectors (0.25° resolution) measured from the Seawinds sensor on the QuickSCAT spacecraft (e.g., Friele 2000). Bathymetry was extracted using data from ETOPO2 (Smith and Sandwell 1997).

Data for each environmental parameter were extracted from the global time series within a 1° longitude by 2° latitude grid (the approximate error of the geolocation method) centred on the date of each location. The mean \pm s.d. of the data at a given location were used in subsequent analyses.

7.3 Results

7.2.1 Short-term effects

All 13 males were caught after two weeks, and there were no differences in body mass between equipped and the randomly selected adults without geologgers (equipped males 566.2 ± 15.8 g, $n = 13$; non-equipped males 592.0 ± 12.9 g, $n = 20$; $t_{31} = 1.29$, $P > 0.2$). Power analysis revealed that for a power ($1-\beta$ error probability) of 0.95 the minimum detectable difference between the means was approximately 67 g (R. V. Lenth 2006–09, Java Applets for Power and Sample Size, see <http://www.stat.uiowa.edu/~rlenth/Power>, accessed 1 September 2009). This indicates that we would have needed a difference of at least 67 g in the means to detect a significant difference between the two groups. Given that I could not detect what amounted to a 12% change in body mass, the data should be considered cautiously as it could not reveal a change of the requisite magnitude. No abrasions or injuries were observed during this time, and no sand or soil had accumulated inside the modified band.

7.2.2 Band recovery and assessment

During November and December 2008, 20 geologgers, or 74% of those fitted, were recovered from adult birds (10 males, 10 females). Despite searching all burrows within a 10-m radius of the marked burrows, none of the remaining seven birds equipped with geolocators could be found. Results from another study in the same colony of birds without geologgers returning to breed between 2007 and 2008 indicated a return rate of 82.5% (i.e., 33 of 40 birds banded in 2007 returned in 2008), which is comparable to the return rate of equipped birds. All returned birds fitted with geolocators were of the same mass compared with birds without geologgers

(equipped adults 652 ± 13.6 g, $n = 20$; non-equipped adults 632 ± 12.9 g, $n = 20$; $t_{38} = 1.04$, $P > 0.3$). Power analysis revealed that for a power of 0.95 the minimum detectable difference between the means was approximately 64 g (following Lenth 2006–09). Given this, the dataset was inadequate to detect a 10% change in body mass.

Two birds had minor callusing on their legs (a 10×10 mm area of flaking skin on the inside of the leg), but no other birds showed any sign of abrasion or injuries. No goose barnacles or other marine organisms were found on the bands. In 90% of cases, bands showed some evidence of scratching on their surface. However, the abrasions did not threaten the integrity of the band or the attachment design.

Follow-up searches were made in November and December 2009 for the seven birds that failed to return. Despite extensive burrow searches, none of those birds was found. In December 2010, the 21st logger was removed from a male bird (band number: 162-37012) that had been captured at the colony (Dr Yutaka Watanuki, Hokkaido University, Japan, pers. comm.). The bird weighed 585 g and was in reportedly good health. The 21st bird represented an overall recovery rate of 77% after three years and demonstrated that the new banding technique could last at least three years after deployment.

7.2.3 Trans-equatorial migration and wintering

Of the 20 tagged birds, 14 were from breeding pairs with the remaining tags individuals of a pair. Twelve of 20 recovered loggers provided complete records of tracks during breeding and migration, and a further four loggers providing partial tracks ($n = 16$, 8 males and 8 females) (Figure 7.2). The 21st logger retrieved in December 2010 was not included in the subsequent analysis because it failed to

download and was sent to the British Antarctic Survey, Cambridge, UK for a manual data recovery.

At the end of the breeding season, tagged birds travelled south to a stopover region of deep cold water below the Antarctic Convergence and east of the Ross Sea between degrees 60° - 70° S and degrees 110° - 180° E, where they remained for an average 26.1 (\pm 16.4 days) (Table 7.2). This previously unknown oceanic stopover for Short-tailed Shearwaters was located in cold, highly productive waters characterised by high *chl a* concentrations (Table 7.3). Between 15 April and 9 May 2008, all 16 birds continued their migration north through the South Pacific, passing the Equator on 26 April (\pm 6 days) (Table 7.2). Not surprisingly ocean temperatures were high at this time with low *chl a* concentrations and low wind speeds (Table 7.2; Figure 7.3, 7.4, 7.5). After crossing the Equator, birds followed a north-western path towards the east coast of Japan until 30° N where seven birds took a route that was different from the others by shifting to a north-east flight path, towards the south-central Bering Sea around the Aleutian Islands. The remaining nine birds continued their flight path to the east coast of Japan (Figure 7.2). All birds ceased their northward passage at approximately 40-50° N, and shifted to a pattern of predominantly east-west movements (Fig 7.6). Movements across the Pacific Ocean were fast, with the mean duration of the northward migration being 13 ± 1.5 days (Table 7.2). All birds subsequently remained north of 40° N and between 120° E and 150° W for the duration of the boreal summer (Figure 7.7). This region, which includes the Sea of Japan, Sea of Okhotsk, and Bering Sea is particularly productive, and supports large volumes of key prey species, including *Euphausia pacifica* (Euphausiacea), for many seabirds.

Table 7.2 Timing of migration stages of Short-tailed Shearwaters.

Bird ID	Sex	Arrival at Southern Ocean stopover	Time spent at stopover	Start of migration	Date passing Equator on northbound migration	Arrival at wintering site	Duration of northbound migration	Time spent at wintering site	Departure from wintering site	Date passing Equator on southbound migration	Duration of southbound migration	Arrival at breeding site
8041	f	18/3	31	18/4	23/4	30/4	13	-	-	-	-	-
8042	m	14/3	37	19/4	24/4	30/4	12	-	-	-	-	-
8043	f	5/4	16	20/4	24/4	1/5	12	149	26/9	13/10	22	17/10
8045	m	24/2	55	19/4	22/4	29/4	11	159	4/10	9/10	16	19/10
8047	f	9/4	10	18/4	23/4	29/4	12	155	30/9	7/10	16	15/10
8049	f	13/3	37	18/4	23/4	29/4	12	156	1/10	12/10	17	17/10
8050	f	8/4	14	21/4	29/4	4/5	14	136	17/9	6/10	24	10/10
8051	m	10/4	9	18/4	24/4	29/4	12	141	16/9	1/10	18	3/10
8053	m	29/3	19	16/4	24/4	29/4	14	157	2/10	14/10	17	18/10
8054	m	17/2	61	15/4	22/4	30/4	16	158	4/10	8/10	17	20/10
8056	f	3/3	44	15/4	21/4	30/4	16	-	-	-	-	-
8057	m	13/4	27	9/5	16/5	20/5	12	134	30/9	14/10	19	18/10
8060	m	12/4	19	30/4	4/5	11/5	12	-	-	-	-	-
8062	m	11/4	13	23/4	1/5	7/5	15	146	29/9	12/10	19	17/10
8064	f	5/4	14	18/4	24/4	29/4	12	139	14/9	16/9	17	30/9
8066	m	11/4	12	22/4	1/5	4/5	13	146	27/9	6/10	15	11/10
Mean		26 March ± 18 days	26 ± 16 days	20 April ± 6 days	26 April ± 6 days	2 May ± 6 days	13 ± 1.5 days	148 ± 9 days	26 Sept ± 7 days	7 October ± 7.7	18 ± 2 days	13 Oct ± 6 days

Table 7.3 Oceanographic characteristics with the kernel distribution during different tracking periods in 2007 – 2008. Values are mean \pm sd. SST: sea surface temperature. SSH: sea surface height.

Stage of Migration	Water depth (m)	SST ($^{\circ}$ C)	Chl <i>a</i> (mg m^{-3})	SSH (m)	Wind Intensity (m/s)
Post-breeding	-3569 ± 1451	8.84 ± 8.33	0.34 ± 0.68	0.07 ± 0.07	1.97 ± 4.22
Northward migration	-3829 ± 1565	23.39 ± 5.96	0.18 ± 0.21	0.05 ± 0.12	0.73 ± 2.13
Wintering site	-2650 ± 1948	9.6 ± 4.31	1.21 ± 1.13	0.007 ± 0.04	0.17 ± 1.0
Southward migration	-4061 ± 1530	24.42 ± 5.66	0.18 ± 0.30	0.08 ± 0.07	N/A
Pre-laying	-2975 ± 1493	9.1 ± 5.29	0.35 ± 0.18	0.05 ± 0.06	N/A

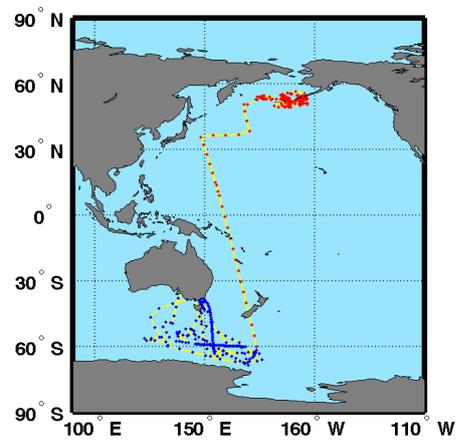
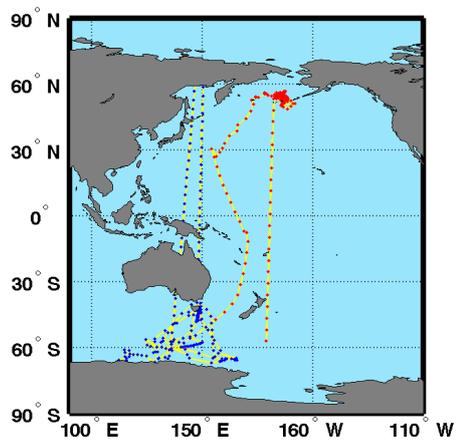
Mean time spent in their wintering region was 148 ± 9.0 days. Individuals chose one of two important wintering regions, the first around northern Hokkaido, Japan and second, west of the Pribilof Islands, Bering Sea (Figure 7.7). These areas were characterised by cold, highly productive waters (Table 7.3). All birds began their return migration to the breeding colony in mid-September to early October (Fig 7.7; Table 7.2). Birds travelled in a south-westerly direction through the central Pacific, east of the Hawaiian Islands, passing the Equator on 7 October (± 7.7 days). Birds continued travelling in a south-westerly direction towards the Australian east coast, entering Australian waters between $25 - 30^{\circ}$ S. Birds then travelled south along the east coast of Australia until reaching the Furneaux Group, Bass Strait in mid to late October (13 October (± 6.5 days). Duration of the birds' southward migration was 18 (± 2.6) days. Total distance travelled over one year was approximately 120,000 km (Table 7.4). Maximum range a bird travelled away from the colony varied between individual birds (Fig 7.8).

Table 7.4 Distances travelled for each bird during the breeding, migration and pre-breeding stages.

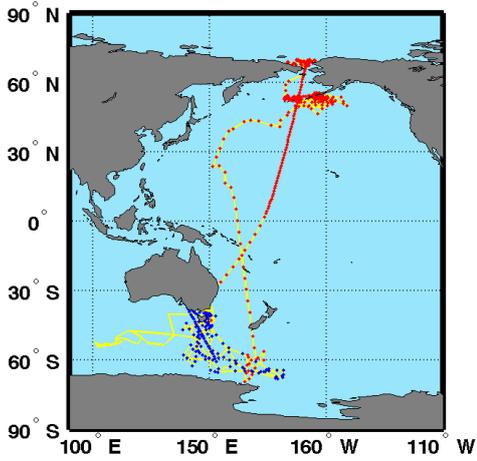
Bird ID	Sex	Distance travelled during breeding (km)	Distance travelled during migration and wintering site (km)	Distance travelled pre-egg laying (km)	Total distance travelled in one year (km)
8041	f	60,462	34,121	Failed	95,084
8042	m	41,581	31,786	Failed	73,531
8043	f	39,423	59,374	19,089	118,240
8045	m	57,751	65,636	16,233	140,744
8047	f	37,373	63,373	21,877	123,242
8049	f	33,935	70,648	13,141	118,600
8050	f	41,925	70,019	16,248	128,314
8051	m	34,015	83,667	22,643	140,438
8053	m	40,602	71,582	18,915	131,686
8054	m	60,086	59,832	13,471	133,638
8056	f	51,625	47,847	Failed	100,022
8057	m	46,021	52,009	24,659	123,384
8060	m	38,721	34,580	Failed	73,852
8062	m	61,247	76,212	19,029	157,207
8064	f	39,015	59,929	24,541	124,111
8066	m	45,944	72,995	17,339	136,427
Mean ± s.d.		45,607 ± 9,595	59,600 ± 15,714	18,932 ± 3,897	119,907 ± 3,447

STSH 8041

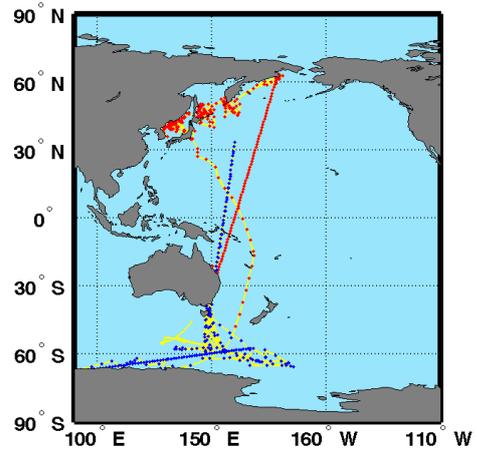
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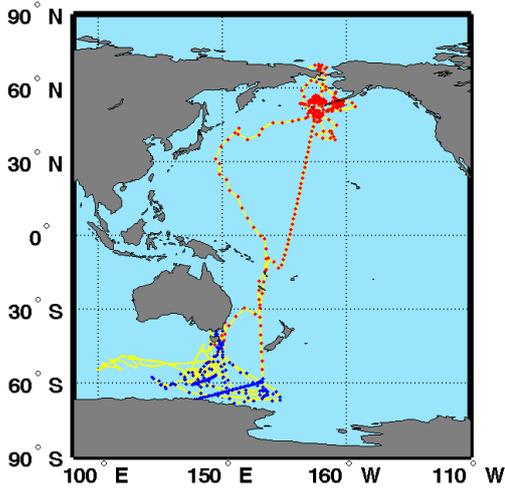
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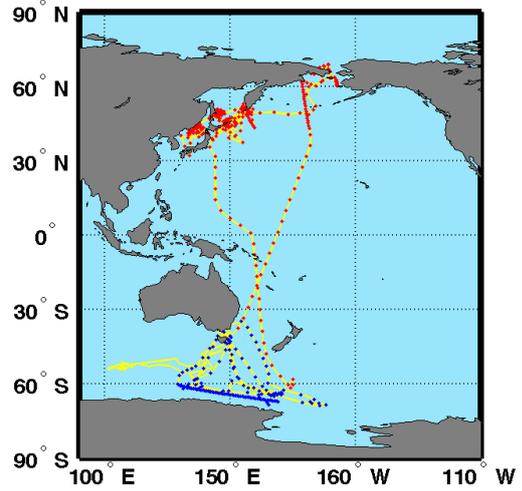
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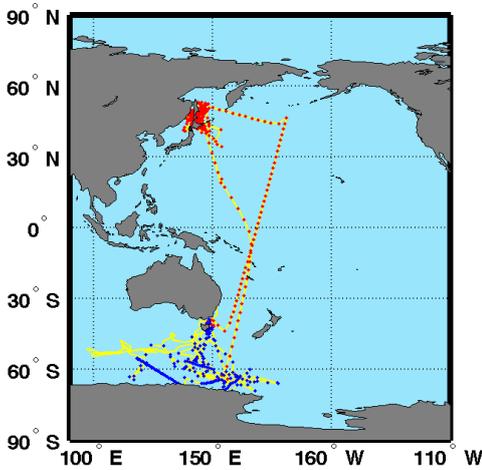
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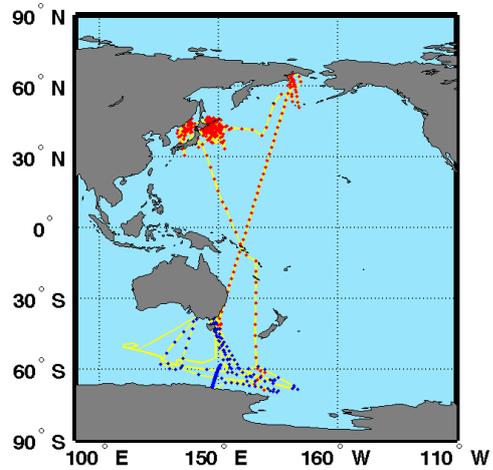
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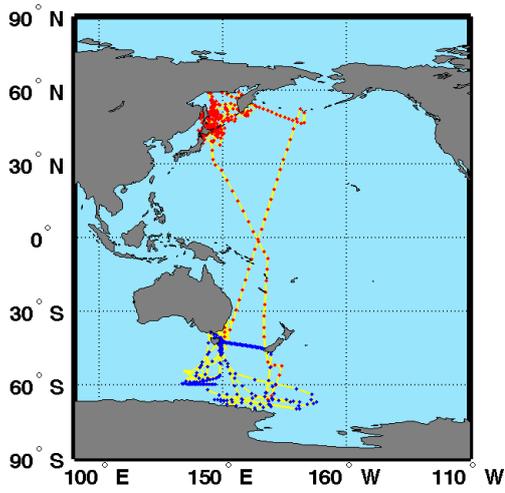
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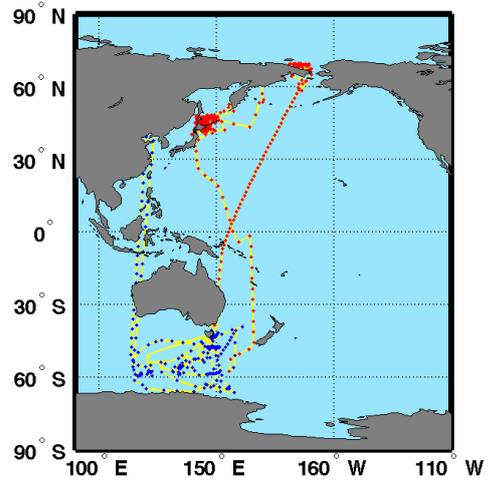
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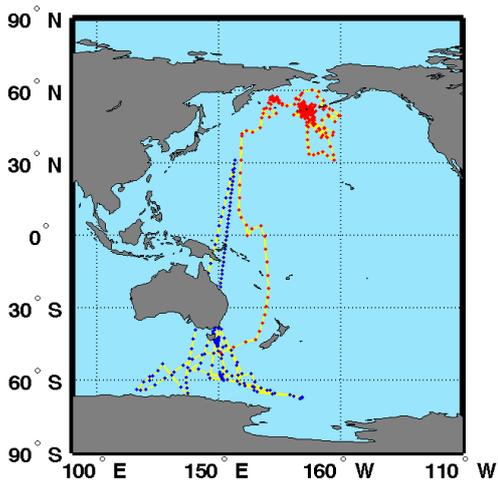
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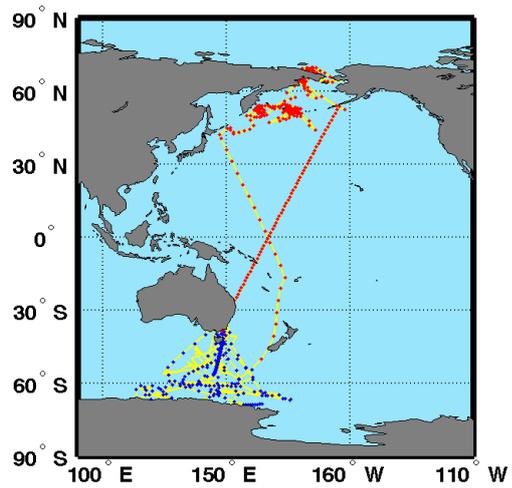
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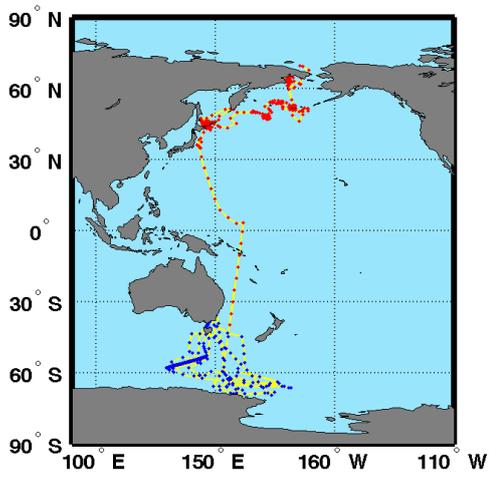
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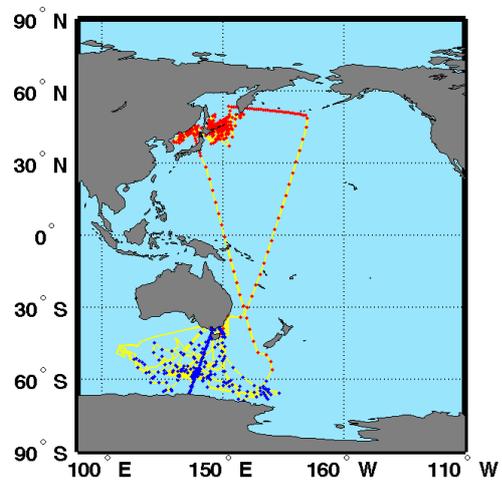
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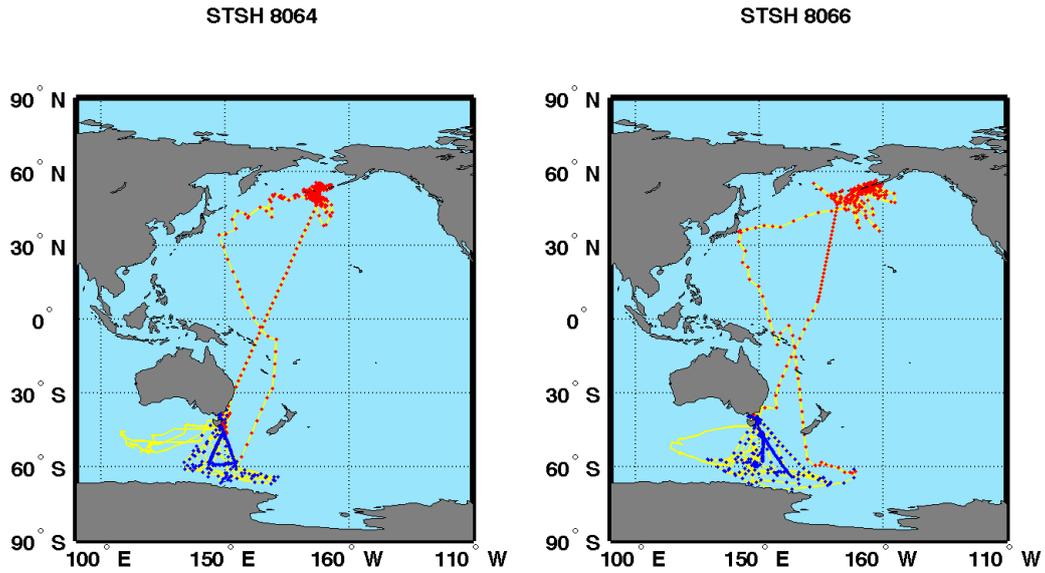


Figure 7.2 Maps showing individuals tracks of all 16 birds from November / December 2007 to December 2008. Filtered and interpolated (2 locations per day) track (yellow line) with red dots denoting migration, blue dots marking breeding, and plain yellow line post-migration/pre-breeding.

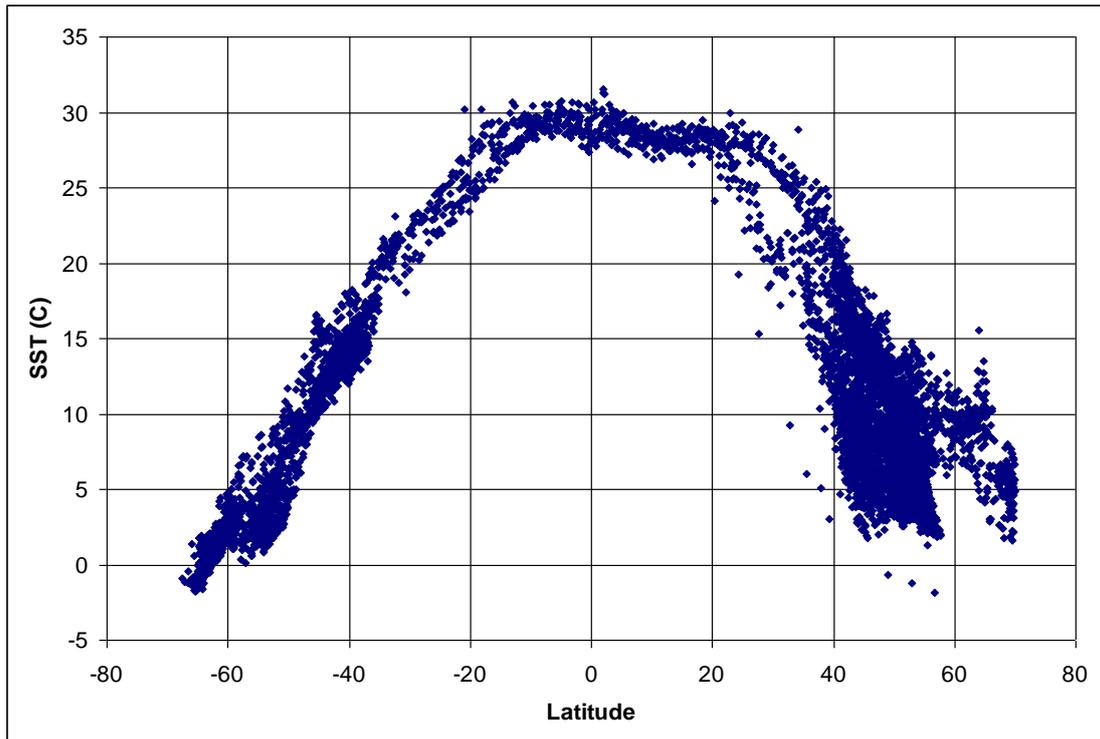


Figure 7.3 Location of Short-tailed Shearwaters and associated Sea Surface Temperature (SST) ($^{\circ}\text{C}$). SST were recorded remotely by satellite and overlaid onto each location.

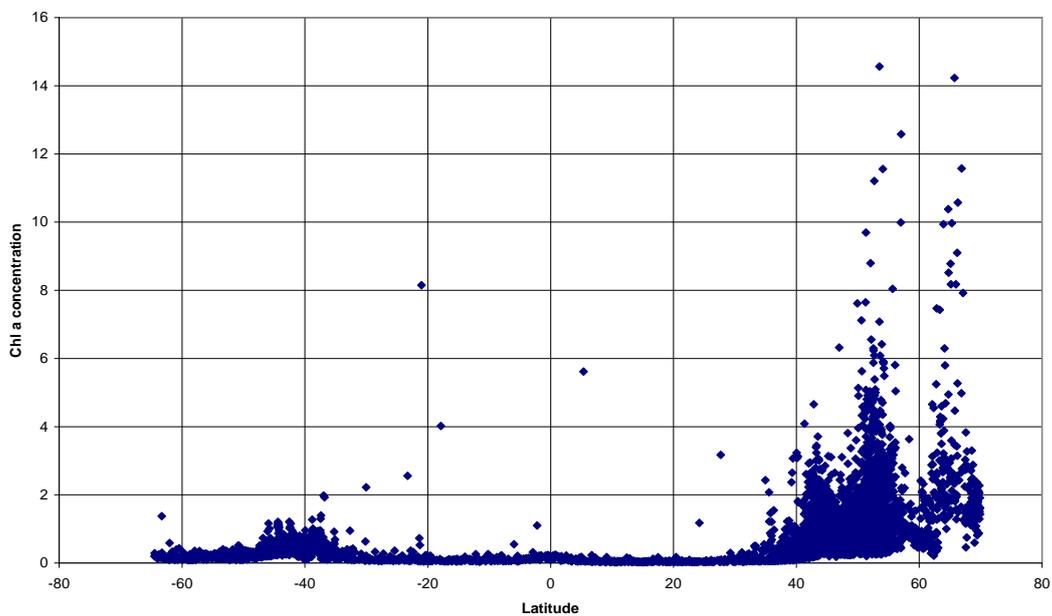


Figure 7.4 *Chl a* concentrations experienced at each location recorded for non-breeding Short-tailed Shearwaters. Values were measured remotely by satellite and overlaid onto each location. Note the paucity of high concentrations when shearwaters cross the equatorial region.

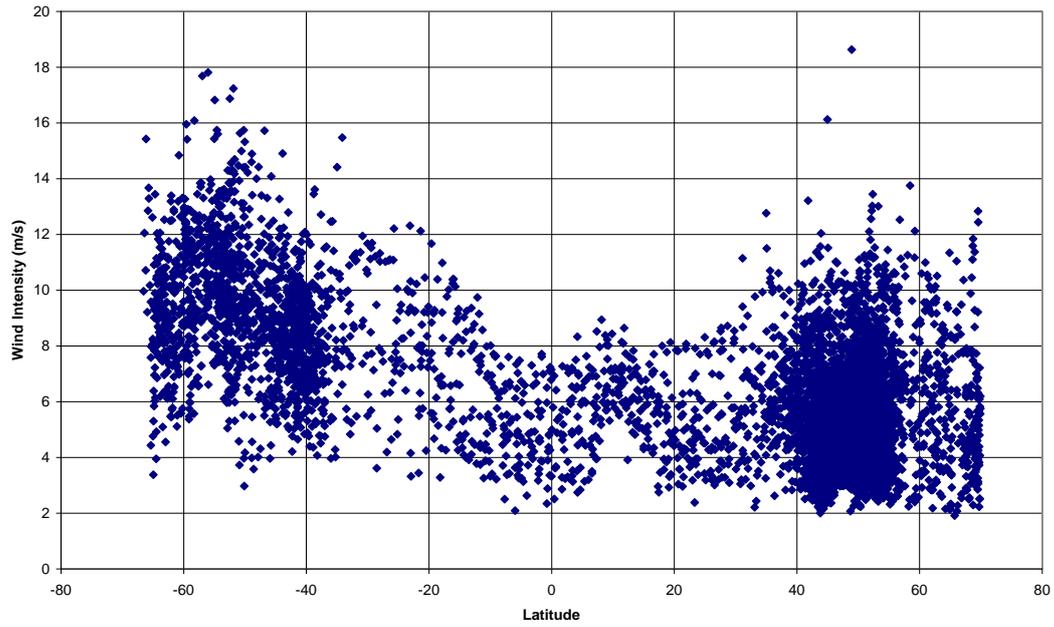


Figure 7.5 At lower latitudes, after breeding, Short-tailed Shearwaters experience wind intensity that is greater than anywhere else on their migration. Note the low wind intensity values for latitudes around the Equator.

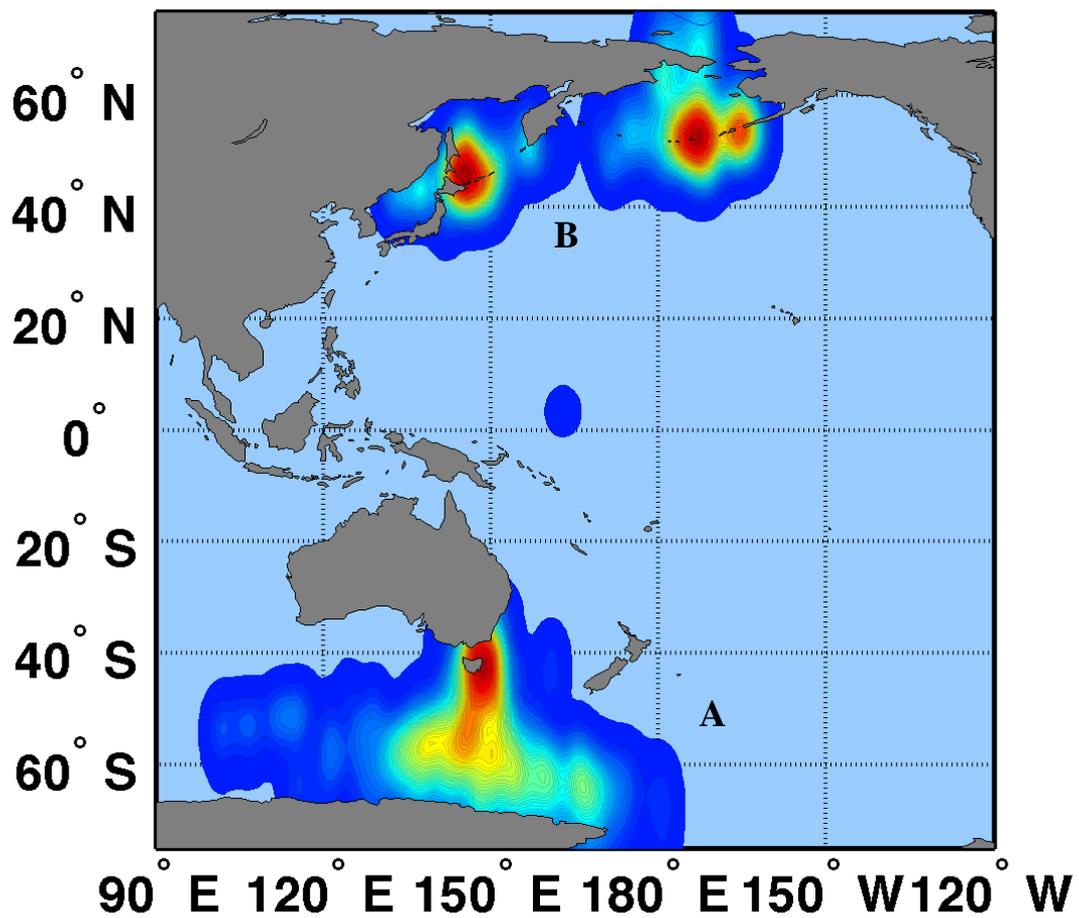
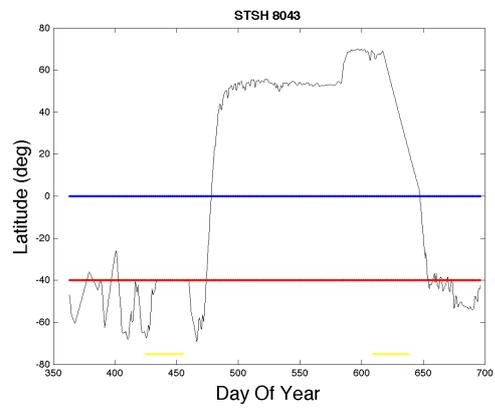
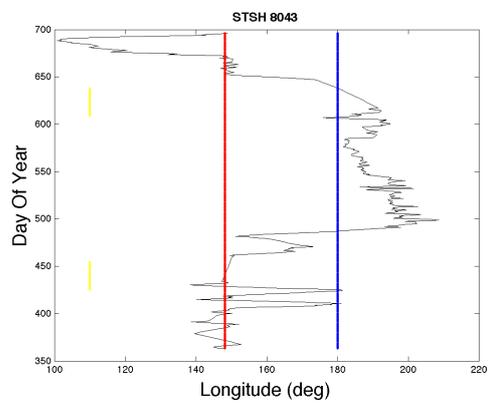
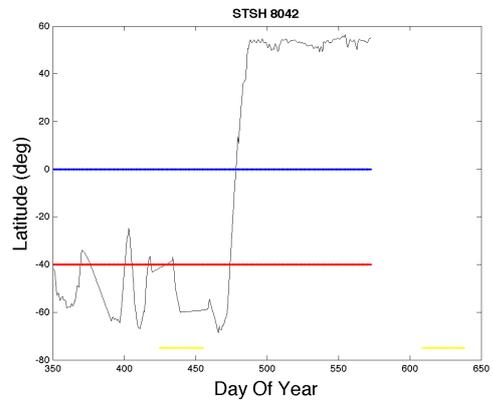
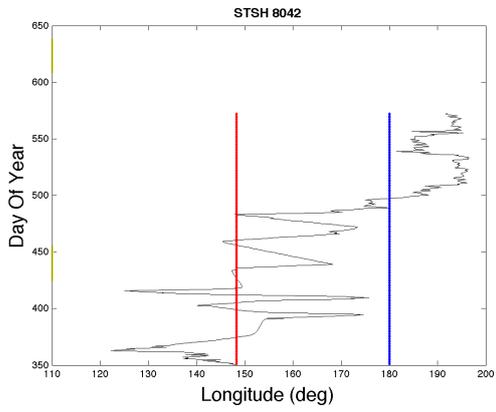
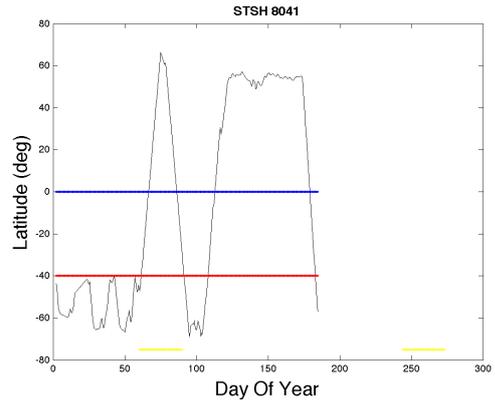
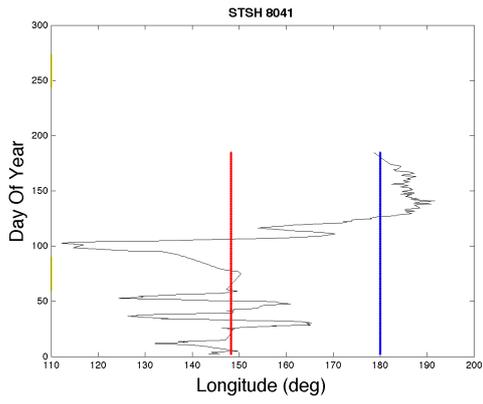
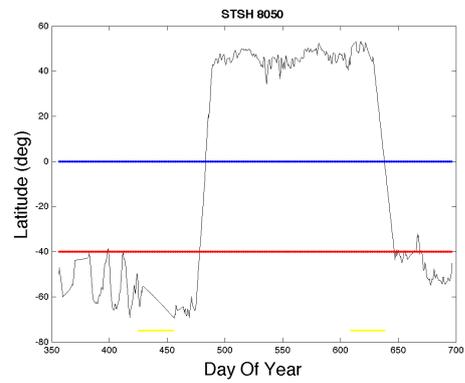
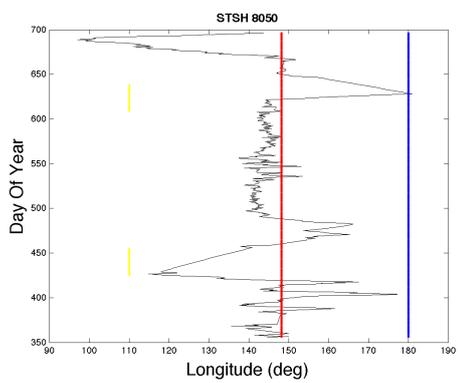
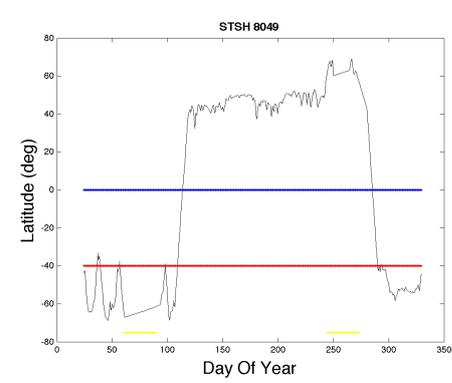
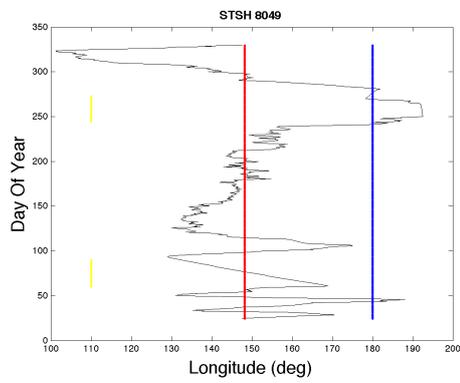
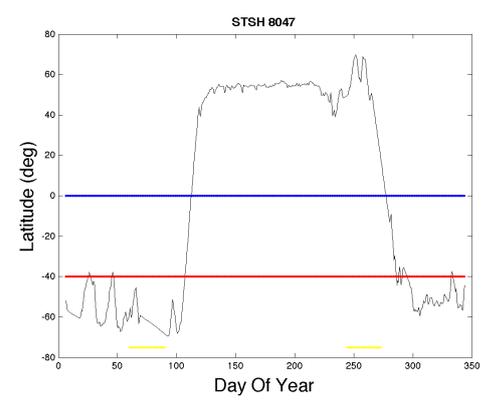
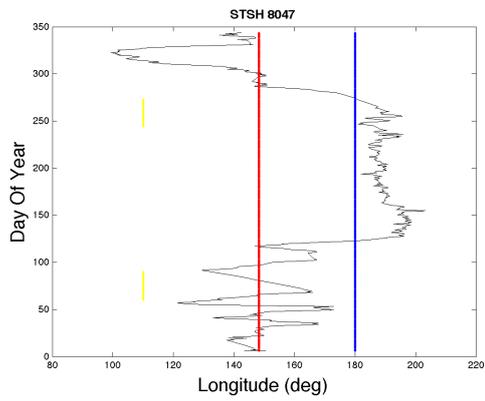
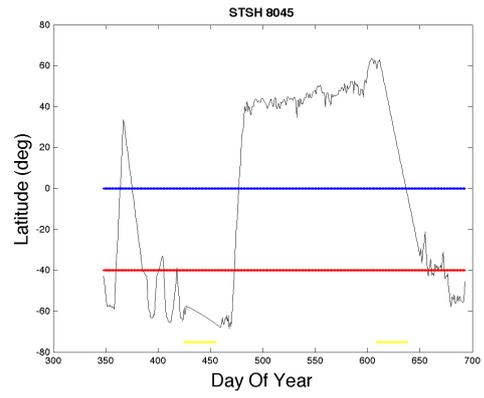
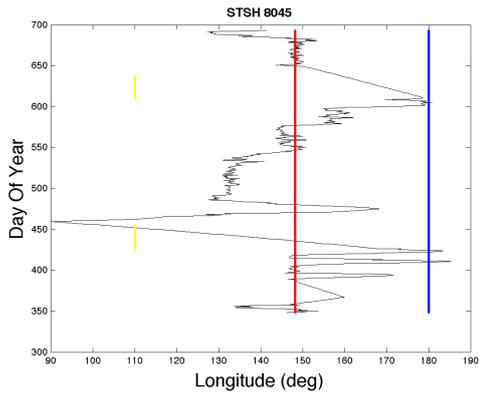
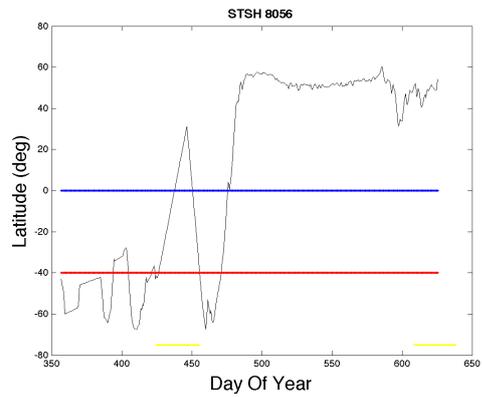
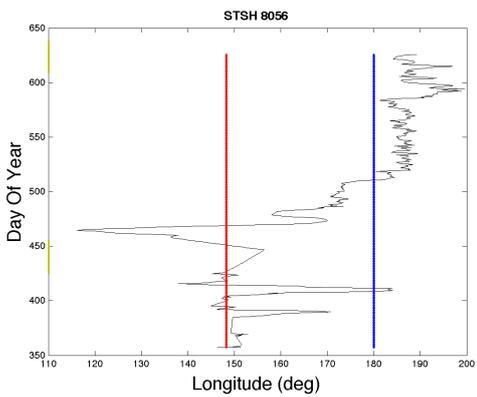
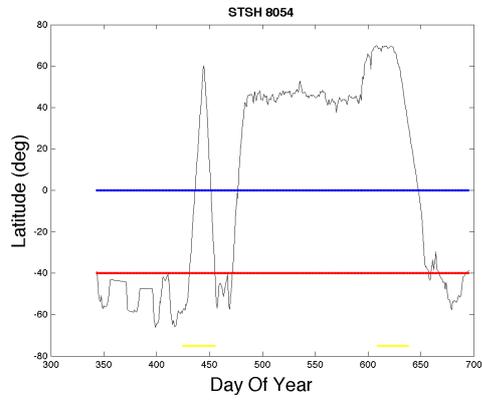
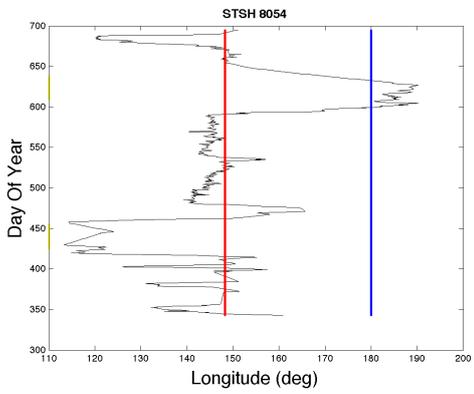
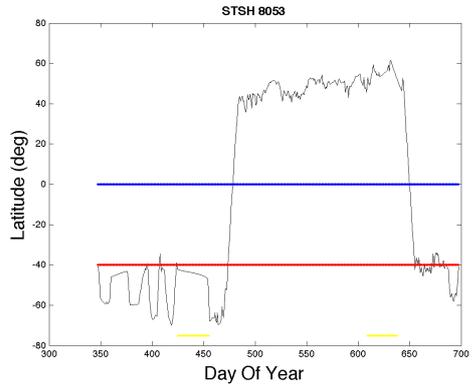
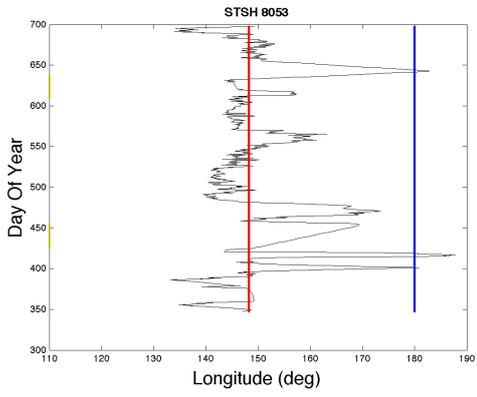
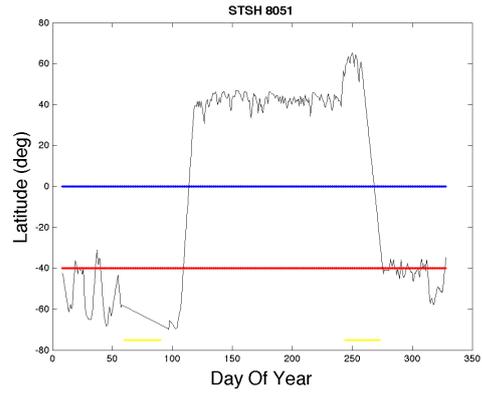
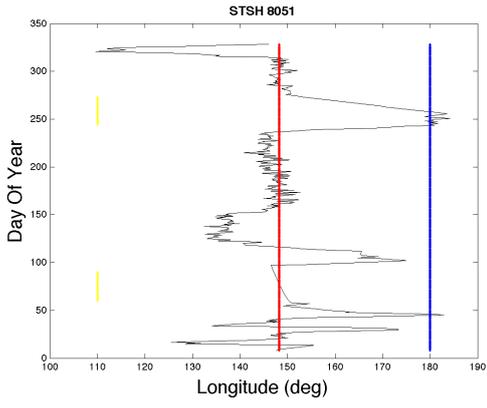
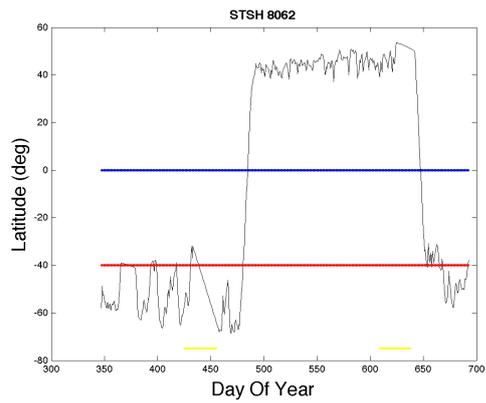
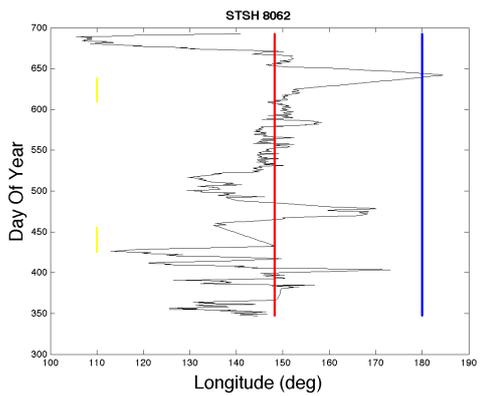
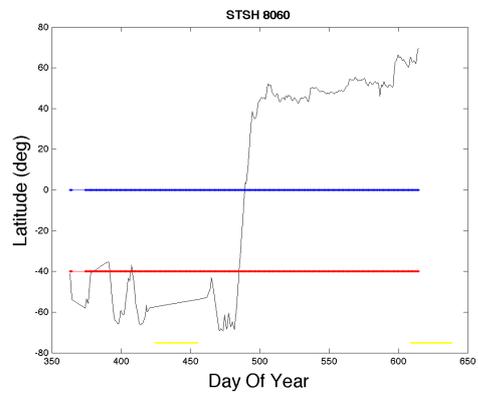
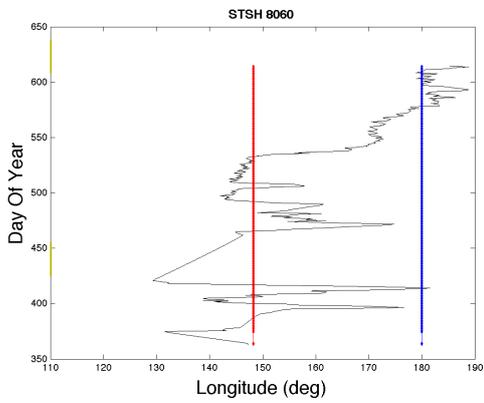
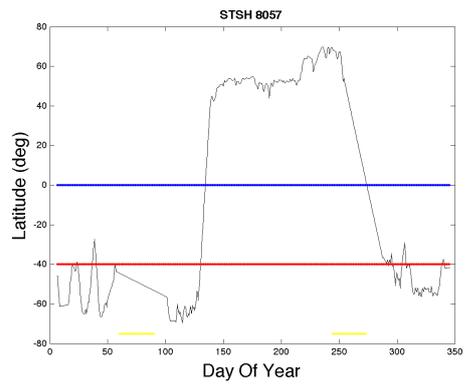
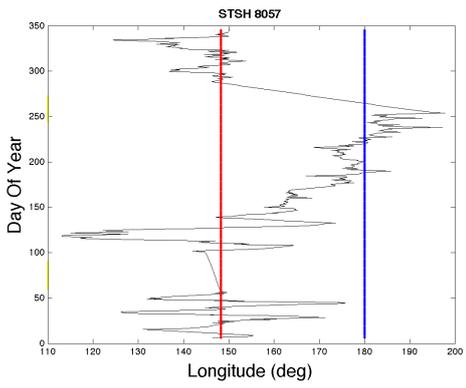


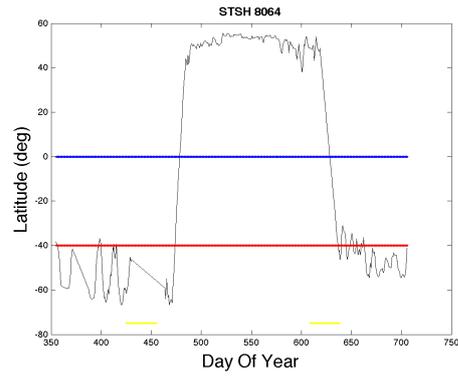
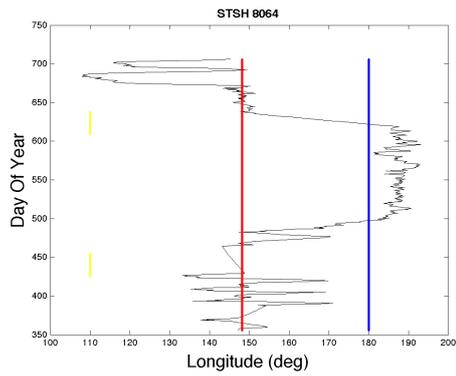
Figure 7.6 25%, 50%, 75%, and 100% utilisation distribution (UD) kernels during a) breeding period, and b) non-breeding period of Short-tailed Shearwaters.







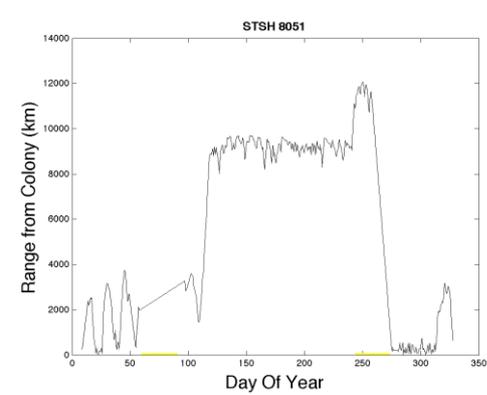
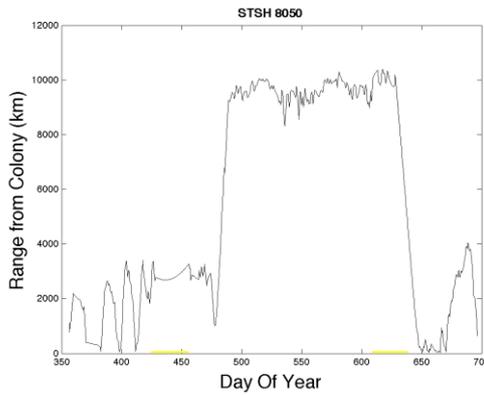
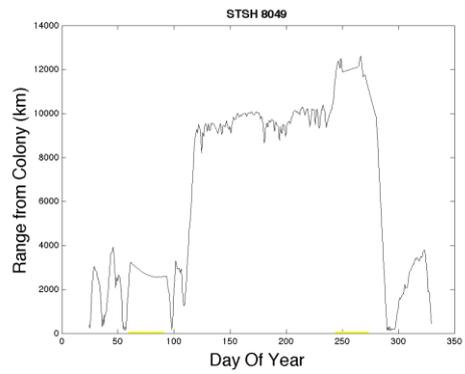
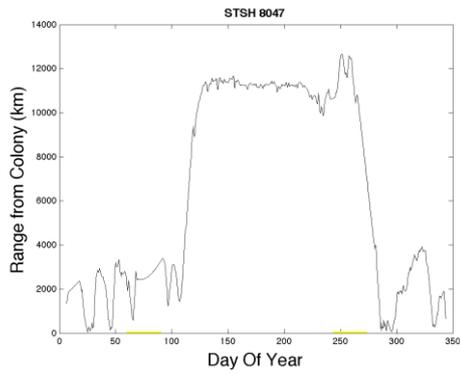
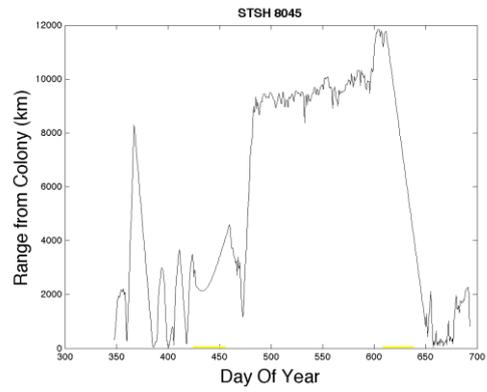
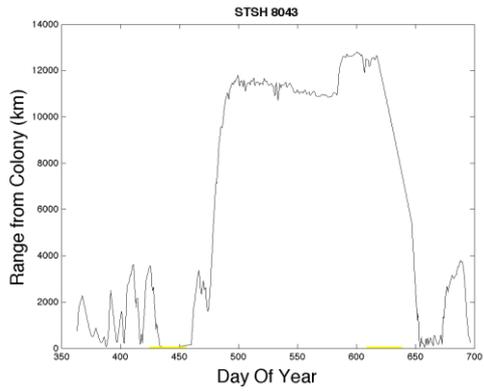
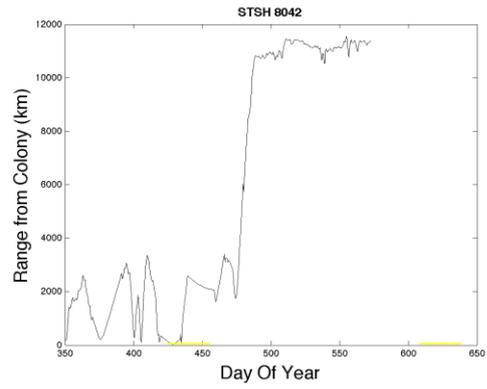
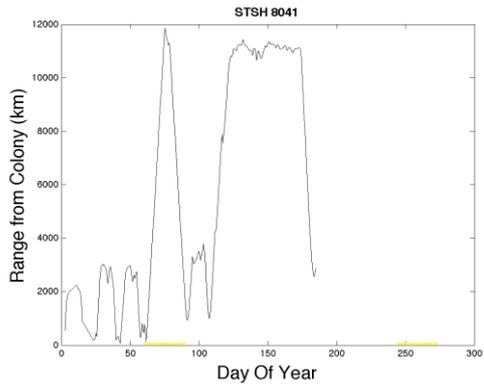




A

B

Figure 7.7 Plots showing a) Longitude vs. day of the year, which shows the changes in longitude over time. The red line denotes the longitude of the colony (148°), the blue line denotes the International Date Line (180°), and the yellow dots on the y-axis mark the equinox periods. These plots are useful (when also compared to the changes in latitude) to determine when birds come and go from the colony. When day of the year exceeds 365, the year has rolled over into the next year (2008); and b) Latitude vs. day of the year, which shows the changes in latitude over time. The red line denotes the latitude of the colony (40°), the blue line marks the equator (0°), and the yellow dots on the x-axis mark the equinox periods. Note: These plots show how latitude changes during the equinoxes.



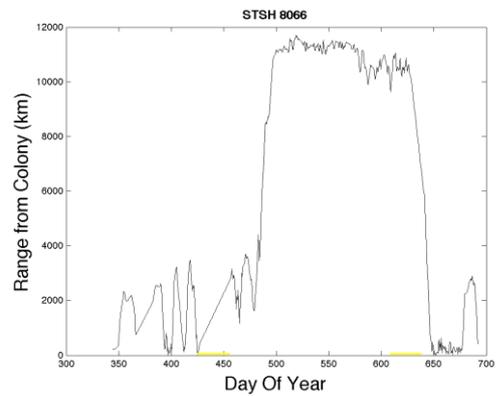
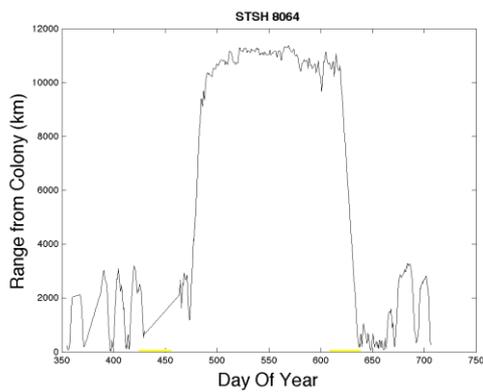
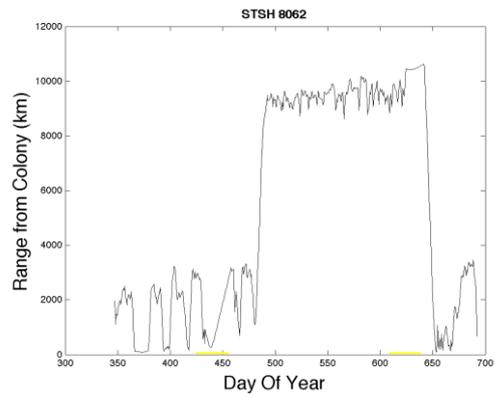
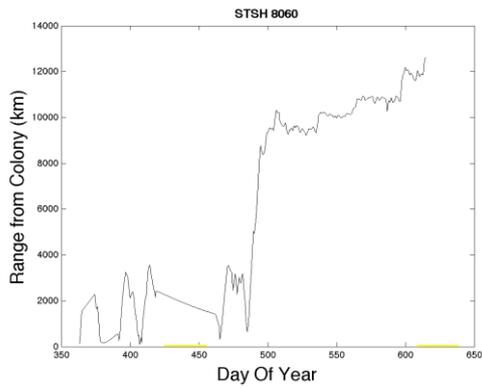
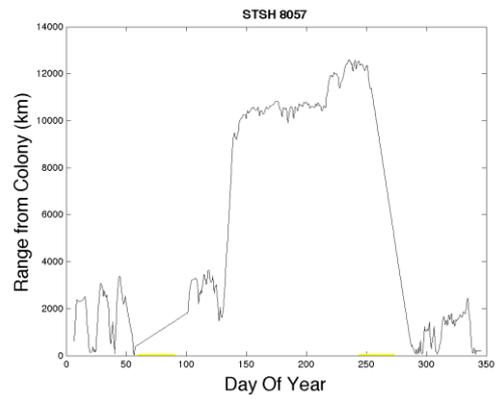
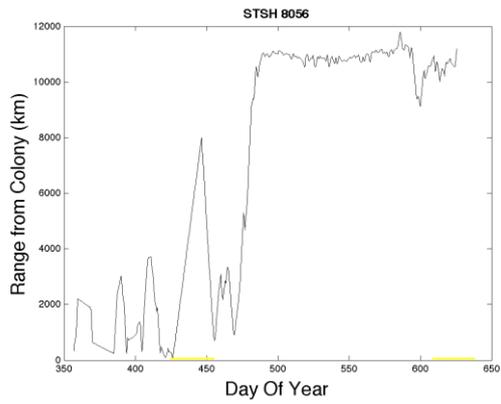
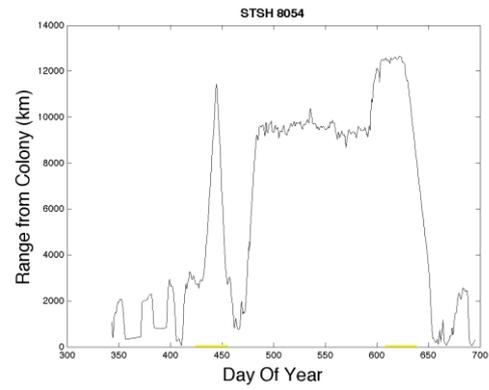
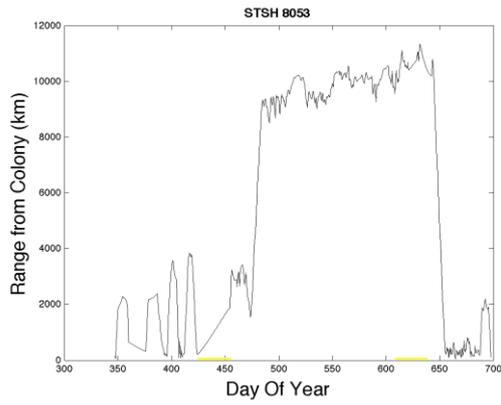


Figure 7.8 Maximum range (or distance km) from the colony in relation to day of the year, which shows the straight line distance (great circle) of each bird's position and the colony. Note: These plots are useful for determining when the birds come and go from the colony as well as the maximum range from the colony when breeding and on migration.

7.4 Discussion

7.4.1 Trans-equatorial migration

Several authors have attempted to unravel the migratory behaviour of Short-tailed Shearwaters based on band recoveries and at-sea surveys (Serventy 1953, 1956, 1967, 1961, Maruyama et al. 1986; Skira 1991), but only now have I been able to provide information about individual movements in much greater detail. Upon the completion of breeding, shearwaters travelled south to cold Antarctic waters where they engaged in intense feeding in highly productive waters to gain sufficient body condition to undertake their migration. The rapid transit north suggests that they exploit the prevailing global wind systems as do other trans-equatorial shearwaters (Shaffer et al. 2006) and Arctic terns (Egevang et al. 2010). The efficiency of shearwater flight paths is illustrated by the northward migration from the Southern Ocean to the North Pacific, covered in only 13 days. Short-tailed Shearwaters exhibited clear synchrony in timing of migration, all leaving the Southern Ocean stopover site, crossing the equator, and arriving at their wintering region within a few days of each other (Table 7.2). At-sea observations suggest that flock sizes of migrating shearwaters are large (100s – 100 000s), and results from other studies of migrant seabirds also indicate high levels of synchrony in timing of passage through oceanic flyways (Shaffer et al. 2006; Egevang et al. 2010). There was no indication that birds from the same colony travelled together in the same flocks, and no evidence to support persistent associations during migration between individuals, including members of a pair.

The tracking data reveal that Short-tailed Shearwaters spend their boreal summer in two areas in the western and central North Pacific, the first being the Oyashio and Sōya Currents off Japan and the Sea of Okhotsk and the Liman Current in the Sea of Japan, and the second being the central Aleutian Islands and the south

Bering Sea. The timing of their arrival to the wintering ground occurs in conjunction with the arrival of Sooty Shearwaters, when oceanic productivity in the North Pacific exceeds that found in the South Pacific (Shaffer et al. 2006). The North Pacific wintering grounds are highly productive waters, supporting millions of seabirds as a result of physical forcing, converging water masses, or coastal upwelling, all of which promote primary and secondary production that attract fish, squid, and krill (Gould et al. 2000; Hunt et al. 2002; Ito 2002). For the most part, individuals chose one of two wintering sites. However, some individuals that began their winter around Japan did move into the Bering Sea before the migration south. Birds that began their winter in the Bering Sea did not move across to Japanese waters. Movement between wintering sites was not observed for Sooty Shearwaters (Shaffer et al. 2006) and suggests Short-tailed Shearwaters are not restricted to either wintering regions. Movements between wintering sites allow the population to mix in the Bering Sea before returning to their breeding grounds. It is possible that some individuals exhibit wintering site fidelity, as demonstrated by an emerging number of studies on albatrosses and Streaked Shearwaters (Yamamoto et al. unpublished data).

The routes used for both the northbound and southbound migrations reveal a high level of divergence with those of Sooty Shearwaters, which also winter in the Bering Sea and waters around Japan (Shaffer et al. 2006). Despite breeding in a geographically close region (Australia and New Zealand), each species exploits a unique strategy to migrate to the Northern Hemisphere. It would appear from banding studies of Flesh-footed Shearwaters, another migratory species from the Australasian region, that they may migrate in a similar way to Short-tailed Shearwaters to the North Pacific but remain in warm waters and do not penetrate the Aleutian Islands (Serventy et al. 1971).

This study in part confirms previous assumptions about the migration routes of Short-tailed Shearwaters (Serventy 1953, 1956, 1967, 1961, Maruyama et al. 1986; Skira 1991) and identifies a previously unknown stopover site deep in the Southern Ocean before the birds continue their migration northward. Thus, the long-term changes in duration and extent of winter sea ice, and declines in abundance of Antarctic krill in this region should be viewed with considerable concern. Travelling through the western Pacific Ocean sector is a key element of these birds' migration strategy that might help buffer them from inter-annual variability in biological productivity (Shaffer et al. 2006). Increases in global temperatures and increases in the severity and frequency of El Nino Southern Oscillation events may significantly influence major ocean ecosystems. Declines in food availability or shifts in the distribution of key prey species could lead to population declines as a result of increased mortality during migration and a reduction in breeding success in the southern hemisphere. Therefore, the long-term monitoring of this species could serve as an important indicator of the impacts of global climate change and the health of the Pacific Ocean (Shaffer et al 2006).

7.4.2 Band design and recovery rate

Compared with other GLS studies of shearwaters (Table 7.1) the retrieval rate of 74% among equipped birds in this study after 12 months exceeded the retrieval rate in all studies except for those on Manx Shearwaters (Guilford et al. 2009) and Streaked Shearwaters (Yamamoto et al. 2008). In those studies, 100% and 79% respectively were recaptured with a geolocator at their breeding colony after one year. In this study, return rates between birds with and without geolocators were comparable. This has been found in similar studies (Igual et al. 2004; Takahashi et al. 2008). There are

a variety of reasons for the absence of our control and study birds in the colony, including their intermittent breeding behaviour, where 14% of each sex may skip breeding during any given year depending on environmental conditions, and a further 15% of males and 13% of females can be present but not associated with an egg in any given year (Bradley et al. 2000). Natural attrition also claims 7–11% of birds between the ages of 6 and 15 years (Bradley et al. 1989). It is also possible that I failed to find the birds at the colony or that some birds that skipped breeding the season following geolocator deployment did return to the colony but were not captured because they returned and left during the night (fieldwork was conducted only during the day, as required by our research permits). The 21st bird that was found on Great Dog Island in December 2010 demonstrates that birds can survive up to 3 years post-deployment. With continued monitoring of the study site in the coming years, even more birds could be found. This possibility is particularly exciting given that the MK14 battery lasts up to 4 years and the potential for continuous, multi-year data from individuals is likely.

The reasons behind low return rate in other studies are not clear. However, some researchers did have difficulty locating burrows in the following season (Phillips et al. 2006). The large variation between the return rates of two studies on Streaked Shearwaters may simply reflect variations in the nest-site fidelity or nesting behaviour of the species (Takahashi et al. 2008; Yamamoto et al. 2008). None of the other researchers suggested that their attachment method contributed to the low return rates, although this is a possibility. In their study, Guilford et al. (2009) modified the plastic band to fit the tarsus of Manx Shearwaters, but those researchers do not suggest that this was the reason for their 100% return rate. However, low recovery rates (30–40%) do not necessarily mean that the attachment methods were

problematic if the natural recapture rates were low (see Takahashi et al. 2008). Similarly, the high recovery rates of some studies (70–80%) do not necessarily mean that attachment methods were effective if the natural return rates were as high as that or even higher. Future studies would benefit from comparing rates of return of adults without geologgers, and not simply assessing body mass upon return. Power analyses in these types of studies are also helpful given the low sample sizes of most GLS studies. In this study, we were unable to detect a change in body mass that was less than 10%, yet for a bird that relies on distant foraging grounds this could be ecologically significant, particularly during the incubation period.

For long-term deployments of tracking devices to be successful, they require an adequate attachment method that will be durable for a sufficient amount of time for data to be collected while also being able to withstand the harsh environmental conditions that seabirds experience on land and at sea. The results of this study indicate that the use of a modified metal band to attach GLS loggers on shearwaters was an adequate solution for up to 3 years. Apart from flaking skin observed on two adults, an outcome that was also reported by Shaffer et al. (2006) in Sooty Shearwaters, this method revealed no obvious negative effects on Short-tailed Shearwaters and its use on other species of shearwater of similar size could be recommended to help minimise unwanted influences on return rates. For smaller, more sensitive, species such as gadfly petrels (*Pterodroma*) and some smaller *Puffinus* shearwaters, further investigation is needed into the effects of the attachment of geologgers on reproductive success, rates of return, chick quality, and survival. The possible physiological effects of attachment of geologgers and the associated effects of handling by researchers have also received little attention (Carey 2009; but see Navarro and González-Solís 2007; Navarro et al. 2008). This may require minor

modifications to each band to suit particular species, and extensive laboratory and field testing are therefore advisable before any deployment occurs.

Chapter 8: Effects of Data-logger Attachment on the Return Rate, Body Condition, and Reproductive Performance of Short-tailed Shearwaters

8.1 Introduction

Recent advances in bio-logging devices have greatly advanced some areas of seabird research (for a review see Burger and Shaffer 2008). In addition, recent improvements in the size and mass of devices carried by small and medium sized seabirds have given researchers greater information about foraging locations, breeding and wintering ranges (Phillips et al. 2006, 2007; Catry et al. 2009), migratory directions and pathways (Croxall et al. 2005; Guilford et al. 2008; Shaffer et al. 2006; Egevang et al. 2010), and important staging points (Guilford et al. 2009). These tracking devices have also provided important information about the lifestyles and habits of seabirds, particularly on the overlap between their foraging ranges and fisheries — matters of great concern to research scientists and conservationists (Baker et al. 2002; Phillips et al. 2006). While acknowledging these advances, researchers must also recognise that tracking devices may themselves have an effect on birds' behaviour, reproductive success, and survival (for reviews see Phillips et al. 2003 and Carey 2009).

In order to ascertain individual bird locations and activity at-sea, the use of global location sensing (GLS) devices — also known as loggers and data loggers — has increased in recent years (Croxall et al. 2005; Igual et al. 2005; Shaffer et al. 2006, 2009). These devices' low mass, ease of use, and longevity have encouraged researchers to attach them to a wide range of small and medium sized petrels and shearwaters (Procellariidae) (Rayner et al. 2008; Carey et al. 2009; Guilford et al. 2009). Yet only a few studies report the effects, such as body condition and return

rate, of attaching loggers to their study animals (Carey et al. 2009 and references therein). The added mass and increased aerodynamic drag, in addition to altering the bird's centre of gravity caused by an externally attached GLS device, can increase energy expenditure and alter normal behaviour (Navarro and González-Solís 2007; Navarro et al. 2008). Prey capture while diving could also be reduced if a bird's hydrodynamic profile is affected (Wilson et al. 1986; Ropert-Coudert et al. 2000, 2007a, b). Effects imposed on adults carrying GLS devices may translate to effects on breeding success (Adams et al. 2009). Possible effects include nest abandonment, decreased foraging ability, failure to provision offspring adequately, and failure to return to the colony (Phillips et al. 2003). To avoid such unwanted behavioural outcomes, Phillips et al. (2003) suggested that device loads for procellariiform seabirds should not exceed 3% of a bird's body mass. If a GLS device alters a bird's typical behaviour, equipped birds are clearly not representative of the species under investigation.

Despite studies on other seabirds (Wanless et al. 1988, 1989, Söhle et al. 2000; Söhle 2003; Chiaradia et al. 2005; Ropert-Coudert et al. 2010; Beaulieu et al. 2010a; Ritchie et al. 2010), studies investigating the effects of attaching GLS data loggers to small and medium sized seabirds are lacking (Carey 2009; but see Adams et al. 2009). In this study, the effects of attaching GLS devices to Short-tailed Shearwaters (*Puffinus tenuirostris*) are investigated and compared with an un-equipped control group. Specifically, the birds' hatching and fledgling success in the year of attachment were monitored, along with pre-fledging chick size (skeletal measurements) and chick mass. The size and mass of a pair's offspring was monitored as an indirect indicator of foraging performance. In the following year, return rates, body condition, and reproductive success of returning adults were

recorded in order to determine any long-term effects of GLS attachment. If GLS devices were having a detrimental effect on Short-tailed Shearwaters it was hypothesised that attaching them to birds would produce a reduction in their body condition, reproductive success and return rates.

8.2 Methods

8.2.1 Field procedures

Data were collected over two breeding seasons during November to March in 2007/08 and again in 2008/09 on Great Dog Island. In 2007/08, 80 breeding birds were weighed with Pesola 1000 (± 10) g scales and measured with Vernier callipers to ± 0.02 mm during the incubation period (Chapter 2). Adults were banded with an Australian Bird and Bat Banding Scheme (ABBBS) band at this time if they had not been banded in a previous study (Meathrel and Carey 2007). All burrows were marked with a polyvinylchloride pole and a unique number was assigned for the duration of the project.

In 2007/08 GLS devices were deployed on 27 birds (13 pairs and one individual of another pair: 13 males and 14 females), and 53 birds were randomly selected as controls (26 pairs and one individual of another pair; 26 males and 27 females). GLS devices (MK13, British Antarctic Survey, Cambridge, UK) were embedded in transparent resin, which measured $20 \times 8.5 \times 6.5$ mm and weighed 1.8 g. The GLS device plus the band used to attach it to the bird represents about 5.4 g of extra mass, which is 0.7 - 1 % of the mass of an average adult Short-tailed Shearwater (Chapter 7; Carey et al. 2009). The devices were mounted on modified aluminium bands using UV resistant cable ties that could be placed on a bird's leg (Chapter 7; Carey et al. 2009). Hatching, fledging, and overall breeding success (i.e., chicks

fledged from eggs laid) were recorded in manipulated (i.e., GLS equipped birds) and control burrows (i.e., adults with only the ABBBS band) in the year of GLS attachment. Chicks were measured and banded following the same procedure described for adults before fledging. During the following breeding season (2008/09) burrows were monitored during egg laying until all breeders were identified. Adults that returned were recaptured at the nest during the incubation period. Once captured, the birds were weighed, and if a GLS device was present it was removed. Eggs were measured as described in Chapter 2 and egg volume was calculated using the equation $v = 0.51 lb^2$ (Hoyt 1979), where l = length and b = breadth. Burrows were inspected again in January and March 2009 to ascertain survival, hatching, and pre-fledging size.

8.2.2 Statistical analyses

All tests were performed with SPSS version 17.0 (SPSS Inc., Chicago, IL, December 2008). Differences between measurements of equipped and non-equipped male and female adults were tested with Student's t -tests. A sequential Bonferroni adjustment was used as multiple measures of the same individual were made, resulting in a critical $P = 0.008$ (see Sokal and Rohlf 1995). For all other tests the significance was set to $P < 0.05$. Principal components analysis (PCA) was used to characterise variability in body dimensions within the total sample. As in studies reported in the third and fourth chapters the first principal component (PC1) comprised head length, bill length, bill depth, wing length, and tarsus length, and was used as a single composite measure of body size. Return rates and breeding success of equipped and control birds were compared using χ^2 tests. Effects on body condition of individuals in the year of recapture were investigated by combining the five morphometric

measures in a body size index (PC1) in a PCA. An ANCOVA model was then used with body mass as the dependent variable, body size index (PC1) as a covariate, and sex and presence of GLS device as fixed factors. All data are presented as means \pm standard deviation (s.d.).

8.3 Results

8.3.1 Morphometrics

The body masses of equipped versus non-equipped male and female birds were statistically different at the time of deployment of GLS devices, and remained significant after Bonferroni adjustment (Table 8.1). Non-equipped males were heavier than equipped males (non-equipped males 623.84 ± 46.7 , equipped males 566.15 ± 56.9 , $t_{37} = 3.37$, $P = 0.002$), while equipped females were heavier than non-equipped females (equipped females 651.42 ± 41.6 , non-equipped females 592.22 ± 72.0 , $t_{39} = 2.83$, $P = 0.007$). There were no significant differences between equipped and non-equipped males and females on the five skeletal measurements or PC1 scores (Table 8.1).

Table 8.1 Differences in mass and body measurements of GLS equipped and non-equipped Short-tailed Shearwaters. Data presented are mean \pm s.d., and sample sizes are shown in parentheses.

	Males				Females			
	GLS equipped (13)	Non-equipped (26)	t_{37}	P	GLS equipped (14)	Non-equipped (27)	t_{39}	P
Mass (g)	566.15 \pm 56.9	623.84 \pm 46.7	3.37	0.002	651.42 \pm 41.6	592.22 \pm 72.1	2.83	0.007
Head length (mm)	82.44 \pm 1.9	83.03 \pm 2.4	0.76	0.45	80.46 \pm 1.5	81.69 \pm 2.2	1.85	0.07
Bill length (mm)	32.66 \pm 1.2	32.80 \pm 1.3	0.29	0.77	31.37 \pm 1.0	31.66 \pm 1.3	0.72	0.47
Bill depth (mm)	9.06 \pm 0.2	8.88 \pm 0.3	1.64	0.11	8.30 \pm 0.4	8.25 \pm 0.3	0.49	0.63
Wing length (mm)	273.31 \pm 5.1	272.53 \pm 6.6	0.36	0.71	264.42 \pm 22.6	268.96 \pm 6.4	0.98	0.33
Tarsus length (mm)	59.64 \pm 1.6	59.43 \pm 1.4	0.40	0.69	58.86 \pm 1.5	58.21 \pm 1.3	1.38	0.17
PC1 score	0.61 \pm 0.8	0.58 \pm 0.8	0.10	0.91	-0.67 \pm 0.7	-0.52 \pm 0.8	0.56	0.57

8.3.2 Reproductive success in the year of deployment

Hatching success in 2007/08 was slightly higher in the burrows of equipped birds than in burrows of non-equipped birds, although these differences were not statistically significant (Table 8.2, equipped 78.6 %, $n = 14$; non-equipped 63.0 %, $n = 27$, $\chi^2 = 1.04$, $d.f. = 1$, $P = 0.31$). Survival of all chicks was high until pre-fledging, and at that time no difference was detected between chicks that had been raised by adults carrying GLS devices and those that had not (equipped 81.8 %, $n = 11$; non-equipped 88.2 %, $n = 17$; $\chi^2 = 0.22$, $d.f. = 1$, $P = 0.64$).

There was no significant difference in mean mass of pre-fledged chicks raised by adults carrying GLS devices (577.7 ± 101.2 g, $n = 9$) and chicks raised by adults without GLS devices (522.0 ± 140.3 g, $n = 15$; $t_{22} = 1.04$, $P = 0.31$). Chicks reared by non-equipped adults tended to be larger in skeletal measurements, but these differences became non-significant after Bonferroni adjustment (Table 8.3). PC1 accounted for 55 % ($\lambda = 2.77$) of the total variance explained by the components, and four of the five skeletal variables loaded heavily and positively (> 0.70) on this PC; the exception was bill depth, with a loading of -0.27 . There was a significant difference in PC1 scores between chicks reared by GLS equipped and non-equipped adults (equipped -0.66 ± 0.8 , $n = 9$; non-equipped 0.40 ± 0.8 , $n = 15$, $t_{22} = 2.91$, $P = 0.008$) indicating that chicks raised by non-equipped adults were, overall, skeletally larger.

Table 8.2 Hatching and fledging success of adults that were GLS equipped and non-equipped.

Group	Hatching success		Fledging success		Overall reproductive success	
	2007/08	2008/09	2007/08	2008/09	2007/08	2008/09
Non-equipped	63.6%	75%	88.2%	100%	55.5%	75%
GLS equipped	78.6%	75%	81.8%	100%	64.2%	75%

Table 8.3 Differences in body measurements between pre-fledging chicks reared by GLS equipped and non-equipped parents. Data presented are means \pm s.d.

	GLS equipped (<i>n</i> = 9)	Non-equipped (<i>n</i> = 15)	<i>t</i> ₂₂	<i>P</i>
Mass (g)	577.77 \pm 101.2	522.0 \pm 140.3	1.03	0.31
Head length (mm)	75.2 \pm 2.5	77.2 \pm 2.2	2.03	0.05
Bill length (mm)	29.5 \pm 1.6	31.2 \pm 1.6	2.39	0.02
Bill depth (mm)	7.8 \pm 0.5	7.5 \pm 0.3	1.59	0.12
Wing length (mm)	115.6 \pm 18.6	130.6 \pm 14.7	2.17	0.04
Tarsus length (mm)	56.2 \pm 1.4	57.8 \pm 1.9	2.07	0.05
PC1 score	-0.66 \pm 0.8	0.40 \pm 0.8	2.91	0.008

8.3.3 Recapture rate

In 2008/09, the recapture rate was 53.7 % (43 of the 80 birds that had been banded were recaptured; Table 8.4). The return rate was higher for GLS equipped than for non-equipped birds, and this difference was significant (equipped = 74.1%, $n = 27$; non- equipped = 43.4%, $n = 53$, $\chi^2 = 6.77$, $d.f. = 1$, $P < 0.01$).

Table 8.4 Return rates of male and female Short-tailed Shearwaters non-equipped and equipped with GLS devices.

	Non-equipped		GLS Equipped		χ^2	P
	Percent (%)	n	Percent (%)	n		
Males	53.8%	14	76.9%	10	1.95	0.16
Females	33.3%	9	71.4%	10	5.38	0.02
Total	43.4%	23	74.1%	20	6.77	<0.01

There was no significant difference between the return rates of GLS equipped males and non-equipped male birds (Table 8.4). GLS equipped females, however, returned at a significantly higher rate than did non-equipped females (equipped = 71.4%, $n = 14$; non-equipped females 33.3%, $n = 27$, $\chi^2 = 5.38$, $d.f. = 1$, $P = 0.02$). The recapture rate within the non-equipped group was 43.4%, and although the recapture rate was slightly higher for males than for females, the difference was not statistically significant (non-equipped males 53.8%, $n = 26$; non-equipped females 33.3%, $n = 27$, $\chi^2 = 2.26$, $d.f. = 1$, $P = 0.13$). Recapture rates within GLS equipped birds was 74.1% and there was no difference in recapture rates between male and

female birds within the GLS equipped group (equipped males 76.9%, $n = 13$; equipped females 71.4%, $n = 14$, $\chi^2 = 0.10$, $d.f. = 1$, $P = 0.74$).

8.3.4 Adult body condition

After controlling for body size, no significant effect of GLS attachment on body mass of returning individuals could be detected (Table 8.5). Neither was there an interaction between GLS attachment and sex (Table 8.5). Upon return to the colony, non-equipped birds had slightly greater mean body mass than did those that were GLS equipped (663.4 ± 51.2 g, $n = 23$; 652.0 ± 60.6 g, $n = 20$ respectively).

Table 8.5 Results of the two-way ANCOVA performed for exploring effects of sex and geolocators (Geo) on body condition of Short-tailed Shearwaters (*PCI* principal component 1).

	$F_{(1, 42)}$	P
Size index (PC1)	2.8	0.10
Sex	0.04	0.84
Geo	0.13	0.72
Sex \times Geo	0.11	0.74

8.3.5 Egg size and reproductive success in the year of retrieval

Egg size in the year of recapture did not differ between groups on any dimension that was assessed (Table 8.6). Hatching success for equipped and non-equipped pairs was high in the 2008/09 season (75.0% for both groups), and all chicks survived until pre-fledging (Table 8.2). There was no significant difference in body mass between chicks raised by GLS equipped adults versus chicks reared by non-equipped adults

(mean body mass in equipped reared chicks 488.3 ± 121.3 g, $n = 6$; mean body mass in non-equipped reared chicks 510.0 ± 98.3 g, $n = 6$, $t_{10} = 0.34$, $P = 0.7$). There were no differences between GLS equipped and non-equipped reared chicks on any of the five skeletal measurements (all $t_{10} < 1.24$, $P > 0.24$). PC1 accounted for 49% ($\lambda = 2.44$) of the total variance explained by the components, and three of the five skeletal variables loaded heavily and positively (> 0.81) on this PC; exceptions were bill length with a loading of -0.36 and bill depth with a loading of -0.24 . There was no significant difference in PC1 scores between chicks reared by GLS equipped and non-equipped adults (equipped -0.13 ± 1.15 , $n = 6$; non-equipped 0.13 ± 0.90 , $n = 6$, $t_{10} = 0.44$, $P = 0.65$).

Table 8. 6 Mean egg measurements for pairs that were GLS equipped and those non-equipped in the 2008/09 season. Data presented are means \pm s.d.

	GLS equipped ($n = 8$)	Non-equipped ($n = 8$)	t_{14}	P
Egg mass (g)	88.1 ± 10.3	87.5 ± 6.1	0.14	0.8
Egg length (mm)	69.8 ± 2.4	69.5 ± 1.7	0.33	0.7
Maximum egg breadth (mm)	47.0 ± 1.9	47.0 ± 0.9	0.11	0.9
Egg volume (cm ³)	79.2 ± 8.9	78.5 ± 4.4	0.18	0.8

8.4 Discussion

For procellariiform seabirds, Phillips et al. (2003) recommended that a maximum mass for attached devices should be less than 3% of an individual's body mass.

However, studies have found that even lightweight devices 0.7-3.0% of body mass have been associated with a reduction of body mass, attendance of offspring,

provisioning rates, and frequency of foraging trips (Wanless et al. 1988; Ackerman et al. 2004; Adams et al. 2009). Identifying any effects is imperative for animal welfare but also for the accuracy of tracking data and subsequent interpretation (Phillips et al. 2003). The present study has demonstrated that attaching GLS devices to Short-tailed Shearwaters does not profoundly affect the birds' body condition, return rate or reproductive success. This finding supports Phillips et al.'s (2003) suggestion and implies that the GLS attachment did not impair the foraging, prey capture, or flying ability of the adult birds and that they were behaving 'normally'.

Any differences in hatching and fledging success between equipped and non-equipped adults were not significant. In fact, in the 2007/08 year of attachment, adults that were equipped with GLS devices had a higher hatching and overall reproductive success than did adults that were not equipped. Furthermore, adults carrying a GLS device reared chicks that were 9.6% heavier than were chicks of adults that were not equipped with a GLS device. The differences observed between the chicks' PC1 scores seem to contradict the equal body mass between the two groups for reasons that are unclear but the difference in offspring skeletal size raises an interesting observation and is a possible avenue for further research. Small differences between the two groups may reflect differences in parental effort and foraging behaviour. These results contrast with those of a recent study by Adams et al. (2009) in which there was a 35% reduction in chick body mass for Sooty Shearwater (*P. griseus*) chicks that were reared by adults carrying GLS devices. These researchers also found that the effects on chicks were more apparent when both parents carried a GLS device.

Recapture rates of returned adults after 12 months showed that the extra mass and attachment location did not affect the birds negatively. The significantly higher

rate of return recorded for adults that had GLS devices attached in this study was unexpected given the results of similar studies (Iguar et al. 2005; Phillips et al. 2006; Takahashi et al. 2008). To assess effects of loggers on return rates accurately, a comparison of equipped and control (unequipped) birds from the same population, breeding area, and year seems to be required for each GLS study. This slight modification to the research design would not be difficult to implement and the addition of extra birds could be used to quantify the impacts of handling by investigators (Chapter 4). This would be particularly relevant when naïve birds are used in future GLS studies.

This study also did not indicate the presence of any sex-specific effects of attaching GLS devices on return rates and body condition. Attachment of GLS devices on Short-tailed Shearwaters may have impacted on the adult birds' body condition, but any changes may have been only short-term and not detected due to the methods employed in this study. Despite a small reduction in body mass, the mean body mass of returning GLS adults was 1.7% lower than that of non-equipped adults. This small difference is unlikely to be ecologically significant given that the natural variation in an individual's body mass can be as high as 20-30% (Lill and Baldwin 1983; Chapter 6). In a similar GLS tracking study, Iguar et al. (2005) found a significant (1.6%) reduction in body mass (after controlling for body size) in equipped Cory's Shearwaters (*Calonectris diomedea*); these researchers also found that there was a 6-20% greater return rate among the non-equipped adults, but this was not statistically significant. After trans-equatorial migration, only 56% of GLS equipped Sooty Shearwaters returned to their breeding grounds in New Zealand, and these birds had a 4% mass reduction compared to non-equipped adults, but these differences were not significant (Adams et al. 2009). In Sooty Shearwaters, body mass of adults

carrying imitation satellite tags was reduced by 8.3% at recapture before breeding, but this resulted in no effects on chick condition or colony attendance (Söhle 2003).

In the current study, adults' return rate and body condition indicated that they did not incur any deleterious effects by carrying GLS devices throughout their post-breeding and trans-equatorial migration. Furthermore, there were no differences in egg size between the two groups, indicating that females were able to provision themselves adequately and produce an egg during the pre-laying exodus. Once GLS devices were removed from adult birds no carry-over effects of GLS attached were detected. During the period of this study no detectable differences were observed in the reproductive success of birds that returned to the colony, as hatching and fledging success did not differ between the two comparison groups. These results suggest that appropriately sized data-loggers are a relatively benign method of obtaining at-sea foraging and behavioural information from seabirds. Subsequent research might reveal whether these results are consistent across different years, colonies, and age of birds and their breeding experience. GLS devices are rapidly becoming smaller and lighter, and if this trend continues the potential for long-term negative effects will decrease. Nevertheless, monitoring individuals and assessing their health and reproductive output should be considered an integral part of all future GLS studies.

Chapter 9: Summary of Major Findings and Directions for Future Research

9.1 Summary of major findings

The main aims of this study were to investigate the effects of investigator disturbance on Short-tailed Shearwaters (*Puffinus tenuirostris*) and to quantify the effect of investigator disturbance on these birds' reproductive success. The major findings of the research are outlined below.

The ability to accurately determine the sex of Short-tailed Shearwaters was an important component of this study. Short-tailed Shearwaters exhibit no sex-linked plumage dimorphism (Marchant and Higgins 1990), and therefore identification of the sex of birds in the field outside the egg laying period is difficult. However, knowledge of the gender was essential to answer many of the questions in this study. A discriminant function analysis based on several external morphometric measurements was assessed for its utility in sexing Short-tailed Shearwaters. This analysis predicted the sex of adults with a high degree of accuracy — about 84% — based on two measurements: bill depth and head length. Within pairs, gender could be assigned 92% of the time based on a single measurement, bill depth, with males having a deeper bill. Despite several other studies on Short-tailed Shearwaters (Bradley and Meathrel 2006; Einoder et al. 2008), this study did not reveal any assortative mating within pairs, which suggests that they mate randomly based on morphological traits. Reducing the handling time a researcher needs to determine sex is desirable as it may decrease the stress that birds experience when handled.

The frequency of handling during the incubation period was used to quantify the effects of investigator disturbance on the length of incubation, hatching success, chick survival, and chick body size and mass. I was able to demonstrate that

excessive handling (i.e., daily and every three days) did have a significant effect on hatching success. Even handling incubating birds weekly reduced the hatching success of Short-tailed Shearwaters compared to the control group, albeit not significantly. This study highlights the vulnerability of naive birds to intensive scientific investigations. This study also highlights the sensitivity of Short-tailed Shearwaters, and perhaps shearwaters and petrels in general, to research procedures. Once the investigator disturbance ceased, at the end of the incubation period, its effects were still evident towards the end of the chick fledgling period with a significant difference observed in chick body mass and size among birds where handling had occurred. Reasons for this observation are unclear. However, one possibility is that handling adults during the incubation period increased levels of the stress hormones such as corticosterone (Buttemer et al. 1991; Astheimer et al. 1992). An increase in circulating corticosterone levels may direct behaviour away from reproduction and towards self-maintenance such as feeding. Stress hormones were not measured in this study but raise an avenue for further research. Stress hormones in relation to investigator disturbance have not been extensively studied across seabird taxa and any future research would provide valuable knowledge. It would be interesting and beneficial to repeat the handling experiment between naive and habituated shearwaters to understand individual birds' responses to handling. It may be the case that birds that had been subject to long-term studies react less negatively to handling than to birds that had not previously been disturbed. Consequently, it is worth asking whether long-term studies really represent a bird's natural behaviour or whether researchers are observing biased (i.e., habituated) behaviour. Further research is obviously required, and it would also be interesting to assess the stress

hormone levels of birds that are the subject of long-term studies and those that are truly 'naive'.

The long-term effects of handling incubating Short-tailed Shearwaters were equally detrimental as the short-term effects. One year after the initial handling experiment, I observed a significant reduction in the return rate of birds. Handling birds also increased divorce rates between pairs, and a number of birds moved away from burrows that they had used in the previous year. Unfortunately, determining the effects on reproductive success of birds that did return to the colony was difficult in the present research because of the low sample size and conclusions need to be drawn with caution. In any case, the birds that did not return to the colony were unlikely to have bred elsewhere because Short-tailed Shearwater, like most procellariids, are extremely site faithful (Bradley et al. 1991). Rarely have individuals been observed breeding to two different locations (Serventy 1967; Serventy and Curry 1984; Wooller et al. 1989). The extent to which these birds were affected in the long-term was not anticipated at the start of this study and it highlights the long-lasting outcomes that researchers can have on some populations. Results from the short- and long-term experiments of handling demonstrate that researchers studying long-lived seabirds should be aware of the effect that their presence can have on reproduction. This is particularly relevant when studying naive birds that have not previously experienced investigator contact.

Determining a species incubation routine and body mass regulation is an important aspect in a pelagic seabirds' biology, yet we know very little about the majority of the Procellariiformes. One reason for this is inevitably the intense nature of these studies because researchers are required to have regular contact with birds. A number of researchers who have investigated incubation routine and body mass

regulation have reported that a number of birds abandon early into the incubation period, possibly as a result of excessive handling (Johnstone and Davis 1990; Chaurand and Weimerskirch 1994). In this study, results from a less intensely handled group of birds demonstrated that accurate data can be obtained once knowledge of a species' tolerance to handling can be determine before an investigation begins. In this study, individuals that were handled minimally throughout the incubation period had lower hatching success than did control birds, but there were no differences in chick survival, mass, or skeletal size. Recapture rates after 12 months were similar for both experimental and control groups, and no long-term effects were seen in the subsequent breeding season. The difference in hatching success could have been influenced by the heavy rain experienced on Great Dog Island during early incubation which led to wet, flooded burrows across the colony (M. Carey pers. obs.). It is difficult to determine the effects of the rain on the control burrows because those burrows were not monitored intensely (to avoid disturbance). Equally, it is difficult to disentangle the effects of rain versus the handling regime in the experimental burrows. Knowing which variable led to the failure of some burrows, or the relative importance of different variables, are missing elements in this research. Data presented for the incubation routine and body mass regulation are interesting and raise a number of new questions regarding the evolution of shared parental investment and egg neglect in procellariid seabirds.

The growing interest in at-sea behaviour of seabirds provided an excellent opportunity to investigate the effects of attaching devices to seabirds, particularly small to medium sized seabirds. Attachment method is crucial to the success or failure of any tracking project. However, such things as the design of the attachment and length of deployment are important considerations. An animal's welfare is

fundamental in any research program, but a researcher also needs to be confident that data collected by the bird is accurately depicting a birds' natural behaviour. The design of the new attachment method of global location sensing (GLS) loggers was particularly important in this study. Previous studies had used a round band, or slightly modified Darvic band, to attach GLS devices (Phillips et al. 2006; Shaffter et al. 2006; Takahashi et al. 2008; Yamamoto et al. 2008; Guilford et al. 2009). The shape of these bands could have had undesirable effects on the equipped bird's behaviour or caused injury to the laterally compressed tarsus. The new method designed in this research takes into account the laterally compressed tarsus of shearwaters to aid in reducing both the aerodynamic and hydrodynamic of the birds' profile. The new design, based on the size 16 shearwater band (ABBBS), is also light, keeping well within the recommendations of Phillips et al. (2003). This new attachment method appears to be satisfactory for the long-term deployment of GLS devices given that it produced no obvious negative effects. The new design could be used on similar sized birds in order to reduce unwanted outcomes and maximise return rates. This may require only minor modifications to each band to suit each particular species, along with extensive laboratory and field testing before any deployment.

As a consequence of the new banding method, I was able to obtain the first tracks of the trans-equatorial migration of Short-tailed Shearwaters. The migratory movements of small and medium sized seabirds remain largely unknown, despite their status as top marine predators and indicators of marine health. Tracks revealed that after breeding, shearwaters fly south to a previously unknown stopover site below the Antarctic convergence and west of the Ross Sea. They remain in this area for approximately 26 days before flying rapidly north through the western Pacific Ocean.

At around 30°N they diverged in their flight paths, with some birds flying to waters around Japan and others continued north to the Bering Sea. Transit times on both northward migration paths were approximately 13 days. The birds then spent the bulk of the boreal summer north of Hokkaido, Japan, or in the south-central Bering Sea before returning south through the central Pacific Ocean to their breeding grounds.

These results show, for the first time, the complete migration of these long-lived seabirds and reveal individual variation in their wintering distribution. The results of this study also, in part, confirm previous assumptions about this species (Marshall and Serventy 1956; Serventy 1957, 1961, 1967) as well as present new knowledge of their movements in the Pacific Ocean. Combined with other similar studies, the data revealed important pelagic hotspots for marine seabirds, migration bottlenecks, and potential conflicts with industrial fisheries (González-Solís *in prep*; Appendix 1 – Conference Abstract). Knowledge of these areas is fundamental for identifying marine protected areas (MPA) and therefore is important in the conservation and management of seabirds on a global scale.

To ensure that tracked birds were acting ‘normally’ despite attachment of the GLS devices, equipped and non-equipped birds were monitored in the year of deployment and in the year post recovery of the GLS devices. The birds’ body condition and reproductive success were monitored to gauge how well they performed throughout the breeding and non-breeding stages. Results indicated that in the short-term there were no consequences in terms of adult body condition, hatching success, chick survival, or chick body mass resulting from the attachment of a GLS device. For equipped birds, however, there was a significant difference in chick skeletal size, in that chicks raised by those adults were smaller. Despite being skeletally smaller, chicks of equipped birds were, on average, 50 g heavier than chicks raised by non-

equipped adults. In the following year, almost 12 months after deployment, there was a significant difference in the recapture rate of these birds. It was expected that if the GLS devices were having a detrimental effect on a bird, equipped adults would return in fewer numbers. In fact, the opposite was true: Equipped adults returned in significantly higher numbers than did non-equipped adults. No differences were observed between body conditions of the returned adults. The reproductive success of adults that were equipped was equal to that of non-equipped adults indicating that, after retrieval of the GLS devices, no further consequences could be detected. The results of this research suggest that the data obtained in the tracking study are accurate, and that birds were acting ‘normally’ and did not alter their behaviour in any way. The fact that some size differences between chicks occurred in the year of deployment may reflect an age difference among chicks, age and experience of the parents, or sample size effects.

9.2 Implication of the research

The results of this research clearly demonstrate that Short-tailed Shearwaters can be negatively affected by research procedures, particularly handling. This validates the observations made by Serventy and Curry (1984) where excessive handling and nightwork reduced the population of Short-tailed Shearwaters on Fisher Island. The present research also explains the behaviour of Northern Fulmars (*Fulmarlis glacialis*) in the North Atlantic (Ollason and Dunnet 1980) and confirms the results on Blackmer et al. (2004). The degree of which individuals are affected by handling depends on its frequency. The severity of the impact can be long-lasting and has the potential to interrupt breeding behaviour and an individual’s lifetime reproductive

success. Observations from other colonial nesting seabirds are in accord with this conclusion (Table 9.1). Results from the handling experiment suggest that Short-tailed Shearwaters are particularly sensitive to investigator disturbance. It is clear that handling birds excessively is an unacceptable practice and that researchers need to be aware of this when planning their research programs. Studies that require regular handling of adults during the incubation stage should be kept to a minimum, and strict guidelines should be enforced where intense studies are conducted on small populations or threatened species unless the researchers can demonstrate that handling their subjects will not have any negative consequences — either short- or long-term.

Handling birds, their eggs, and their young is often essential for behavioural and ecological studies. This necessitates researchers capturing birds at the nest, in the burrow, in the air, and at sea for many reasons including banding, sexing, obtaining morphometrics, and taking blood. Possible ways to limit the impact of such work include reducing both the number of times a bird is handled throughout the breeding season and the amount of time taken on each occasion. Marks and Leasure (1992) have suggested that the interference to a burrow entrance and its internal structure caused by reaching into the burrow to check its contents may be perceived by the incubating adult as a signal that the burrow is about to collapse. Likewise, creating ‘trapdoors’, a common practice to view or obtain easy access to the nesting chamber in burrows of nesting petrels, might increase the frequency of nest abandonment (Sinclair 1981). If such is the case, the use of remote monitoring systems and burrowscopes should be encouraged, at least in studies where handling is not necessary and where the accuracy and practicality of using a burrowscope in rough terrain and inclement weather are not serious issues (Jones et al. 2003; Schulz et al. 2005). If trapdoors must be used, they should be constructed outside the breeding

season to avoid disturbance to the burrow, and researchers should be mindful that, although the time of day of inspection may not have an effect on the birds' reproductive success, the frequency of inspection does (Blackmer et al. 2004). Innovations should also be encouraged. For example, the use of an artificial nesting habitat by Gould's Petrels has had no reportable adverse effects on reproduction or survival, and has even been used to establish a new breeding colony as a safeguard against extinction (Priddel et al. 2006b). Gould's Petrels and Madeiran Storm-petrels (*O. castro*) nesting in artificial burrows have both produced a higher annual breeding success than do birds using natural nest sites (Bolton et al. 2004; Priddel et al. 2006b). Innovations of this kind allow essential research to continue with minimum impact.

Perhaps more importantly, past studies where regular handling has occurred should be viewed with caution in terms of how accurate their results are, particularly the results concerning demographic parameters. Where researchers do not take into account their own impact, their data should be viewed with some suspicion and as probably not providing an accurate depiction of a particular species or population. As a result of biased data, a misallocation of funds and resources could result, further threatening species recovery and conservation outcomes.

A code of research procedures is needed for researchers working on procellariiform seabirds, including promotion of best practice methods for research in which invasive procedures and repeated occurrences of disturbance are proposed. The guidelines could be similar to those already protecting vulnerable seabird populations on the Great Barrier Reef and some of the sub-Antarctic research stations.

Table 9.1 A summary of the effects of investigator and human disturbance on colonial nesting seabirds. Disturbance type I = investigator, H = human. Symbols indicate the response of the species, + positive, – negative and • no response.

Species	Disturbance type	Observed effect					Reported findings and comments
		Behaviour	Reproductive success	Nest distribution	Physiological parameters	Breeding population (size trends)	
Sphenisciformes - Jackass Penguin (<i>Spheniscus demersus</i>) (Hockey and Hallinan 1981) - (van Heezik and Seddon 1990)	I	–	–				Regular passage through the nesting colony prevented birds prospecting for nesting sites. Repeated passage reduced productivity of the population.
	I H	•					Medium-term disturbance, consisting of twice daily approaches to within 10 m over a period of three months, appeared to have no detrimental impact on beach group size or composition. Regularly disturbed beach groups were less responsive to direct or gradual approach than either partially disturbed or undisturbed groups.
- Magellanic Penguin (<i>S. magellanicus</i>) (Yorio et al. 2001)	H					–	Negative effects on seabird reproduction in Patagonia are through direct destruction of nests or their contents and desertion of offspring, particularly at locations where seabirds nest in association with or near to colonies of avian predators.

<p>Sphenisciformes (cont.)</p> <p>- Humboldt Penguin (<i>S. humboldti</i>) (Ellenberg et al. 2006)</p>	H		-		-		<p>Breeding success was significantly reduced at frequently visited sites. Heart rate telemetry during disturbance experiments revealed that Humboldt Penguins respond more strongly to human presence than do any other penguin. A person passing an incubating penguin at 150m distance already provoked a significant heart rate response. Recovery times were up to half an hour after direct human approach, causing increased energy expenditure without any overt behavioural reaction.</p>
<p>- Adélie Penguin (<i>Pygoscelis adeliae</i>) (Muller-Schwarze 1984)</p> <p>- (Wilson et al. 1989)</p> <p>- (Woehler et al. 1994)</p>	<p>I H</p> <p>I</p> <p>I</p>	-	-	-		-	<p>An estimated 9-36% decline in nests between 1971 and 1982/83.</p> <p>Birds with ~ 1 cm clipped from their tail feathers stayed at sea 50% longer than unmarked controls. The length of foraging trip and incidence of nest desertion increased with increasing device volume.</p> <p>Breeding success (chicks fledged per nest) was significantly lower for</p>

<p>Sphenisciformes (cont.)</p> <p>- (Giese 1996)</p> <p>- (Bricher et al. 2008)</p>	<p>I H</p> <p>H I</p>		<p>-</p>			<p>Shirley Island colonies than for those at Whitney Point. Investigator visitors to Shirley Island from Casey station are believed to be responsible for the observed changes in the distribution and abundance of breeding pairs and for maintaining the stable population by reducing overall breeding success through disturbance associated with visits.</p> <p>Penguins were exposed to two forms of human activity currently occurring in Antarctica: nest checking for scientific purposes and recreational visits (disturbance treatments). For both larger and smaller colonies, hatching success and chick survival were highest at control colonies and lowest at colonies in subjected to recreational visits. Hatching success was 35% lower in the colony subjected to nest checking (compared to the control colony) and 47% lower in the colony subjected to recreational visits. For chick survival these reductions were 72% and 80% respectively.</p> <p>- This study used GIS and decision trees to examine whether potential changes in snow cover and/or</p>
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<p>Sphenisciformes (cont.)</p> <p>- (Beaulieu et al. 2010b)</p>	<p>I</p>		<p>—</p>			<p>proximity to human activities were able to explain the varying population trends of colonies at two breeding localities near Casey, East Antarctica. At the less visited site, Whitney Point, wind exposure and snow accumulation correctly predicted the broad trends of colonies in most (84%) instances, whereas at Shirley Island their predictive accuracy fell to 58%. At Shirley Island, proximity to human activity correctly predicted the broad trends for 84% of colonies.</p> <p>The authors aimed to identify critical periods of the breeding cycle of Adélie Penguins when the reproductive success may decrease because of instrumentation. Pairs were followed at least during the incubation period but the majority was monitored during the entire breeding season. Reproductive success was affected in pairs where males were instrumented. This was not due to extra chick mortality during chick rearing but to a significantly lower hatching success. The low hatching rate observed in equipped males was associated with a higher egg rotation rate, perhaps as a stress response to the presence of the instrument. Even</p>
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<p>Sphenisciformes (cont.)</p> <p>- (Lynch et al. 2010)</p>	<p>H</p>		<p>+</p>				<p>though the causal effects remain unclear, instrumentation severely affected hatching success.</p> <p>Over the course of five seasons, the breeding productivity of Adélie Penguins breeding at Petermann Island were monitored to identify drivers of rapid community change. The impact of tourist visitation on breeding success was also investigated. Consistent with larger trends in this region, the Adélie Penguin population decreased by 29% between the 2003/04 and 2007/08 seasons. Interestingly, Adélie Penguin colonies frequently visited by tourists had higher reproductive success than those visited only occasionally.</p>
<p>- Chinstrap Penguin (<i>P. Antarctica</i>) (Muller-Schwarze 1984)</p>	<p>I H</p>					<p>–</p>	<p>The number of breeding pairs had increased at remote sites and decreased as a response to human interference. At three colonies the number of nests decreased 83%, 99% and 98% as a result of human presence. At a remote colony, not visited by researchers or tourists, the author noted a 207% increase in breeding pairs since 1965.</p>
<p>- Gentoo Penguin (<i>P. papua</i>) (Muller-</p>	<p>I H</p>					<p>–</p>	<p>At Port Lockroy colony, over three breeding seasons, counts indicated</p>

<p>Sphenisciformes (cont.) Schwarze 1984)</p>						<p>that there had been a -20%, + 11% and +18% changes in nest counts since 1971. Other regularly visited colonies suggested that there had been a 91% and 14% reduction in the number of nests. Two less often visited colonies had increased in a decade, from 800 nests in 1971/72 to 1,514 in 1982/83 (+89%) and 229 nests to 453 (+98%).</p>
<p>- (Nimon et al. 1996)</p>	<p>I</p>				<p>• / -</p>	<p>During experiments in which a person appeared at a distance of 15 – 20 m, gradually approached to 3m, and then observed incubating penguins, neither penguins that were present during the placement nor their unmarked partners exhibited significantly higher heart rates than during periods when no people were present. However, when sudden brief increases of up to 50% for 10 sec periods could occur in response to certain stimuli, such as abrupt movement when a person was only a few meters away.</p>
<p>- Holmes (2007)</p>	<p>H</p>	<p>-</p>				<p>Gentoo Penguins demonstrated significantly increased levels of vigilance for 5 minutes and significantly increased self-maintenance for 5 – 10 minutes following approaches by pedestrians.</p>

<p>Sphenisciformes (cont.)</p> <p>- (Lynch et al. 2010)</p>	H		—				<p>Over the course of five seasons, the breeding productivity of Gentoo Penguins breeding at Petermann Island were monitored to identify drivers of rapid community change. The impact of tourist visitation on breeding success was also investigated. Consistent with larger trends in this region, the Gentoo Penguin population increased by 27% between the 2003/04 and 2007/08 seasons. Gentoo Penguin reproductive success was lowest in colonies frequently visited by tourists.</p>
<p>- Emperor Penguin (<i>Aptenodytes forsteri</i>) (Regel and Pütz 1997)</p>	I				—		<p>Birds were exposed to various man-induced stimuli. Stimuli resulted in typical body temperature rises that varied with the duration and strength of the stimulus. On average, the temperature rose by 1.5 K, the maximum researched being 2.6 K following a stimulus of more than 2 hr duration. Depending on the intensity of disturbance, minimal energy expenditure ranged between 3.2 kJ/kg and 9.7 kJ/kg, being slightly higher in chicks. This represented up to 10% of the daily energy demand.</p>
<p>- King Penguin</p>	H	—					<p>Suggested by Holmes (2007) that the</p>

<p>Sphenisciformes (cont.)</p> <p><i>(Aptenodytes patagonicus)</i> (Holmes 2007)</p> <p>- (Hughes et al. 2008)</p>	I	—	•				<p>increased agonistic activity by King Penguins, appeared to be in indirect consequence of the approaches, whereby the pedestrian instigated the sudden movement of molting, loafing, or resting birds into or alongside breeding animals.</p> <p>The short-term behavioural effects of helicopter overflights on breeding King Penguins were examined. Noise from the aircraft engines and helicopter blades increased sound levels in the colony from background level of 65-69 dB (A) to a maximum mean peak level of 80 dB (A) during overflights. Penguin behaviour changed significantly during all overflights at all altitudes compared to the pre- and post-flight periods. Pre-overflight behaviour resumed within 15 minutes of the aircraft overhead and no chicks or eggs were observed to be taken by predators during overflights. Non-incubating birds showed an increased response with a reduced overflight altitude, but this was not observed in incubating birds.</p>
<p>Royal Penguin (<i>Eudyptes schlegeli</i>) (Holmes et al. 2005)</p>	H	—			—		<p>In response to a single pedestrian visit using the current recommended approach distance of 5 m for visitors,</p>

							penguins showed an increased heart rate (1.23 times the average resting heart rate) and vigilance (six-fold increase), however, no penguins fled their nests. These responses were significantly greater than observed during Subantarctic Skua (<i>Catharata skua lonnbergi</i>) overflights, suggesting incubating Royal Penguins viewed a single pedestrian at 5 m as a greater threat than a predator in flight.
Pelecaniformes							
- White Pelican (<i>Pelecanus erythrorhynchos</i>) (Bunnell et al. 1981)	H					-	Only one breeding colony of White Pelican exists in British Columbia, Canada. The earliest nesting record, from 1953, counted 140 nests. For three years centred around 1960, the colony averaged 146 productive nests. In the three-year period 1978-1980, the average number of productive nests was 107. Over a 20 year period the mean rate of decline was about two breeding pairs per year. The major factors contributing to the decline of the pelican appeared to be disturbance by humans (low flying aircraft) and Coyote predation.
- Brown Pelican (<i>P. occidentalis californicus</i>)	H			-			Disturbances had severe detrimental effects on productivity in ground nesting Brown Pelicans. Brown

Pelecaniformes (cont.) (Anderson and Keith 1980)							<p>Pelicans suffered severe setbacks as a result of even one disturbance early in the nesting season. Effects of disturbances were manifested mostly through immediate losses of eggs and young (mostly predation). Nest abandonment occurred mostly during the early stages of nesting. Injury and death of young pelicans were recorded until downy young were about three weeks of age, when they became capable of defending themselves against avian predators such as Western Gulls (<i>Larus occidentalis</i>) and Ravens (<i>Corvus</i> sp.). Western Gulls often attacked even large chicks. Often Western Gulls walked ahead of human intruders pecking holes in eggs, but not totally consuming contents. Gulls farther away from human carried eggs away from the colony and consumed them elsewhere. Gulls often gathered over intruders and their calling frequently attracted more gulls and further alarmed more distant pelicans. Such situations often caused nest desertions in the pelican colonies at greater distances from the intruders and resulted in even greater losses.</p>
- Atlantic Gannet	H					-	A comparison between past surveys

<p>Pelecaniformes (cont.)</p> <p>(<i>Morus bassanus</i>) (Nettleship 1975)</p>							<p>and those performed in 1969 and 1973 showed that after increasing greatly over 80 years, the breeding population decreased 16% in four years. Reduced fertility because of contamination by toxic chemicals and disturbance at the colony by tourist boats and visitors on land were seen as the likely agents of decline.</p>
<p>- Masked Boobies (<i>Sula dactylagra</i>)</p> <p>- Red-footed Boobies (<i>S. sula</i>)</p> <p>- Blue-footed Boobies (<i>S. nebouxii</i>) (Burger and Gochfeld 1993)</p>	<p>H</p>	<p>–</p>		<p>–</p>			<p>Burger and Gochfeld (1993) examined short-term changes in behaviour of Masked, Red-footed and Blue-footed Boobies when tourists walked by, and examined display stations and nest placement as a function of distance from a regularly trans-versed tourist path. Whether displaying boobies walked, flew, or remained on their station, when tourists passed, was related to their distance from the trail. Boobies displaying at stations on or up to 2 m from the trail, walked or flew from their station 62 to 95% of the time depending on the species. All species of boobies performed more head and body turns, and gave out more calls, after tourists passed than before, while the rate of preening did not differ. All three species of boobies avoided nesting right along the trail, despite similarities of habitat.</p>

<p>Pelecaniformes (cont.)</p> <p>- Blue-footed Boobies (<i>S. nebowxii</i>) (Del Viejo 2004)</p>	H		-				<p>Human entry to the colony was the most widespread factor affecting all four colonies studied. The level of intrusion varied in relation to the colony's accessibility. The causes of these losses were passing boats, and the mooring of boats on the shore for the fisherman to rest, amongst various other human activities. On El Rancho Island, 75 Blue-footed Booby fledglings were killed by fisherman to obtain bait for crabs (<i>Portunidae</i>). This caused a decline of at least 50% in the colony.</p>
<p>Double-crested Cormorants (<i>Phalacrocorax auritus</i>) (Kury and Gochfeld 1975)</p> <p>-(Ellison and Cleary 1978)</p> <p>- (Henny et al. 1989)</p>	H I I	- -	- -				<p>Human intrusions into the nesting areas made adults leave the colony, facilitating predation on eggs and chicks by gulls. Repeated human disturbance caused birds to regurgitate fish. If repeated over many days, the authors suggest that it might significantly harm growing young by depriving them of food.</p> <p>The investigators caused the immediate failure of some sub-colonies of late-nesting birds by facilitating gull predation.</p> <p>The distribution of nesting colonies in</p>

							the study area changed after 1984. The cormorants were most likely responding to increased human disturbance at their nesting islands, coupled with additional protection and reduced human activity on other potential nesting islands. The protected island recorded the highest nesting population ever recorded in 1988.
Charadriiformes - Western Gull (<i>Larus occidentalis</i>) (Robert and Ralph 1975)	I		-				This study suggested that under defined conditions, the presence of an investigator can be detrimental to breeding success. Hatching failure was found to be directly proportional to the amount of disturbance in a plot. However, mortality of young was inversely proportional to the amount of disturbance. The latter mortality was apparently the result of occasionally disturbed chicks reacting to the presence of the investigator by running into other territories and being attacked by adults. Young gulls that were more frequently disturbed were less frightened, and less subject to attack by adults. Overall, mortality of young, comparing the completely undisturbed plot with a disturbed plot, was higher on the disturbed plot.

<p>Charadriiformes (cont)</p> <p>- Glaucous-winged Gull (<i>L. glaucescens</i>) (Gillett et al. 1975)</p>	I		-			•	<p>The presence of investigators increased chick mortality in areas where they worked. Their presence had no effect on egg morality. There was no overall population decline on the island and instead the authors suggested the population was increasing. 55% of chick mortality occurred during the first week after hatching. The increase in mortality resulted largely from chick moving into adjacent territories and being attacked by neighbouring adults as the result of investigator entering the chicks' home territory.</p>
<p>- Ring-billed Gull (<i>L. delawarensis</i>) (Fetterolf 1983)</p>	I		-				<p>Human activity grossly altered adult and chick behaviour. Adults fought 10 – 15 times more often during disturbance than before and attacks on chicks increased between 400 – 600 fold. Chicks running from their nest during pre-disturbance watches were not observed, yet runs were very common during and after disturbance. As a result, most peaking deaths occurred after disturbance. Hatching success was lowest in the most disturbed plot where nest checks were shortest before the post-hatching period. Longer disturbances and direct entry to the plot during experimental</p>

<p>Charadriiformes (cont)</p> <p>- (Brown and Morris 1994)</p>	<p>I</p>		<p>—</p>			<p>disturbances in post-hatching therefore reduced hatching success compared to the moderately and least disturbed plots. Entering the plot by investigators increased adult fighting which forced incubators off nests more frequently for longer periods and probably increased embryonic mortality due to excessive cooling or heating. Fledging success, and consequently net reproductive output, was seriously affected by investigator activity.</p> <p>From 1989 to 1991, the authors studied the effects of investigator disturbance on the breeding success on individual pairs nesting at two colonies. Clutch size, hatching success/pair and fledging success/pair were measured for pairs nesting in study plots subjected to various levels of investigator disturbance. Visits into the study areas before and during egg-laying period had no significant effect on nesting density or clutch size distribution. Similarly, visits during the incubation phase had no effect on the hatching success of study pairs. Although the authors did not enter the study area during the brooding period, they established that visits during</p>
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Charadriiformes (cont)							hatching had no effect on the hatching or fledging success of study pairs.
- (Brown 1995)	I	•	•				Ring-billed Gulls adults were tolerant of trapping on the nest, and blood sampling, and returned to their nests quickly after release. No pairs permanently abandoned their clutch. Brown suggested that these results indicate that taking blood from a species that is known to be tolerant of trapping and handling has minimal effect.
- (Brown and Morris 1995)	I	—	•				The frequency of charges, jabs, and wingpulls increased during the period of investigator activity in the colony, while the duration of beakpulls decreased. Chick mobility increased with age, and older (>7 days) chicks strayed off their natal territories and were attacked more frequently during disturbances than before disturbance. No chicks were fatally attacked during investigator disturbance and stray chicks returned to their natal territories quickly after disturbance. The mean fledging success of pairs disturbed during this study was not different for that for undisturbed pairs.
- Black Skimmer	H		—	—			The authors reported significant

<p><i>(Rynchops niger)</i></p> <ul style="list-style-type: none"> - Common Tern (<i>Sterna hirundo</i>) - Gull-billed Tern (<i>S. nilotica</i>) - Least Tern (<i>S. antillarum</i>) - Royal Tern (<i>S. maxima</i>) - Sandwich Tern (<i>S. sandvicensis</i>) (Erwin et al. 2003) 							<p>changes in the use of the dredged material islands. Population declines and changes in bird habitat use appeared to be at least partially associated with the conditions and management of the existing dredged material islands, coastal policy changes associated with creating new dredged material islands, and competing demands for sand for beach augmentation by coastal communities. The authors point out that as these and other coastal habitats become less suitable for colonial waterbirds, other man-made sites, such as bridges and buildings have become increasingly more important.</p>
<p>Common Tern (<i>S. hirundo</i>)</p> <p>Least Tern (<i>S. albifrons</i>)</p> <ul style="list-style-type: none"> - Black Skimmer (<i>R. niger</i>) - Herring Gull (<i>L. argentatus</i>) (Erwin 1980) 	H		-			-	<p>In heavily disturbed areas, natural barrier islands have been developed, greatly reducing the extent of beach habitat. Consequently, the authors demonstrated that birds had shifted colony sites to dredge deposition sites, or to a lesser extent, marsh islands. Increasing numbers of the large, dominant Herring Gull and its ability to invade both march and dredge island habitats appeared to affect nesting Common Terns and Laughing Gulls (<i>L. atricilla</i>) adversely.</p>

<p>Charadriiformes (cont)</p> <p>- Least Tern (<i>S. albifrons</i>) (Brubeck et al. 1981)</p>	I	-	-				<p>Effects of trapping, banding, and patagial tagging on the parental behaviour of terns in five colonies. Adult terns were captured with nest traps or with cannon-nets at loafing areas. The authors compared parental behaviour and nest outcome among experimental groups that differed from each other in the extent of experimental manipulation. Observations were made at 89 nests. Terns that were nest-trapped and marked with patagial tags deserted nests at a greater rate than did terns that were handled less extensively. Brooding terns that were nest-trapped and tagged accepted significantly more fish from their foraging mates than did birds that were subjected to lesser degrees of handling. No differences occurred in the rate of food delivery to chicks or in chick survival rates among experimental groups or controls.</p>
<p>- Black Skimmer (<i>R. niger</i>) (Safina and Burger 1983)</p>	I	-	-	-			<p>Black Skimmers were subjected to either daily or weekly nest checks in order to study the effects of investigator activity on reproduction. Pre-laying adults left the sub-colonies that were disturbed daily and settled in relatively undisturbed sub-colonies;</p>

Charadriiformes (cont)						some pairs in these areas deserted nests early in incubation. Nest density, late nesting, hatching success, and fledging success were inversely correlated with disturbance. As a consequence of disturbance, a few chicks ate younger con-specifics. Low fences placed around groups of nests depressed fledging in areas disturbed weekly, but enhanced it in sub-colonies disturbed daily.
- Common Murre (<i>Uria aalge</i>) - Black-legged Kittiwake (<i>Rissa tridactyla</i>) (Beale and Monaghan 2005)	H		•/–			Beale and Monaghan examined the relationship between daily visitor numbers and daily failure rates of nests in two species of seabirds. Daily failure rates for Black-legged Kittiwakes were weakly correlated with daily visitor numbers but indicated that capping daily visitor numbers slightly reduced overall breeding success. This was not the case for Common Murres, where failure rate declined seasonally but was not significantly correlated with visitor numbers.
- Black Guillemot (<i>Cephus grille</i>) (Cairns 1980)	I	–	–			Breeding success, breeding synchrony and condition of young at fledging were measured in two colonies. Nest productivity was lower, but maximum chick mass were higher, in an area

Charadriiformes (cont)							disturbed daily than in an area disturbed once every 4 days. Intra-specific agonistic behaviour was more frequent in a high density sub-colony, but nesting density was uncorrelated with breeding success and synchrony. No relationship was found between habitat structure and breeding success.
- Least Auklet (<i>Aethia pusilla</i>) - Crested Auklet (<i>A. cristatella</i>) (Piatt et al. 1990)	I		-				The authors studied the breeding success, chick growth and diets of two species of auklets. Hatching success, fledging success and productivity was significantly lower in intensively studied plots than in control plots. No information of chick growth or diet effects.
- Atlantic Puffin (<i>Fratercula arctica</i>) (Rodway et al. 1996)	I		-				The authors monitored the reproductive success over two breeding seasons to determine if the effects of the disturbance persisted through subsequent breeding seasons. Chick productivity was reduced by 38% in disturbed study plots compared to control plots in the first year. Effects of disturbance persisted one year and were not apparent two years after the disturbance.
- (Pierce and Simons 1986)	I		-				Investigator activities within the colony during incubation period

Charadriiformes (cont)							<p>apparently had two effects. First, it reduced breeding success directly in some nests due to desertion. Second, it may have lengthened the incubation period in nests that were temporarily deserted. Tufted Puffin nestling development was not adversely affected by periodic visits to collect growth data.</p>
<p>- Razorbill (<i>Alca torda</i>) (Lyngs 1994)</p>	<p>I</p>		<p>–</p>				<p>The overall breeding success of ‘heavy disturbance areas’ was significantly lower than that of ‘slightly disturbed areas’. Growth rate, age and weight at departure and post0departure survival of heavily disturbed chicks were not affected. Birds laying smaller eggs were apparently most influenced by the disturbances. As egg size increases with age of females in this species, Lyngs suggested those younger breeders are more sensitive to disturbance than older birds.</p>

9.3 Directions for future studies

This research has resolved a number of outstanding questions relating to investigator disturbance, but it has also produced a number of new ideas and given rise to some new challenges. Clearly, more research on the effects of investigators on all birds is necessary. The effect of handling is well established for several populations, but for most species, many questions remain. For example, for surface nesting shearwaters, at what distance from the nest, at what frequency, at what stage of the breeding season, and for how long will particular species of birds accept investigator disturbance before negative consequences occur? Studies of nesting Wandering Albatross and giant petrels indicated that simply walking through the colony can dramatically increase heart rates and cause reproductive failure (Weimerskirch et al. 2002; de Villiers et al. 2006; Wheeler et al. 2009). The same is true for other surface nesting penguins, gulls and boobies (Table 9.1).

For studies that involve tracking devices, there are currently unprecedented opportunities for researchers intending to investigate at-sea behaviour of pelagic seabirds. As tracking devices become smaller they will allow even smaller seabirds to be monitored. However, with each study there should be a parallel investigation into the effects of attaching a device to the individual. This would appear to be especially important once device loads exceed 3% of a bird's body mass. Effects are most likely to be seen in a bird's body condition and in the amount of effort it invests in reproductive behaviour. Researchers should also investigate the effects in the long-term, and in the post-recovery period, of tracking devices having been attached. Very few studies have been able to quantify disturbance adequately, and this gap in our knowledge offers opportunities for further research, possibly in conjunction with existing or new projects.

Measuring the effects of investigator disturbance will require studies of physiology, behaviour, and breeding biology as well as parallel studies of other known variables, such as predation and food availability, which affect bird populations. Appropriate methods should be used in these studies, and more attention needs to focus on minimising the unwanted effects associated with attempts to collect accurate data. The publication of these studies should be widely advocated, even if no negative outcomes are found. Ethics committees and government agencies should also promote research concerning disturbance, and encourage best practice methods in order to minimise any negative outcomes arising from research on the species being studied.

Answering some of the questions raised in this research is likely to benefit a variety of bird species, as well as providing practical information for scientists and managers. These outcomes may be particularly important for limiting the impact of the growing tourism and ecotourism industry in the Great Barrier Reef, Lord Howe Island, sub-Antarctic islands, and Antarctica (Great Barrier Reef Marine Park Authority 1997). Managers of these areas must enforce strong precautionary guidelines to protect breeding seabirds against human disturbance, and to ensure that minimal or no negative outcomes arise from visits by researchers and tourists.

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Appendix I: List of conference presentations during candidature

Carey, M.J., Phillips, R.A. and Silk, J.R.D. Trans-equatorial migration of Short-tailed Shearwaters – testing old theories with new technology. Ecological Society of Australia's 2010 Annual Conference. 6 - 10 December 2010, Manning Park Centre, The Australian National University, Canberra, ACT.

Abstract:

Trans-equatorial migration of Short-tailed Shearwaters – testing old theories with new technology

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Although Short-tailed Shearwaters (*Puffinus tenuirostris*) have been studied extensively during their breeding season, our understanding of their movements outside this period remains largely unknown. Early results from banding studies and museum collections implied a broad 'figure-of-eight' movement across the Pacific Ocean. Recent oceanic transects suggested birds migrated in broad fronts in the western and central Pacific. Here, we present the first tracks of the trans-equatorial migration of Short-tailed Shearwaters from a colony on Great Dog Island, Tasmania, Australia. Data were obtained from global location sensors (GLS loggers), which enable the estimation of bird location twice per day based on ambient light levels. We deployed 27 GLS devices in 2007 and retrieved 20 in December 2008. Tracks revealed that after breeding, shearwaters fly south to the Antarctic convergence for a brief period before flying rapidly north through the western Pacific to the coastal waters off Japan. Short-tailed shearwaters spent the bulk of the winter either in this region or further north in the Bering Sea, before returning south through the central Pacific to their breeding grounds in Australia. Birds used local waters around the colony before the commencement of egg laying. For the first time, our results show the complete migration of this long-lived seabird and reveal individual variation in their wintering distribution. Our results, in part, confirm previous assumptions as well as present new knowledge of their movements in the Pacific Ocean.

Carey, M.J., Phillips, R.A. and Silk, J.R.D. Post-breeding migration of Short-tailed Shearwaters – testing old theories with new technology. 1st World Seabird Conference. 7-11 September 2010, Victoria, British Columbia, Canada.

Abstract:

Post-breeding migration of Short-tailed Shearwaters – testing old theories with new technology

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Short-tailed Shearwaters (*Puffinus tenuirostris*) have been studied extensively during their breeding season however our understanding of their movements outside this period remains a mystery. Early results from banding studies and museum collections implied a broad 'figure-of-eight' movement across the Pacific Ocean. Recent oceanic transects suggested birds migrated in broad fronts in the western and central Pacific. Here, we present the first trans-equatorial post-breeding migration of Short-tailed Shearwaters from a colony on Great Dog Island, Tasmania, Australia. Data were obtained from global location sensors (GLS) using ambient light levels. We deployed 27 GLS devices in 2007 and retrieved 20 in December 2008. Tracks revealed that after breeding, shearwaters fly south to the Antarctic convergence for a brief period before flying rapidly north through the western Pacific to the coasts off Japan. Short-tailed shearwaters used either of two wintering regions off northern Japan or the Bering Sea, before returning south through the central Pacific to their breeding grounds in Australia. Birds used local waters around the colony before the commencement of egg laying. For the first time, our results show the complete migration of this long-lived seabird and reveal variation in their wintering distribution. Our results, in part, confirm previously known information as well as present new knowledge of their movements in the Southern Ocean.

Gonzalez-Solis, J., Felicísimo, A., Tremblay, Y., Reid, T., **Carey, M.**, Hodum, P., Takahashi, A., Muñoz, J., Sigurðsson, I., Thompson, D., Ryan, P., Cuthbert, R., Hedd, A., Montevecchi, W., Trathan, P., Phillips, R., Shaffer, S. Global migration dynamics of trans-equatorial shearwaters. 1st World Seabird Conference. 7-11 September 2010, Victoria, British Columbia, Canada.

Abstract:

Global migration dynamics of trans-equatorial shearwaters

Jacob Gonzalez-Solis, Angel Felicísimo, Yann Tremblay, Tim Reid, **Mark Carey**, Peter Hodum, Akinori Takahashi, Jesus Muñoz, Ingvar Sigurðsson, David Thompson, Peter Ryan, Richard Cuthbert, April Hedd, William Montevecchi, Phil Trathan, Richard Phillips, Scott Shaffer

In each of the two major oceans of the world, the Atlantic and the Pacific, millions of shearwater migrate across the equator twice a year. Some species breed in the northern, and “winter” in the southern hemisphere, while others conduct the opposite migration, but all pursue for an endless summer. Understanding the global dynamics of these movements can help us to better assess major driving factors, multi-specific hot-spots and the risks faced by shearwaters during their journeys. Using geolocation data, we analysed the trans-hemispheric migration of ten shearwater species, including those breeding in both hemispheres and the two major ocean basins: Cory's (*Calonectris borealis*), Scopoli's (*C.diomedea*), Cape Verde (*C.edwardsii*), Streaked (*C.leucomelas*), Manx (*Puffinus puffinus*), Great (*P.gravis*), Flesh-footed (*P.carneipes*), Pink-footed (*P.creatopus*), Short-tailed (*P.tenuirostris*) and Sooty (*P.griseus*) shearwaters. Concurrent data on marine habitat traits were obtained from the NASA. Spatiotemporal overlap among species revealed a few major large-scale hotspots in both oceans. In the Atlantic, most species followed relatively narrow corridors showing a figure of eight migration associated with the northern and southern oceanic gyres. In the Pacific, however, most species migrated between hemispheres within a western, or a broad eastern corridor. We discuss the consequences for management and conservation of shearwaters in each ocean.

Carey, M.J. The effects of data-logger attachment on breeding Short-tailed Shearwaters. 5th Australasian Ornithological Conference, 29th Nov – 4th December 2009, Armidale, NSW, Australia .

Abstract:

The effects of data-logger attachment on breeding Short-tailed Shearwaters.

Mark J. Carey, Department of Environmental Management and Ecology, La Trobe University, Wodonga, Victoria, 3690, Australia.
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Concern has been raised about the potential negative effects of attaching tracking devices to a number of seabird species. Of particular concern are their possible effects on a bird's reproductive and foraging performances. The extra weight carried by the individual, design of the device and location of attachment all potentially have serious effects on an individual's flight, diving and foraging abilities. These devices may also lead to a bias in results or an inaccurate interpretation of these results as birds with them may not be behaving 'normally'. Here, the possible effects of a 5.4g Global Light Sensing (GLS) data-logger attached to a modified aluminium band were investigated on Short-tailed Shearwaters (*Puffinus tenuirostris*) breeding on Great Dog Island, Furneaux Group, Tasmania. Return rates, breeding success and body condition were compared between equipped and non-equipped birds over two breeding seasons from 2007 - 2009. No evidence of negative effects of data-loggers on return rates, egg size, chick quality or adult body condition were found. These results suggest that appropriate data-loggers are a relatively benign method of obtaining at-sea foraging and behavioural information from seabirds. Monitoring tracked individuals and their reproductive output should be considered an integral part of all future GLS studies.

Carey, M.J. Incubation routine, body mass regulation and egg neglect in Short-tailed Shearwaters (*Puffinus tenuirostris*). 5th Australasian Ornithological Conference, 29th Nov – 4th December 2009, Armidale, NSW, Australia.

Abstract:

Incubation routine, body mass regulation and egg neglect in Short-tailed Shearwaters (*Puffinus tenuirostris*).

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The incubation routine and fluctuation in mass of male and female Short-tailed Shearwaters (*Puffinus tenuirostris*) were studied on Great Dog Island, Furneaux Group, Tasmania in 2006-07. Factors influencing egg neglect during incubation and foraging trips at-sea were also investigated. Thirty pairs were monitored over the entire incubation period; shifts averaged between 13 – 15 days, except for a short shift by the female at egg laying. Birds lost an average of 14.4 g / day or 19.3 % of body weight during their incubation shift. There were no differences between the sexes. Birds deserted their nest at higher masses than when they were relieved by their partner. Temporary egg neglect, ranging from 1 to 17 days was observed in all monitored burrows throughout the incubation period. Time spent at-sea increased in the second half of the incubation period while, net mass gain remained similar across the entire incubation period. No relationship was found between the number of days spent at-sea and the mass gained on the foraging trip. A large number of nests were abandoned in this study, perhaps due to the excessive handling of the birds. Alternative sampling methods are recommended in future studies of this nature so that the bird's behaviour is less affected.

Carey, M.J. The effects of investigator disturbance on the hatching success, chick survival and quality of Short-tailed Shearwaters (*Puffinus tenuirostris*). 36th Annual Meeting of the Pacific Seabird Group, 22 – 25th February 2009, Hakodate, Hokkaido, Japan.

Abstract:

THE EFFECTS OF INVESTIGATOR DISTURBANCE ON THE HATCHING SUCCESS, CHICK SURVIVAL AND QUALITY OF SHORT-TAILED SHEARWATERS (*PUFFINUS TENUROSTRIS*).

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Studies have suggested that research procedures can have a detrimental effect on the reproductive success of a number of bird species, yet little experimental investigation to test this have been conducted on procellariiform seabirds. Investigators studying long-lived birds should understand how their research procedures affect their study animals and take precautions to mitigate any adverse effects. In an abundant procellariiform, the Short-tailed Shearwater (*Puffinus tenuirostris*), the frequency of investigator disturbance was examined during the incubation period to determine if it influences hatching success, chick survival and quality. All birds in this study received little or no investigator disturbance prior to this study. *Weekly, every three days* and *daily* handling of incubating birds reduced hatching success by 39, 61 and 100% respectively, compared to the control group. Most failures were caused by egg abandonment by the parents, particularly in the early stage of incubation and during incubation change over between parents. Chick survival did not differ among treatment groups and while *control* chicks tended to be heavier, overall body size was not significantly different between groups. These results demonstrate that *weekly, every three days* and *daily* investigator disturbance during incubation greatly reduced the hatching success of naïve Short-tailed Shearwaters while having no discernible effect on chick survival or size. These findings are significant in broader terms because any investigator disturbance that reduces reproductive success could exacerbate population declines, particularly of rarer species or small populations, and interfere with the accurate assessment of demographic parameters.

Carey, M.J. and Meathrel C.E. The effects of investigator disturbance on the hatching success of Short-tailed Shearwaters *Puffinus tenuirostris* on Great Dog Island, Tasmania. 4th Australasian Ornithological Conference, 3 – 5th 2007, University of Western Australia, Perth.

Abstract:

The Effects of Investigator Disturbance on the Hatching Success of Short-tailed Shearwaters *Puffinus tenuirostris*

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Investigators studying long-lived birds should understand how their research procedures affect their study animals and take precautions to mitigate adverse effects, especially when threatened species are involved. In an abundant procellariiform, the Short-tailed Shearwater *Puffinus tenuirostris*, we examined whether the frequency of investigator disturbance during the incubation period influenced hatching success. All birds in this study had received no investigator disturbance in the past 12 years. *Weekly, every three days* and *daily* handling of parents reduced hatching success by 39, 61 and 100% respectively, compared to the control group. Most failures were caused by egg abandonment by the parents, particularly in the early stage of incubation and during incubation change over between parents. Once an egg had been deserted, mammalian and reptilian predators quickly took advantage of the exposed egg. Our results demonstrate that *weekly, every three days* and *daily* investigator disturbance during incubation greatly reduced the hatching success of naïve Short-tailed Shearwaters. These findings are significant in broader terms because any investigator disturbance that reduces reproductive success could exacerbate population declines, particularly of rarer species, and interfere with the accurate assessment of demographic parameters.

Appendix II: Printed copies of published work during candidature

Carey, M.J. (2011) Investigator disturbance reduces reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*. *Ibis* **153**: 363-372.

Carey, M.J. (2011) Incubation routine, foraging trip duration and body mass regulation in Short-tailed Shearwaters. *Emu* **111**: 166-171.

Carey, M.J. (2011) Sexual size dimorphism, within-pair comparisons and assortative mating in the Short-tailed Shearwater (*Puffinus tenuirostris*). *Notornis* **58**: 8-16.

Carey, M.J. (2010) Predation of Short-tailed Shearwater eggs on Great Dog Island, Tasmania. *Australian Field Ornithology* **27**: 59-64.

Carey, M.J. (2009) Islands in the Strait. *The Bird Observer* **863**: 12-14.

Carey, M.J. , Meathrel, C.E. and May, N.A. (2009) A new method for the long-term attachment of data-loggers to shearwaters (Procellariidae). *Emu* **109**: 310-315.

Carey, M.J. . (2009) The effect of investigator disturbance on procellariiform seabirds: a review. *New Zealand Journal of Zoology* **36**: 367-377.



Investigator disturbance reduces reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris*

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Research procedures can have a detrimental effect on the reproductive success of the study species. In this study, the frequency of investigator disturbance on Short-tailed Shearwaters *Puffinus tenuirostris* was examined experimentally throughout the incubation period to assess whether disturbance influences hatching success, pre-fledging chick survival and chick body size. Handling of incubating birds every day, every 3 days and once a week reduced hatching success by 100, 61 and 39%, respectively, compared with pairs that were not disturbed. Most failures resulted from egg abandonment by the parents, particularly during the early stage of incubation. Chick survival did not differ between treatment groups, but control chicks were significantly heavier and had larger bill depths and longer wings. The difference in chick body mass and size observed between the control and disturbed chicks might be due to physiological or behavioural mechanisms in adults or carry-over effects from the incubation stage to the next life-history stage. Reduced offspring quality has the potential to affect post-fledging survival and recruitment. These findings are significant in broader terms because any investigator disturbance that reduces reproductive success, survival and offspring fitness could interfere with the accurate assessment of demographic parameters and exacerbate population declines.

Keywords: animal behaviour, handling, impact, Procellariiformes, *Puffinus tenuirostris*, seabirds.

There have been long-held concerns over the impact of investigators in ecological studies of wildlife, particularly in studies of avian species (Götmark 1992, Carney & Sydeman 1999, Nisbet 2000, Phillips *et al.* 2003, Carey 2009). Nisbet (2000) first made the clear distinction between human or recreational disturbance and investigator disturbance, and thus provided a formal description of the implications of investigator effects. In behavioural, demographic and ecological studies, researchers should aspire to unbiased observations when studying wildlife in order to observe individuals under natural conditions without altering those conditions. However, without experimental studies that explore the effects of investigator disturbance it is difficult to determine the magnitude of that disturbance, consider strategies for avoiding it, or at least make appropriate adjustments to take

it into account. Many researchers have not assessed the effects their activities might have had on birds' normal behaviour (Götmark 1992, Nisbet 2000). However, whereas some researchers have claimed that no disturbance effect occurred in their studies (Saffer *et al.* 2000a, O'Dwyer *et al.* 2006), others indicate that researchers do have an impact (e.g. Weimerskirch *et al.* 2002, Blackmer *et al.* 2004). This observer effect has the potential to create biased results that, in turn, could compromise our understanding of a species' ecological and behavioural attributes (Serventy & Curry 1984).

Studies of investigator disturbance have included a wide range of avian taxa, particularly colonial nesting waterbirds such as gulls, terns, pelicans, cormorants and penguins (for reviews see Carney & Sydeman 1999, Nisbet 2000). In contrast, experimental studies that quantify investigator disturbance of procellariiform seabirds have received less attention (Carey 2009). The potential negative

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effects of investigator disturbance on birds include predation of eggs and young (Hockey & Hallinan 1981), desertion of nests (Giese 1996), reduction in fledging success (Pierce & Simons 1986, Whidden *et al.* 2007), physiological changes such as increased heart rates (Weimerskirch *et al.* 2002) and acute stress-induced levels of plasma corticosterone (Brewer *et al.* 2008). The causes of these effects have been attributed to handling birds, among others, during research activities. Handling of adults and their young is necessary for some behavioural and ecological studies. Birds are handled to attach rings for individual recognition, to make morphological measurements, to acquire blood samples or to attach tracking devices. Handling, even when conducted in a prompt and professional manner as required under current animal ethics permits, may trigger adverse outcomes, so it is important to determine the handling frequency that birds can tolerate before negative effects are observed.

In this study, the frequency of handling during the incubation period was used to quantify investigator disturbance on the length of incubation (average 53 days; Serventy 1967), hatching success, chick survival to fledging, and chick body size and peak mass of Short-tailed Shearwaters *Puffinus tenuirostris*. Anecdotal accounts of investigator disturbance affecting these seabirds report some evidence that handling of adults during the incubation period can have a negative effect on hatching success (Allan 1962, Morse & Buchheister 1979, Warham 1990, Marks & Leasure 1992), but there is little published experimental evidence to support this. Handling of adults during the incubation period and subsequent effects on the survival and quality of their offspring have also received little experimental investigation despite the possible compromised outcomes (Gangloff & Wilson 2004, Carey 2009). Based upon anecdotal accounts from previous studies and evidence supported by Blackmer *et al.* (2004), I predicted that hatching success would be lower as the frequency of handling increased and that there would be an observed difference in pre-fledging chick survival and body size.

METHODS

Study site and species

This research was conducted between November 2006 and March 2007 on Great Dog Island, one of

the Furneaux group of islands located off the southeastern coast of Australia (40°15'S, 148°15'E). Great Dog Island (377 ha) is located in Franklin Sound and is classed as a Conservation Area/Short-tailed Shearwater Reserve. A large Short-tailed Shearwater colony with an estimated 952 000 burrows covers much of the island (Skira *et al.* 1996) and is Tasmania's third largest shearwater colony (Skira & Brothers 1988).

Short-tailed Shearwater is a medium-sized (approximately 600 g) procellariiform that breeds on islands and headlands of southeastern Australia (Marchant & Higgins 1990). It is abundant, with estimates of 23 million breeding birds, all of which perform a trans-equatorial migration to the northern Pacific in April and May each year (Serventy 1967, Skira 1991). These birds are long-lived, form long-term pair bonds and are highly philopatric to their nesting burrows (Serventy 1967, Serventy & Curry 1984, Wooller *et al.* 1989, Bradley & Wooller 1991, Skira 1991). Egg-laying in this species is notably synchronous (Serventy 1963, 1967, Meathrel *et al.* 1993), with a single egg laid during a 16-day period (Meathrel *et al.* 1993). Parents incubate the egg alternately at 12–14-day intervals for approximately 53 days (Serventy 1967, Serventy & Curry 1984). Eggs hatch in late January, at which point parents begin feeding the chick. Chicks fledge after a brief starvation period during April and May (Serventy 1967, Serventy & Curry 1984, Skira 1991).

Field procedures

Pairs used in this study had experienced no previous handling by researchers except for 12 birds that had been ringed as chicks 10–12 years prior to this study as part of an investigation into parental attendance and chick provisioning patterns (Hamer *et al.* 1997). Thirty active burrows in each of four treatments (total $n = 120$) were chosen during daily inspections of approximately 300 burrows during the egg-laying period between 22 and 27 November 2006. An active burrow was defined as one with an incubating bird. All active burrows were located within 24 h of egg-laying. Burrows were located in an area of 20 × 100 m to avoid confounding influences of microclimate and temporal bias. Each burrow was marked by a polyvinylchloride pole with a unique number for the duration of the project. Once an active burrow was found it was randomly allocated to one of four

treatments of investigator disturbance. The disturbance experiment started as soon as the active burrows were found. Burrows were disturbed during daylight hours between 07:30 and 13:00 h throughout the investigation. All burrows were inspected according to the time schedule of their respective treatment group: only once, at the beginning of the study (control); every day; every 3 days; or every 7 days (hereafter referred to as control, 1D, 3D and 7D groups, respectively). A maximum of two investigators were in the plot at any one time. All burrows were clearly marked with coloured flagging tape and were only approached if a disturbance event was imminent. This ensured that the minimally disturbed control group was not adversely affected because of visits to neighbouring burrows and avoided any possible bias of researchers walking overhead. Average burrow density of the study plot was $0.47/\text{m}^2$; however, the density of study burrows used in this study was $0.06/\text{m}^2$. The investigator disturbance ended once it was determined whether the egg had hatched, and the time between onset of incubation and hatching was recorded to the nearest day. To that effect, burrows were inspected for the presence of a chick from 53 days after egg-laying onwards. If an egg was still present after 53 days from incubation, the burrow was checked daily until the fate of the egg could be determined (i.e. hatched or failed to hatch). Eggs that failed to hatch were classified as infertile, predated or abandoned. If an egg was no longer present in a particular burrow during the experiment, the burrow was still inspected at the appropriate disturbance interval to identify burrow use by non-breeding or failed birds.

Experimental treatment groups and disturbance procedures

Pairs in the control group received the minimum amount of disturbance possible and their burrows were not approached by researchers during the experiment until hatching. Field procedures for the 1D, 3D and 7D treatment groups simulated investigator disturbance that might be experienced by incubating birds during routine monitoring in a scientific study where regular handling is required to obtain demographic or individual physiological parameters (Prince *et al.* 1981, Johnstone & Davis 1990, Chaurand & Weimerskirch 1994, Booth *et al.* 2000).

Control group

If a burrow was allocated to the control group, the incubating bird and the egg were not removed from the burrow. Thus, only one member of a control pair received investigator contact and the other was not handled during the incubation period. After determining that a burrow was active by briefly feeling for the presence of an adult and an egg, it was left undisturbed for 53 days (the average length of the incubation period; Serventy 1967) until it was re-visited to determine hatching success. If an adult shearwater was present on the second visit, the bird was removed from the burrow and placed in a calico bag while the burrow was inspected for a chick. If a chick was found, it was carefully removed (if it could be reached), weighed and measured. Measurements taken for both adults and chicks were head length from the tip of the maxillary unguis (upper nail of the bill) to the rear of the skull, bill length from the maxillary unguis to the posterior extremity of the nares (nasal tubes), bill depth measured vertically at the proximal base of the nares, and length of the tarsometatarsus (hereafter tarsus) with Vernier callipers to ± 0.02 mm. Wing length, from the carpal joint to the end of the 10th primary feather, was measured with a standard, butt-end wing ruler to the nearest 1 mm. Chicks were weighed with a 300-g (± 2) Pesola scale and adult birds were weighed with a 1000-g (± 10) Pesola scale. Adults were ringed with an Australian Bird and Bat Banding Scheme (ABBBS) band at this time. If an egg was present, it was removed and inspected for any evidence of hatching (i.e. starring or pipping). The egg was then returned to the burrow along with the adult.

Treatment groups

During the first visit to a burrow in the 1D treatment group the egg and the incubating bird were removed. To account for the influence of egg size on hatching success, eggs were weighed with a 300-g Pesola scale. The body mass and morphometric measurements (head length, bill length, bill depth, wing and tarsus) of the adult bird were also recorded as described for the control group. All adults encountered were ringed with ABBBS bands. After handling, the egg and adult were returned to the burrow where they were left undisturbed until the following day, when the adult bird was removed from the burrow, the band number checked, and its body mass recorded. Morphometric measurements were not taken

again, and handling took < 2 min. Once the presence of the egg was determined, the adult was returned to the burrow, thus completing the investigator disturbance until the following day. When the first incubation changeover occurred, 12–14 days into the incubation period, the partner was banded, weighed and measured as described above. The frequency of handling continued daily thereafter. Because Procellariiformes frequently leave eggs unattended in nesting burrows (Mathews 1954, Warham 1990), cold and unattended eggs found at any time during the investigation were checked every day to determine whether the burrow had been abandoned (i.e. neither parent attending the egg) or if a parent had returned to continue the incubation (defined as temporary egg neglect). Thus, this information could be used to calculate temporary egg neglect and parental care.

For the remaining two treatment groups, procedures were the same as in the 1D treatment group initially, then burrows were disturbed every 3 or 7 days, respectively, during the incubation period. Once the average 53-day incubation period had passed, burrows were inspected daily to ascertain hatching date and the size of the hatchling.

Chick survival, mass and size

Once hatching success and hatchling size were determined, all burrows in all four groups were left undisturbed for 9 weeks. Towards the end of March, young birds begin to explore outside their burrows (Serventy 1967). This behaviour increases the possibility that young chicks do not return to their natal burrows, usually because of predation. At this stage, chicks are approximately two-thirds grown (Serventy 1967, Saffer *et al.* 2000b). Therefore, all treatment burrows that contained a chick in January 2007 were inspected in mid-March to ascertain chick survival and size. If a chick was present, it was removed, placed in a calico bag and weighed using a Pesola with a 2500-g (± 20) scale, and the measurements described above for adults were recorded. Chicks were ringed with an ABBBS band and returned to their burrow. If a chick was not present it was assumed that the chick had perished since hatching.

Statistical analyses

Statistical analyses were performed using the SPSS version 17.0 software package (SPSS Inc., Chicago,

IL, USA). One-way ANOVA was used to identify any differences in incubation length and egg mass among treatment groups. To assess whether investigator disturbance influenced the probability that an egg would hatch, a multiple logistic regression model was used in which the nominal dependent variable was hatched or failed to hatch and the explanatory variable was the frequency of disturbance (control, 1D, 3D and 7D). Next, a two-tailed G-test with Williams' correction factor was used to conduct pairwise comparisons of the number of eggs that hatched vs. the number of eggs that failed to hatch among the four treatment groups (Sokal & Rohlf 1995). These six pairwise comparisons were corrected for multiple comparisons using the Bonferroni method; a result was considered significant when $P \leq 0.0083$ ($\alpha = 0.05/6$; Sokal & Rohlf 1995).

To assess whether chick mass and skeletal measurements varied across treatments, ANOVA was used to identify any differences in chick body mass and body measurements between the four groups. Principal components analysis (PCA) was then used to characterize variability in body dimensions within the total sample. The first principal component (PC1) comprised head length, bill length, bill depth, wing length and tarsus length, and was used as a single composite measure of body size (Rising & Somers 1989, Dytham 2003). Effects on body condition of chicks in each treatment were investigated using an ANCOVA model with body mass as the dependent variable, body size index (PC1) as a covariate and treatment group as a fixed factor. Unless specified above, for all tests the significance level was $\alpha \leq 0.05$ and descriptive statistics are presented as means \pm standard deviation (sd).

RESULTS

Laying date and egg size

Egg-laying began on 22 November, and by 27 November, 120 burrows had been allocated to the control or a treatment group. The mean egg-laying date was 25 November and there were no differences between the control and treatment groups ($F_{3,116} = 0.05$, $P = 0.9$). Thirty eggs were weighed from each of the three treatment groups (1D, 3D and 7D; total $n = 90$) and no differences were observed between groups (mean egg mass 98.4 ± 7.4 g, $F_{2,87} = 0.26$, $P = 0.8$). However, mean egg mass increased over the 6 days they were

laid (Pearson's correlation coefficient $r_{90} = 0.33$, $P = 0.001$). The mass of the smallest egg was 67% that of the largest.

Hatching success and incubation length

Overall hatching success significantly decreased with frequency of disturbance (Wald $\chi^2 = 19.52$, $df = 3$, $P < 0.001$, $n = 120$; Table 1). Compared with the control group, investigator disturbance reduced hatching success by 39% in the 7D group, 61% in the 3D group and 100% in the 1D group (Table 1).

All 120 burrows were monitored for the entire 53.5-day (± 0.96) incubation period. The number of hatching checks needed to determine hatching success averaged 1.7 ± 0.9 ($n = 38$) and differed slightly between groups (control: 1.3 ± 0.6 , 3D: 2 ± 0.5 , 7D: 2.1 ± 1.3 ; $F_{2,35} = 3.56$, $P = 0.04$). The duration of incubation differed significantly between treatment groups ($F_{2,35} = 4.60$, $P = 0.02$). *Post hoc* least-significant difference testing revealed that the 7D group had a slightly, but significantly, longer incubation period (54.1 ± 1.3 , $n = 11$) than did controls (53.2 ± 0.5 , $n = 19$, mean difference 0.9 ± 0.3 , $P = 0.01$) and the 3D group (53.1 ± 0.3 , $n = 8$, mean difference 1.0 ± 0.4 , $P = 0.02$). Because none of the 1D nests hatched, the incubation length could not be determined.

Hatchling mass and size did not differ between groups (mass $F_{2,30} = 2.98$, $P = 0.06$; head length $F_{2,30} = 2.66$, $P = 0.08$; bill length $F_{2,30} = 0.38$, $P = 0.68$; bill depth $F_{2,30} = 0.03$, $P = 0.96$; wing length $F_{2,30} = 2.95$, $P = 0.07$; tarsus $F_{2,30} = 1.75$, $P = 0.19$).

Table 1. Comparisons showing the differences in hatching success, fledging survival and overall reproductive success in the four treatment groups.

Treatment	Hatching success	Fledging survival	Overall reproductive success
Control	63.3% ^a ($n = 30$)	57.8% ($n = 19$)	36.6%
7D	36.6% ^{ab} ($n = 30$)	63.6% ($n = 11$)	23.3%
3D	26.6% ^b ($n = 30$)	75.0% ($n = 8$)	20.0%
1D	0.0% ^c ($n = 30$)	n.a.	0.0%

Levels of handling in each treatment group during the incubation period were: control, only once on the day of laying; 7D, every 7 days; 3D, every 3 days; and 1D, every day. Different subscripts of hatching success refer to significant pairwise comparisons between groups.

Although the causes of nest failure could not be identified in all cases, the primary cause of failure was nest abandonment by incubating parents. Of the 82 observed eggs that did not hatch, 75% failed because the parents permanently abandoned their nesting attempt. Sixty per cent of egg abandonments occurred during the first half of the incubation period (Fig. 1). Of eggs that failed to hatch, 6% were because they were either rotten or infertile. The fate of 6% of eggs in the control group could not be determined because of the interval between nest checks. Predation also accounted for some egg failure. Ten eggs were predated during the experiment (12% of eggs that did not hatch or 8% of all eggs monitored) by Blotched Blue-tongue Lizards *Tiliqua nigrolutea* and Australian Water Rats *Hydromys chrysogaster* (Carey 2010). Predation occurred at all times of the incubation period and in all treatment groups.

The minimum number of disturbances sufficient to cause permanent egg abandonment was a single visit in the 1D treatment group (mean 14.1 ± 11.1 visits, range 1–44 visits, $n = 28$). Temporary egg neglect was observed in all 1D burrows at some stage during the incubation period. Temporary egg neglect in the 1D treatment group averaged 3.2 ± 2.4 days (range: 1–17 days, $n = 30$). Only two 1D burrows (6.6%) were active after the 53-day incubation period had passed, and neither of these eggs hatched (Fig. 1).

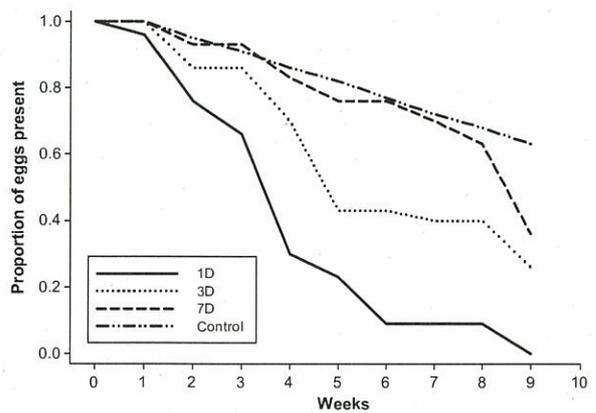


Figure 1. Proportion of active Short-tailed Shearwater nests over time among the four treatment groups. Note, for the control group, a constant rate of egg loss is assumed over the incubation period.

Chick survival, mass and size

All chicks were measured on the same day. Control chicks (mean 56.5 ± 1.7 days) were slightly but not significantly older than 3D and 7D chicks (3D mean 55.3 ± 1.1 days; 7D mean 55.4 ± 0.9 , $F_{2,35} = 2.85$, $P = 0.07$). Chick survival was not significantly influenced by handling adult birds during incubation (Wald $\chi^2 = 0.11$, $df = 2$, $P = 0.74$, $n = 38$; Table 1). Analysis of chick body mass showed significant differences between the three groups ($F_{2,21} = 5.96$, $P = 0.009$), with control chicks being on average $252 (\pm 74.9)$ g heavier than 3D chicks and $138 (\pm 71.3)$ g heavier than 7D chicks (Fig. 2). Significantly larger bill depths and wing lengths were recorded in control chicks than in the 3D and 7D treatment groups (Table 2). PC1 accounted for 55% ($\lambda = 2.78$) of the total variance explained by the components and four variables loaded heavily and positively on this PC (> 0.71 ; the exception was bill depth = 0.15). Despite control chicks being greater in some variables, there was no statistically significant difference in PC1 scores between treatment groups; however, the difference did come close to the 0.05 significance level (Table 2). After controlling for body size, no significant effect of investigator disturbance on body mass was detected between the three groups (ANCOVA: $F_{2,20} = 2.28$, $P = 0.12$); however, between the control and the combined

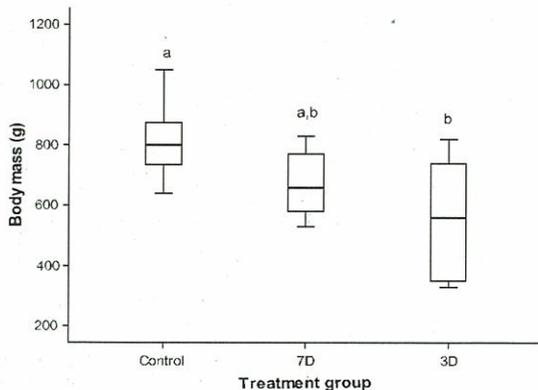


Figure 2. Box plot indicating the differences in peak chick body mass (g) between treatment groups where adults had received different levels of investigator disturbance during incubation on Great Dog Island. The plot shows the median value as a thick bar (50th percentile), the interquartile range as the box (25th–75th percentile) and the full range as the 'whiskers'. Letters denote *post hoc* testing to distinguish significantly different means using a least-significant difference test.

disturbed groups, control chicks tended to be heavier for a given body size (i.e. 3D and 7D, $n = 12$) (ANCOVA: $F_{2,20} = 3.65$, $P = 0.07$).

DISCUSSION

In this study, handling adults daily and every 3rd day significantly reduced the hatching success of Short-tailed Shearwaters. Weekly handling of incubating adults also reduced hatching success but was not significantly reduced compared with the control group. In response to investigator disturbance, Short-tailed Shearwaters reduced their parental effort by abandoning their eggs, which is consistent with life-history theory. Long-lived species such as the Short-tailed Shearwater have a high probability of adult survival, and reproduction in any one year represents a small fraction of an individual's lifetime reproduction (Lack 1954, 1968, Wooller *et al.* 1989). Therefore, parents probably reduced their investment in the current breeding attempt as a means of increasing the probability of future survival and thus future breeding attempts (Stearns 1992). Results from this study and those of others (see Blackmer *et al.* 2004) have demonstrated that frequent handling of incubating adults can alter their hatching success. It seems that Short-tailed Shearwaters are particularly sensitive to investigator handling throughout the incubation period, even more so than some other long-lived species of seabird (Borersma *et al.* 1980, Warham 1990, Marks & Leasure 1992, Blackmer *et al.* 2004, Carey 2009). In a comparable study, Blackmer *et al.* (2004) found that handling incubating birds daily or weekly significantly reduced hatching success of Leach's Storm-petrels *Oceanodroma leucorhoa* by 56 and 50%, respectively. Serventy and Curry (1984) found that handling of Short-tailed Shearwaters over a 25-year period on Fisher Island, Tasmania, resulted in a decline of occupied breeding burrows by 71%. The investigator disturbance contributed to an increase in burrow desertion, decreased breeding success, decreased recruitment of young birds and a delayed start of breeding in some birds. Their study implicated investigator disturbance in the long-term decline of this population and complements findings from other long-term studies (Ollason & Dunnet 1980).

Egg desertion was the primary response to investigator disturbance. This was particularly evident in the daily handling group, where there

Table 2. Differences in body measurements between pre-fledging Short-tailed Shearwater chicks reared by parents that had received different levels of investigator disturbance during the incubation stage. Data presented are mean \pm sd.

	Control ($n = 11$)	7D ($n = 7$)	3D ($n = 6$)	$F_{2,21}$	P
Head length (mm)	81.05 \pm 2.3	79.64 \pm 1.5	77.85 \pm 5.2	2.02	0.15
Bill length (mm)	31.44 \pm 1.5	30.94 \pm 1.4	31.20 \pm 2.0	0.19	0.82
Bill depth (mm)	7.99 \pm 0.4	7.47 \pm 0.5	7.29 \pm 0.4	5.13	0.01
Wing length (mm)	161.81 \pm 13.7	148.57 \pm 10.4	132.83 \pm 25.9	5.85	0.01
Tarsus length (mm)	59.36 \pm 1.2	58.60 \pm 1.5	58.05 \pm 2.1	1.42	0.26
PC1 score	0.45 \pm 0.65	-0.15 \pm 0.4	-0.65 \pm 1.5	2.93	0.07

was a 70% reduction in active nests after the first 4 weeks of incubation. Temporary egg neglect was observed in all burrows disturbed daily, and may have occurred in the control and other two treatment groups. If temporary egg neglect did occur, this might account for the longer incubation period for eggs in the weekly treatment group, but it cannot explain why the 3D group had a normal incubation period. Perhaps egg neglect was less common in the 3D group. The amount of egg neglect that occurred between 3D and 7D groups is difficult to quantify due to the interval between nest checks. Egg neglect resulting in extended incubation periods has been reported for a number of seabirds (Mathews 1954, Boersma & Wheelwright 1979, Warham 1990). Interestingly, in the most disturbed group, 1D, two birds continued incubating their egg well past the expected hatching date. One possibility for this is that the egg neglect in 1D and 3D groups was so severe that the embryo died. A few 3D and 7D embryos survived but developed more slowly, which extended the incubation period. As a result of high levels of investigator disturbance in Tufted Puffin *Fratercula cirrhata* colonies, Pierce and Simons (1986) also found that birds had longer incubation periods.

Although in the current study, investigator handling of adults had an adverse effect on hatching success, it did not affect chick survival up to two-thirds of the way through pre-fledging development. Still, when taking into account overall reproductive success, the control treatment group recorded a 36% success rate which, on average, was 16% higher than in the disturbed treatment groups. Long-term data from Fisher Island suggest the reproductive success of the control group is within the expected range for Short-tailed Shearwaters, where on average 49% of eggs laid produce large chicks (range 18–85%) (Serventy & Curry 1984). Booth *et al.* (2000) handled Little Shearwa-

ters *Puffinus assimillis haurakiensis* every 2 days throughout the incubation period and did not find any effects on chick survival. Overall, 29% of 'study burrows' with a hatched egg were successful in fledging a chick, compared with 30% of burrows in the control group. Similarly, investigator handling of incubating Gould's Petrel *Pterodroma leucoptera* did not seem to produce any differences between chick growth and survivorship (O'Dwyer *et al.* 2006). However, recent evidence suggests that poor early development conditions can lead to a reduction in the growth of the embryo with consequences for the organism later in life (Gorman & Nager 2004, Nilsson *et al.* 2008). This may explain the results from the present study, where investigator disturbance may have had a slight effect on body size, in that chicks from treatment groups were structurally smaller. Furthermore, the more disturbance there was, the smaller the chicks tended to be. Body mass was also affected in chicks from treatment groups. Parent birds that were handled every third day produced significantly lighter chicks than were found in the control group despite no differences between groups in hatching mass and in disturbance after hatching. Nevertheless, it seems that handling adults during incubation could also have some sub-lethal effects on post-hatching offspring development. This finding supports other experimental studies on prenatal developmental conditions, carry-over effects of the incubation stage on the next life-history stage and the importance of incubation as a component of reproductive costs and for nestling quality (Gorman & Nager 2004, Nilsson *et al.* 2008, Pérez *et al.* 2008). Recent evidence demonstrates that reproductive effort during egg formation and incubation can cause intra-individual and intra-generational trade-offs (Nager *et al.* 2000, 2001, Nilsson *et al.* 2008). Variation in incubation effort can have substantial effects on the potential fitness of the

offspring (Gorman & Nager 2004). Carry-over effects on future life-history stages represent another cost that may influence parental care decisions because the production of poor-quality offspring is costly both to the parents and to the offspring themselves (Gorman & Nager 2004). An alternative view for the poor development of offspring is the role of increasing levels of stress hormones such as corticosterone in adults as a result of handling (Buttemer *et al.* 1991, Astheimer *et al.* 1992). In many vertebrate species, including amphibians, reptiles and birds, corticosterone is a main glucocorticoid involved in regulation of fuel, immune reactions and stress responses. Variation in stress-related hormones such as corticosterone in response to investigator or tourist disturbance has been researched across seabird taxa such as penguins (for a review, see Walker *et al.* 2008), gulls (Brewer *et al.* 2008), shearwaters (Navarro *et al.* 2008) and puffins (Whidden *et al.* 2007). An increase in circulating corticosterone levels may direct behaviour away from reproduction and towards activities that promote self-maintenance such as feeding (Astheimer *et al.* 1992). If this is the case, these birds would reduce both food delivery rates and meal sizes during the chick provisioning stage. For some highly pelagic species, whose chicks are fed infrequently, even a small reduction of food could be serious, particularly in the early stages of chick development. Any reduction in delivery rates or meal size could slow growth rates and/or peak fledging mass. Several studies on shearwaters have shown that a higher fledging mass has a positive outcome for post-fledging survival and recruitment into the breeding population (Manx Shearwater *Puffinus puffinus*: Perrins *et al.* 1973, Brooke 1990, Sooty Shearwater *Puffinus griseus*: Sagar & Horning 1998). This may be a physiological mechanism, but there is an assumption that corticosterone levels remain elevated throughout the chick-rearing period despite no further disturbance. This may not be true and provides an avenue for further research. Alternatively, reduced post-hatching development may be a consequence of disturbed parents being in poorer condition during chick-rearing and therefore their chick develops less well. Unfortunately, the data cannot distinguish between these possibilities.

Handling, banding and nest monitoring have occurred in many other studies on seabirds, although the frequency of handling that was associated with nest abandonment is often not

reported (Götmark 1992, Nisbet 2000). Results presented in this study may exaggerate the effects of investigators because naïve birds were used; habituated birds might be less likely to abandon their nests (Burger & Gochfeld 1999). However, these results are consistent with the responses observed in a number of long-lived seabirds. For example, as a result of investigator disturbance, studies have shown a reduced reproductive success in puffins (Rodway *et al.* 1996), albatross (Wheeler *et al.* 2009), storm-petrels (Blackmer *et al.* 2004), boobies (Burger & Gochfeld 1993) and cormorants (Ellison & Cleary 1978). The other important issue to consider is that the results of this study may have been biased because handling commenced so early in incubation. It may not necessarily just be how frequently an adult is handled that is important, but the timing during incubation as well. There are physiological stress-response reasons why impacts in early incubation might be more severe, as birds have yet to switch firmly to a regular incubation schedule and even a low level of stress during this critical period may trigger abandonment (Beaulieu *et al.* 2010).

In summary, this study demonstrates that the handling of adults daily and every 3 days during incubation has a significant impact on Short-tailed Shearwater hatching success and chick body mass and size. It also highlights the vulnerability of birds that have had little or no experience with human disturbance. Investigator disturbance that has a detrimental effect on the individual's reproductive success, colony distribution or population could exacerbate declines of threatened species (Götmark 1992) and therefore knowledge of these effects is important in designing any research programme (Blackmer *et al.* 2004). Researchers would be well advised to consider their impact on the intended study species. Future research on seabirds should explore the effects researchers have on their study animals and existing studies may also benefit from these investigations. This may also help correct biased or misleading data in past studies. Only then can we be sure that researchers are truly recording a bird's natural behaviour.

I thank all field staff involved in this project, particularly the La Trobe University Marine Ornithology Group, Felix De Natris, Victoria McCartney and Julia Mynott. I also thank the Newall family for granting access to Great Dog Island over a number of years. ANZ Trustees Foundation – Holsworth Wildlife Research Foundation kindly provided financial assistance for this project. This manuscript

was greatly improved by thoughtful comments from Robert Trevethan, Steffen Oppel, Alex Bond, Dennis Black, the editor and four referees. This research was conducted under La Trobe University animal ethics permit number AEC05-15-W and Tasmanian Department of Primary Industries and Water permit No. FA 06494.

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Received 21 March 2010;
 revision accepted 24 January 2011.
 Associate Editor: Richard Phillips.

Incubation routine, duration of foraging trips and regulation of body mass in Short-tailed Shearwaters (*Ardenna tenuirostris*)

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Abstract. The energy demands of incubation can present important costs in avian reproduction. In species where incubation is shared, the time that individuals have for foraging may be influenced by their own foraging success and their partner's ability to fast while incubating. To investigate the costs of incubation, 60 pairs of Short-tailed Shearwaters (*Ardenna tenuirostris*) were studied on Great Dog Island, Tasmania, to determine if body mass influences incubation routines, duration of foraging trips and neglect of eggs. Body mass throughout the incubation period varied considerably, with birds losing an average of 20% of their original body mass as a result of complete fasting while on land. Initial body mass of males was positively correlated with time spent incubating, and heavier birds had the ability to extend their incubation shift if their partner was delayed or failed to return from sea. The body mass when birds left the nest to return to sea was associated with days spent foraging, and was inversely related to the mass gained at sea. Temporary egg neglect was observed in both successful and unsuccessful breeding attempts, but increased the risk of breeding failure. No specific mass threshold at which birds left the nest if not relieved by their partner could be determined. Avian reproduction represents a trade-off in use of resources between current survival and reproductive investment. The results suggest that body mass during incubation plays an important role in the reproductive behaviour of Short-tailed Shearwaters, enabling adults to regulate the trade-off between risks of adult mortality and breeding failure.

Additional keywords: egg neglect, incubation costs, marine ecology, Procellariiformes, seabird ecology.

Introduction

Life-history theory predicts that investment in offspring is balanced against the cost associated with future reproduction (Stearns 1992). One way of assessing the potential cost of reproduction in birds is to monitor co-ordination of nest relief and parental body mass (Drent and Dann 1980). During incubation, pelagic seabirds undergo large variations in their body mass as a result of concomitant fasting (Prince *et al.* 1981; Chaurand and Weimerskirch 1994; Tveraa *et al.* 1997). Parent birds must coordinate their incubation shifts with foraging trips at sea to ensure constant warming of the embryo and protection of the egg from predation (Carey 2010). A bird must spend sufficient time at sea to replenish its body reserves to cope with the period of fasting during its subsequent incubation spell (Johnstone and Davis 1990). However, if a partner spends too much time at sea, its mate may be forced to desert the egg as its own energy reserves become critically depleted (Chaurand and Weimerskirch 1994; Tveraa *et al.* 1997). As a consequence, the rate of breeding failure is high during this period (Johnstone and Davis 1990).

Procellariiformes typically have extended incubation periods with long incubation shifts (Warham 1990). This is due, in part, to the large heavy eggs and vast distances travelled to acquire sufficient food (Warham 1990; Weimerskirch and Cherel 1998; Cherel *et al.* 2005). Short-tailed Shearwaters (*Ardenna tenuirostris*) have four long incubation shifts, alternating between parents, spanning a total incubation period of 53 days (Serventy

1967; Fig. 1). A single egg is laid and if breeding fails it is not replaced. The male begins incubation while the female returns to sea to forage after laying (Serventy 1967) though the female may remain with the egg until the male arrives. Thus the first and third incubation shifts are commonly undertaken by the male, and the second and fourth shifts by the female. Each incubation shift lasts ~10–14 days (Serventy 1967).

When food resources are difficult to acquire, Procellariiformes may be forced to increase the length of an incubation shift while their partner is at sea (Chaurand and Weimerskirch 1994; Tveraa *et al.* 1997). This is achieved at the cost of the incubating parent's body condition, and that in turn has consequences for breeding success. For example, Antarctic Petrels (*Thalassoica antarctica*) can lose 20% of their body mass in one 2-week incubation shift, and adults with lower body condition spend more time foraging at sea, which increases rates of nest desertion (Lorentsen and Røv 1995; Tveraa *et al.* 1997). Similarly, if a partner has not returned to take over incubation, Blue Petrels (*Halobaena caerulea*) will abandon a nest when their body condition falls below a set mass threshold (Chaurand and Weimerskirch 1994). Clearly, incubation places a considerable demand on petrels to manage their own energy reserves, and they may therefore need to regulate their body mass closely. However, the role of body mass in the birds' behaviour during incubation remains unknown for most species of shearwater (*Ardenna*, *Puffinus*).

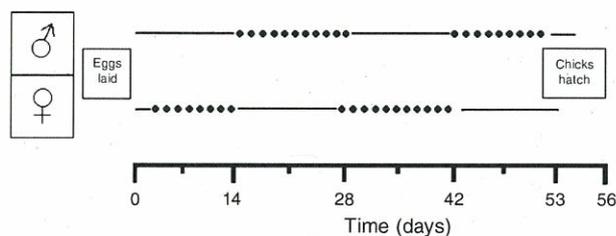


Fig. 1. Diagrammatic representation of the incubation schedule of Short-tailed Shearwaters. Pairs usually perform four (but up to six) incubation shifts in order to hatch the egg. The solid black lines indicate the time spent on the nest. The filled circles indicate the time spent at sea. Labelled boxes show when eggs are laid and when chicks hatch.

For Short-tailed Shearwaters, little is known about the incubation routine for the complete incubation period (Serventy 1967; Serventy *et al.* 1971). In addition, there is little information about the relationships of body mass with incubation schedule, egg desertions or time spent at sea. The aims of this study were to determine accurately the incubation routine of Short-tailed Shearwaters and to investigate the importance of body mass during incubation. In this study, I tested the hypothesis that body mass at the end of an incubation shift would determine the subsequent length of a foraging trip and the body mass upon return to the colony. Adults with lower body mass would be expected to have shorter incubation shifts and longer foraging bouts at sea. The occurrence of egg neglect in relation to body mass was also investigated, where I predicted that adults that were not relieved by their partners would desert their eggs at a lower body mass than would adults that were relieved by their partner. It was expected that neglected eggs were less likely to hatch, thereby demonstrating the importance of body mass for effective parental care in this long-lived pelagic seabird.

Methods

This research was conducted on Great Dog Island, in the Furneaux Group, Tasmania ($40^{\circ}15'07''S$, $148^{\circ}15'08''E$), between 25 November 2007 and 21 January 2008.

Because the peak laying period is between 25 and 29 November (Serventy 1967; Meathrel *et al.* 1993), burrows were initially inspected during that time. Sixty active burrows were marked with a polyvinylchloride (PVC) pole, and a unique number was assigned to each site for the duration of the project. An active burrow was defined as one that contained an adult bird with an egg. When active burrows were encountered, the adults

were removed by hand, and each was placed in a calico bag and weighed with Pesola scales (1000 ± 10 g). Adults were banded with an Australian Bird and Bat Banding Scheme (ABBBS) band. Birds handled during laying were sexed by cloacal examination (Serventy 1956; Boersma and Davies 1987) or by a discriminant function analysis (Carey, *in press*).

Arrivals and departures of birds were detected by placement of fine sticks at the entrance of each burrow. To minimise handling of birds and reduce the adverse effects of investigator disturbance (see Carey 2009), birds were weighed once at arrival (Day 1), and again at Days 10, 12 and 14. If the burrow was still occupied by the same bird after Day 14, that bird was weighed daily until its partner returned. During non-weighing days, burrow entrances were closely monitored (but not inspected) for the anticipated changeover. This sampling regime continued throughout the incubation period until all eggs hatched or failed. If a burrow was found empty or to contain a cold egg, it was inspected every day until an adult bird returned to continue the incubation (defined as egg neglect), the egg was depredated or the burrow was permanently abandoned.

Statistical analyses were performed using SPSS version 17.0 (SPSS Inc., Chicago, IL). Pearson's correlation coefficients were used to test for associations between variables, and either Student's *t*-tests (both independent and paired, as appropriate) or analyses of variance (ANOVA) were used to identify any group differences. Where the assumptions of these tests were not met, the non-parametric equivalents were used. The Chi-square test was used to determine whether the proportion of temporary egg neglect varied during incubation. The significance criterion for all tests was set at ≤ 0.05 . All data are presented as means \pm standard deviation (s.d.).

Results

Incubation schedule

The duration of the main incubation shifts of adults ranged from 9 to 17 days over the 52 day (± 1.9 , $n = 13$) incubation period, except for a short first shift by the female after laying and an occasional sixth shift undertaken by the male bird at the end of the incubation period (Table 1) that, if it occurred, completed the incubation until the egg hatched.

In total, males spent more time on the egg than did their female partners ($t_{24} = 3.62$, $P < 0.01$). Males spent a mean of 26 ± 1.7 days on the egg, and females 23.7 ± 1.6 days (52 and 48% respectively). The time spent incubating the egg increased significantly for males between the second and fourth shifts

Table 1. Duration of incubation shifts, mass at the start and end of incubation shifts, mass on leaving eggs for period of neglect, and the proportion of shifts with periods of egg neglect in Short-tailed Shearwaters

Figures are means \pm s.d.; sample size is given in parentheses; F = female, M = male

Shift	Sex	Duration (days)	Mass at start of shift (g)	Mass when relieved (g)	Mass at neglect (g)	Percentage of periods of neglect
First	F	1.76 \pm 1.34 (21)	—	530.0 \pm 28.98 (16)	523.3 \pm 33.86 (6)	27% (22)
Second	M	12.11 \pm 1.42 (46)	616.1 \pm 45.85 (57)	522.0 \pm 33.59 (35)	514.2 \pm 38.01 (12)	25% (47)
Third	F	13.57 \pm 1.61 (37)	671.7 \pm 36.55 (47)	530.0 \pm 27.10 (31)	532.9 \pm 36.84 (7)	18% (38)
Fourth	M	14.28 \pm 1.51 (25)	732.6 \pm 50.82 (39)	560.0 \pm 31.40 (15)	546.4 \pm 29.76 (11)	42% (26)
Fifth	F	11.50 \pm 1.87 (14)	711.3 \pm 49.65 (31)	600.0 \pm 70.71 (2)	562.0 \pm 43.82 (5)	71% (7)
Sixth	M	2.00 \pm 1.73 (3)	745.0 \pm 68.07 (4)	—	—	—

($t_{69}=6.0$, $P<0.01$, see split of incubation shifts in Table 1), whereas the total time incubating decreased significantly for females between the third and fifth shifts ($t_{49}=3.9$, $P<0.01$, Table 1).

Changes in body mass

With no food delivery by partners during the incubation period, incubating birds inevitably lost body mass as a result of complete fasting within the burrow. The mean loss of mass was $11.0 \pm 2.5 \text{ g day}^{-1}$ (range 4.3–18.0 g day^{-1} , $n=97$ birds), which represented a loss of 1.6% of the initial body mass per day (range 0.7–2.4%, $n=97$). Adults lost a mean of 20.1% of their body mass during an incubation shift. The total body mass lost was closely related to the number of days spent incubating ($r_{97}=0.65$, $P<0.01$). Incubating females lost slightly more mass during an incubation shift than did males (females: $21.6\% \pm 3.9$, $n=42$; males: $19.1\% \pm 5.0$, $n=55$; Mann–Whitney test, $z=2.00$, $P=0.04$). The greatest mass lost by an individual male during an incubation shift was 28.4% of initial body mass; the maximum that an individual female lost was 32.9%.

Overall, the mean mass of males and females at the start of an incubation shift increased significantly between shifts (males: $t_{94}=11.7$, $P<0.01$; females: $t_{76}=4.1$, $P<0.01$; Table 1), whereas the mean mass at the end of an incubation shift when relieved by their partners increased for males but not for females (males: $t_{63}=2.5$, $P=0.01$; Mann–Whitney test, $z=1.7$, not significant (n.s.); Table 1). Body mass at the start of the incubation period was positively correlated with length of incubation for males ($r_{55}=0.53$, $P<0.01$) but not for females ($r_{42}=0.15$, $P=0.33$). Overall, the greater the body mass of an adult, the longer the incubation spell was likely to be ($r_{97}=0.42$, $P<0.01$).

Return from sea

Adults returned to the burrow after varying amounts of time away at sea (mean 15.7 ± 2.3 days, range 11–28 days, $n=85$ birds). While at sea, foraging birds increased body mass by $1\text{--}19 \text{ g day}^{-1}$ (mean $12.2 \pm 4.0 \text{ g day}^{-1}$, $n=85$). The time spent at sea was not related to body mass at return to the nest ($r_{85}=0.08$, n.s.) or mass gained while at sea ($r_{85}=-0.07$, n.s.). Males gained significantly more body mass than did females (males: $206.9 \pm 57.7 \text{ g}$, $n=42$; females: $168.1 \pm 52.3 \text{ g}$, $n=43$; $t_{83}=3.25$, $P<0.01$). Thus, while at sea, the mean daily gain in body mass of males ($13.8 \pm 4.1 \text{ g day}^{-1}$, $n=42$) was significantly higher than that of females ($10.6 \pm 3.3 \text{ g day}^{-1}$, $n=43$; $t_{83}=4.02$, $P<0.01$). For males there was no difference in mean daily gain of body mass between their two stays at sea (first: $14.0 \pm 4.1 \text{ g day}^{-1}$ second: $11.9 \pm 4.4 \text{ g day}^{-1}$, $n=42$; $t_{40}=1.0$, n.s.). Females, however, significantly increased their mean daily gain of body mass during foraging between their first and second stays at sea ($8.6 (\pm 3.2)$ and $11.7 (\pm 2.9) \text{ g day}^{-1}$, $n=43$ respectively, $t_{41}=3.2$, $P<0.01$).

Overall, when birds left the nest to return to sea, their body mass was positively related to the subsequent time spent foraging ($r_{82}=0.22$, $P<0.05$; Fig. 2a). There was no relationship between body mass at the end of an incubation period and body mass upon their next return from sea after foraging ($r_{82}=0.21$, n.s.; Fig. 2b). The mass when birds left the nest to return to sea was inversely related to the mass gained at sea ($r_{82}=-0.37$, $P<0.01$; Fig. 2c). Overall, the duration of a shift and the total mass an incubating

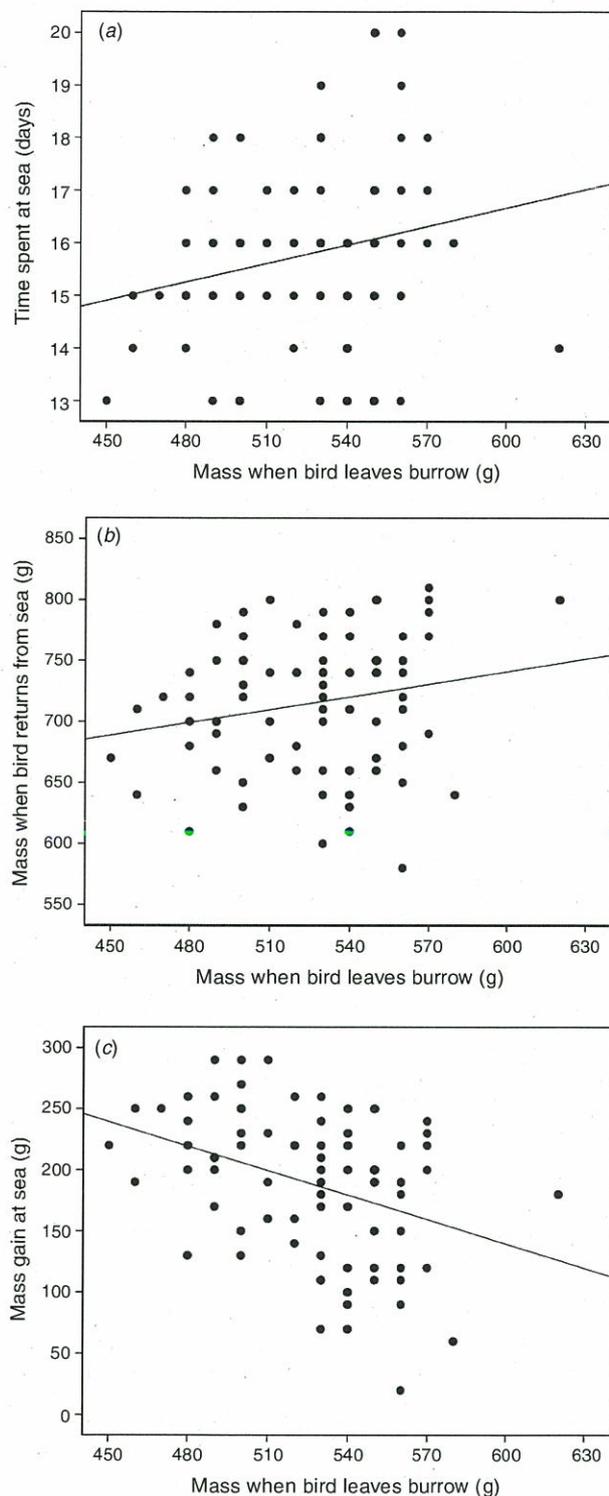


Fig. 2. The relationship between the body mass of Short-tailed Shearwaters leaving their burrow after an incubation shift and: (a) the duration of the foraging trip ($y=0.0117x+9.6456$); (b) the mass when the bird returns to the nest ($y=0.3466x+532.83$); and (c) the mass gain at sea ($y=-0.06653x+538.83$).

bird lost were not related to the subsequent duration at sea, mass on return or the mass gained at sea (Table 2).

Egg neglect

Temporary egg neglect occurred in 93% of burrows. The proportion of temporary egg neglect varied significantly during incubation ($\chi^2_4 = 16.4$, $P < 0.01$), being highest at the end of the incubation period (Table 1). A mean of 1.41 ± 0.91 periods of egg neglect (range 0–4) was observed per burrow during the incubation period. There was significantly less egg neglect in burrows where the chick hatched (0.54 ± 0.52 periods, range 0–1, $n = 13$) than in unsuccessful burrows (1.65 ± 0.85 , range 0–4, $n = 36$; $t_{57} = 4.5$, $P < 0.01$). The observed duration of egg neglect was also significantly less in successful (0.58 ± 0.51 days, $n = 12$) than in unsuccessful burrows (2.6 ± 2.8 days, $n = 27$; Mann–Whitney test, $z = 3.6$, $P < 0.01$, $n = 39$).

Birds that neglected their eggs did so after incubating periods that ranged from 1 to 16 days. Following a period of egg neglect, incubation was re-started by its mate. Body mass did not change over the incubation period for females that neglected their eggs ($F_{2,15} = 1.5$, n.s.; Table 1) but for males body mass when egg neglect occurred was significantly higher in the fourth shift than the second shift ($F_{1,21} = 5.0$, $P = 0.03$, Table 1). For both males and females, no significant differences were detected between the body mass of birds that neglected an egg and the body mass of birds when they were relieved having remained on the nest (males: 529.6 ± 37.4 g, $n = 23$; and 533.4 ± 37.1 g, $n = 50$ respectively; $t_{71} = 0.41$, n.s.; females: 537.8 ± 39.0 g, $n = 18$; 532.9 ± 32.0 g, $n = 49$ respectively; $t_{65} = 0.53$, n.s.; Table 1). For birds that neglected eggs, there was no significant difference in the body mass when eggs were left between males (529.6 ± 37.4 g, $n = 23$) and females (537.8 ± 39.0 g, $n = 18$; $t_{39} = 0.69$, n.s.; Table 1).

Discussion

Co-operation in reproduction decision making can only evolve if pairs can find optimal solutions that allow both survival and reproduction. These results show that body mass during the incubation period plays an important role in Short-tailed Shearwater reproductive behaviour, confirming the fundamental importance of the regulation of body mass in this species. These birds began their incubation shifts with a high body mass that inevitably declined during the shift because they neither ate nor drank at that time. During incubation, these birds lost an average 1.6% of their initial body mass per day, culminating in a 20% reduction of their body mass over an incubation shift. Some individual birds demonstrated an ability to extend their incubation

shift if their partner did not return from sea. In such cases, the incubating bird was able to lose up to one-third of its body mass. This adaptation may help to buffer the late return of a partner if food resources are inadequate or foraging is difficult. Body mass at the start of an incubation shift was evidently important in regulating the length of that particular shift. It seems logical that a higher initial body mass permits a longer incubation shift. Individuals that began their incubation shift at a low body mass could not remain on the egg until their partner returned from sea and would have to abandon the egg for their own welfare and, thus, for the sake of future reproductive output. The body mass at nest abandonment was similar to mass when relieved by a partner. This suggests that relief by partners is timed to occur just before the point of abandonment and perhaps why periods of egg neglect are short, particularly for birds that breed successfully. This study did not find a precise mass threshold at egg abandonment and such a threshold may be difficult to determine in this species given the variability in size of birds. However, the results of this study suggest that birds are not prepared to stay any later than when they reach a body mass at which they would expect to be relieved.

The results of this study reveal that Short-tailed Shearwaters regained their lost body mass when they returned to sea at a more rapid rate than they lost it. Time spent at sea was ~15 days, and birds gained an average of 12 g day^{-1} . Overall, males gained more mass at sea than females. Gain of body mass by females was greater during their second foraging trip than their first, but there were no differences between the two foraging trips undertaken by males. In males there were also no differences in their average daily mass gain between their two foraging trips. The differences in body mass gain observed between males and females may reflect sex-specific foraging ranges in this species. That appears to be the case for giant-petrels (*Macronectes* spp.) (González-Solís *et al.* 2000, 2007; Quintana *et al.* 2010). Alternatively, females may have had difficulty locating food during their first stay at sea as their daily mass gain was lower at that time. During their second trip to sea, an increase in body mass may have resulted from an increase in food availability in the Southern Ocean. At this time, zooplankton volume increases in the Subantarctic (Knox 1984; Atkinson and Peck 1988; Reid *et al.* 2005). Time spent at sea was significantly related to a bird's body mass when it left its burrow. This indicates that birds were required to achieve a body mass that would be sufficiently high to cope with their next incubation shift. During incubation, the time individuals have available for foraging is constrained by their partner's ability to remain on the egg. An extended foraging trip does not necessarily increase the probability of successful foraging (Chaurand and Weimerskirch 1994). It does, however, increase the probability of nest desertion by the incubating bird. Some Short-tailed Shearwaters were observed to have a foraging trip of up to 28 days, but time spent at sea was not related to mass upon return or mass gained while at sea. This could have occurred because they had difficulty foraging effectively. This observation may also support the theory of a threshold in return mass, where the individual will forage to achieve this threshold which will be dependent both on time spent and the quality of the bird. Birds that had difficulty gaining body mass could have been young breeders or inexperienced birds. A bird's age and experience are variables known to affect the breeding success of a wide range of birds, including procellariids such as Manx Shearwater (*Puffinus puffinus*) (Brooke 1978) and

Table 2. The relationship between the duration of incubation shifts and loss of body mass during incubation, and the duration of and mass gain during the subsequent stay at sea in Short-tailed Shearwaters. Values shown are Pearson correlation coefficients (R); n.s. = not significant

	Duration of stay at sea	Mass on return from the sea	Mass gain at sea
Duration of shift ($n = 69$)	0.05 (n.s.)	-0.19 (n.s.)	-0.15 (n.s.)
Total mass loss ($n = 69$)	0.01 (n.s.)	-0.17 (n.s.)	-0.20 (n.s.)

the Northern Fulmar (*Fulmarus glacialis*) (Ollason and Dunnet 1978), which in turn, may be positively correlated with body mass or condition (Sæther 1990; Weimerskirch 1992, 1995; Lecomte *et al.* 2010). In essence, the ability of birds to gain body mass across the incubation period may be directly related to them being more efficient foragers. This explanation has been put forward for the Antarctic Fulmar (*Fulmarus glacialisoides*) (Weimerskirch 1990). Overall, the duration of an incubation shift and the total amount a bird lost during that incubation shift were not related either to how long the bird stayed at sea or to body mass on return from foraging. The association between a bird's mass when it left the nest and the trip duration at sea and the mass gain is logical, as a set mass threshold can be achieved more rapidly if the mass of the bird is already high (Chaurand and Weimerskirch 1994). Thus, if birds reach their desired body mass quickly (from successful foraging) they can return more quickly to land and relieve their mate. If foraging is difficult, they spend a prolonged amount of time at sea to acquire their desired body mass at the risk of their partner abandoning the nest as a result of limited energy reserves.

The incubation routine of Short-tailed Shearwaters had been studied previously, but to only a small extent (Serventy 1967). No detailed work has been conducted, and this is the first comprehensive study of its kind. The results reveal that incubation shifts average 11–14 days, but differ between the sexes. Male birds spent more time incubating than did females, in accord with findings from other studies of procellariiforms (Jouventin *et al.* 1985; Warham 1990). Male birds in the present study were on average 3% larger than their female partners (Carey, *in press*), and there may therefore be different energy budgets for the two sexes that create a potential for differential parental effort (Clutton-Brock 1991). This could explain why incubation by males averaged a total of 26 days compared with the females' 23.7 days (52 and 48% respectively). These results contrast with those of Fisher (1971), who found that noticeable differences in incubation shifts occurred during the early stages of the incubation period, but that birds adjusted their shifts later so that the total time spent by each sex was similar.

The degree of intermittent incubation behaviour has not been studied in Short-tailed Shearwaters, but this study revealed that egg neglect was common. Warham (1990) suggested that eggs may be neglected at any stage of the incubation cycle, but perhaps more at the start when there has been little investment in the breeding attempt, and less so as the point of hatching approaches. This particular pattern was not observed in this study, possibly because changeovers between parents were sometimes delayed to ensure that the on-duty bird had adequate food for the chick. Imber (1976) noted a higher frequency of changeovers three days before hatching in Great-winged Petrels (*Pterodroma macroptera*), and suggested that the duration of the last incubation shift was precisely timed to ensure a changeover at 55 days, the peak time of hatching. The advantage to a pelagic species that is dependent on synchronised breeding shifts is that an uncovered egg does not necessarily result in instant breeding failure even if it does decrease the probability of hatching success (Boersma and Wheelwright 1979). This situation allows adults that have not achieved their desired body mass to persist with foraging without certain breeding failure. Warham (1990) also suggested that the resistance to egg chilling may be a major adaptation to

pelagic foraging that allows them to nest far from their main food source.

Results from this study demonstrate that body mass during incubation plays an important role in the reproductive behaviour of Short-tailed Shearwaters, enabling adults to regulate the trade-off between risks of breeding failure and risks of adult mortality. Subsequent research might reveal whether these results are consistent across different years, colonies, and age of birds and their breeding experience. Further research is needed to identify sex-specific foraging locations of this species and to investigate the effects that age and experience have on individual body mass or condition based on multi-year data.

Acknowledgements

I am indebted to Dennis Black, Felix De Natris, Sophie Kennedy, Victoria McCartney and Danni Smith for their assistance with fieldwork. I thank Leigh Cox for transportation and the Newall family for allowing access to their facilities on Great Dog Island. ANZ Trustees Foundation – Holsworth Wildlife Research Foundation kindly provided financial assistance to this project. This research was conducted under La Trobe University animal ethics permit number AEC05–15-W and Tasmanian Department of Primary Industries and Water permit numbers FA 07166 and FA 08145. Robert Trevethan, Julia Mynott and two anonymous referees significantly improved earlier versions of the manuscript.

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Manuscript received 3 June 2010, accepted 26 November 2010

Sexual size dimorphism, within-pair comparisons and assortative mating in the short-tailed shearwater (*Puffinus tenuirostris*)

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Abstract – Biometric studies of short-tailed shearwaters (*Puffinus tenuirostris*) indicate differences in body mass and linear measurements between sexes. Here the degree of sexual size dimorphism in 390 short-tailed shearwater adults is assessed and a sex-discriminating function is produced to improve methods for sexing live birds in the field. Analysis of body mass and linear measurements showed males to be significantly heavier and larger than female birds in all variables. The largest degree of sexual size dimorphism was in bill depth (7.5%) followed by body mass (5.1%). Bill depth plus total head length were the most accurate variables in a discriminant function model. Together, these 2 variables predicted sex with 84% accuracy. Bill depth alone predicted sex with 82% accuracy. However, application of a sex-discriminating model developed from another colony, did not correctly classify the sex of adult birds as accurately. This can be explained by the existence of significant geographical variation in body size within the species and reinforces the need for colony-specific sex discriminant models. Comparisons within-pairs revealed that bill depth is a more reliable indicator of sex, without the need for a discriminant function analysis. Contrary to previous studies, measurements of male and female partners showed no evidence of assortative mating in any character assessed. If short-tailed shearwaters mate assortatively then it may be based on traits other than structural size.

Carey, M.J. 2011. Sexual size dimorphism, within-pair comparisons and assortative mating in the short-tailed shearwater (*Puffinus tenuirostris*). *Notornis* 58(1): 8-16.

Keywords assortative mating; bill depth; discriminant analysis; morphometrics; sexing; shearwater

INTRODUCTION

Individuals of known sex are vital in many ecological and behavioural studies due to the importance of identifying the roles of each sex in various aspects of breeding biology. However, sex can often be difficult to determine in seabirds (Procellariiformes) because many exhibit monomorphic morphology or plumage characters (Warham 1990). Although males are usually larger than females in many procellariids, there can be a considerable overlap

between the sexes in their size ranges (Marchant & Higgins 1990; Warham 1990). Monotypic birds like shearwaters and petrels are sexed from a variety of methods, such as dissection, observing copulation, cloacal examination at the time of egg-laying (Serventy 1956; Boersma & Davies 1987), sexual voice dimorphism, particularly in the *Puffinus* group (Brooke 1978; Bourgeois *et al.* 2007) and more recently, by molecular methods using polymerase chain reaction (PCR) amplification (Kahn *et al.* 1998). Alternative *in situ* methods are desirable, especially outside the breeding season, when knowledge of a bird's sex is required.

Received 10 Jan 2011; accepted 18 May 2011
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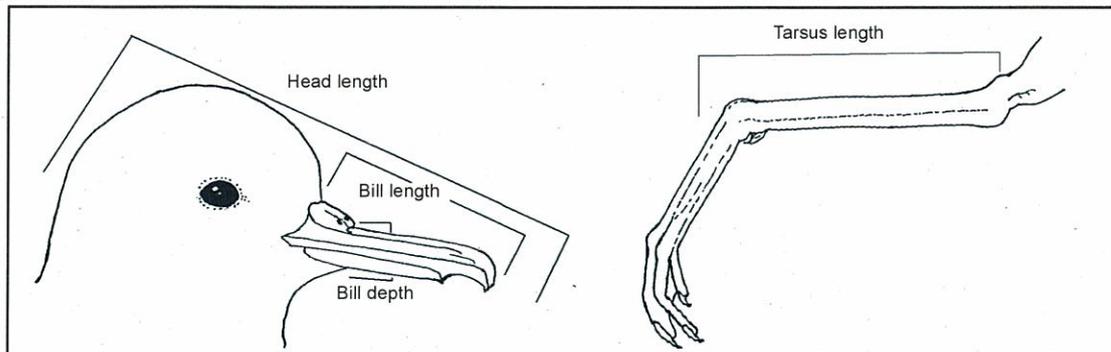


Fig. 1. Location of morphometric measurements taken on short-tailed shearwaters: head length, bill length, bill depth and tarsus. Wing length not shown. Line drawings courtesy of Vicki McCartney.

In situations outside the breeding season where invasive techniques or molecular methods are not possible or undesirable, sex can sometimes be determined from external morphometric measurements. A discriminant function analysis (DFA) combines a number of morphometric measurements and allows relatively accurate predictions of an individual's gender, even when there is considerable overlap in size ranges. These morphometric measurements can be a valuable tool for sexing birds, especially outside the breeding season, as other sexing methods can be applied only during the breeding season (e.g. vocalisations, cloacal examination, and copulation behaviour). Predictive functions from body measurements have been used successfully to discriminate gender in a variety of monomorphic seabirds, including brown noddies (*Anous stolidus*) (Chardine & Morris 1989), razorbills (*Alca torda*) (Wagner 1999), penguins (Amat *et al.* 1993; Renner *et al.* 1998) and gulls (Fox *et al.* 1981; Coulson *et al.* 1983; Hanners & Patton 1985; Evans *et al.* 1993; Torlaschi *et al.* 2000).

The application of a DFA to sex adult birds using external body measurements can be particularly useful because of the relatively non-invasive, cost effective and efficient nature of the technique. The predictive function derived from the DFA is species-specific, but caution must be observed when generalising over the entire geographical range of a species owing to morphometric differences between colonies (Guicking *et al.* 2004; Einoder *et al.* 2008). Thus, it has been suggested that a DFA should only be used in those studies of the local population from which it was derived (Evans *et al.* 1995).

Analyses can also be confounded if individuals mate assortatively by size (Coulter 1986; Fletcher & Hamer 2003). For example, in species where the sexes overlap in size but males are on average larger than females, assortative mating would lead to an increased likelihood of males in small pairs being sexed as females and females in large pairs being

sexed as males. Problems in identifying sex may be greatly reduced by using within-pair comparisons of relative size. Such within-pair comparisons result in improved sex determination in south polar skuas (*Catharacta maccormicki*) (Ainley *et al.* 1985) and cape petrels (*Daption capense*) (Weidinger & Franeker 1998). However, the usefulness of this approach has not been widely evaluated (Fletcher & Hamer 2003).

Short-tailed shearwaters (*Puffinus tenuirostris*) have no plumage differences between males and females although published measurements suggest there may be some morphological dimorphism (Marchant & Higgins 1990; Meathrel *et al.* 1993; Einoder *et al.* 2008). The life cycle and basic biology of short-tailed shearwaters have been described by Serventy (1967) and Serventy & Curry (1984), but few studies examined differences in body size of male and female birds. The objective in this study was to find an *in situ* method of identifying the sex of adult short-tailed shearwaters in the field that could be used outside the egg-laying period. This method provides rapid results and it is cost effective compared to molecular sexing. In this study, data are evaluated on sexual size dimorphism in body mass and 5 linear morphological measurements from randomly sampled males and females, and for known pairs. I also present an equation which can be used to sex live birds, and assess the usefulness of a DFA derived from another colony to sex birds in a different colony. Finally, I use the measurements collected on the large number of pairs in this study to test whether mate choice in short-tailed shearwaters is size-related.

METHODS

Adult short-tailed shearwaters were captured during the breeding seasons of 2006/07, 2007/08 and 2008/09 within a large colony on Great Dog I, Furneaux Group, Tasmania, Australia (40°15'07'S,

Table 1. Body measurements (mean \pm SD) of male (A) and female (B) short-tailed shearwaters according to year of capture on Great Dog I, Tasmania. Superscript letters denote significantly different means using Fisher's LSD *post hoc* testing.

A. Males	2006/07 (<i>n</i> = 90)	2007/08 (<i>n</i> = 90)	2008/09 (<i>n</i> = 13)	$F_{2,190}$	<i>P</i>
Head length (mm)	83.7 (\pm 1.9)	83.1 (\pm 2.1)	84.0 (\pm 1.4)	2.43	0.09
Bill length (mm)	32.7 (\pm 1.4)	32.5 (\pm 1.2)	33.0 (\pm 1.3)	1.21	0.30
Bill depth (mm)	8.9 (\pm 0.3)	8.90 (\pm 0.4)	9.1 (\pm 0.4)	1.64	0.19
Wing length (mm)	272.5 (\pm 5.7)	273.1 (\pm 6.7)	273.2 (\pm 6.3)	0.27	0.76
Tarsus length (mm)	58.8 (\pm 1.3) ^a	59.4 (\pm 1.6) ^b	60.1 (\pm 1.5) ^b	5.86	0.003
Body mass (g)	642.0 (\pm 50.9) ^a	618.8 (\pm 47.7) ^b	660.0 (\pm 60.4) ^a	6.95	0.001

B. Females	2006/07 (<i>n</i> = 88)	2007/08 (<i>n</i> = 87)	2008/09 (<i>n</i> = 22)	$F_{2,194}$	<i>P</i>
Head length (mm)	81.3 (\pm 1.7)	81.5 (\pm 2.0)	80.5 (\pm 2.4)	2.51	0.08
Bill length (mm)	31.5 (\pm 1.1)	31.7 (\pm 1.1)	31.4 (\pm 1.5)	0.87	0.42
Bill depth (mm)	8.3 (\pm 0.3)	8.2 (\pm 0.4)	8.3 (\pm 0.4)	0.30	0.74
Wing length (mm)	269.2 (\pm 6.2)	269.5 (\pm 5.6)	272.2 (\pm 5.6)	2.30	0.10
Tarsus length (mm)	58.2 (\pm 1.7)	58.3 (\pm 1.3)	58.3 (\pm 1.5)	0.21	0.81
Body mass (g)	583.4 (\pm 58.7)	612.3 (\pm 75.3)	615.4 (\pm 53.4)	9.19*	0.01

*Kruskal-Wallis (χ^2), d.f. = 2

148°15'08"E). Body mass (g), plus 5 external body measurements (after Baldwin *et al.* 1931) were taken by one person (MJC) in all 3 breeding seasons (Fig. 1). Adults were weighed using Pesola 1000 g (\pm 10 g) scales and measured using Mitutoyo Vernier callipers (Mitutoyo Corporation, Kanagawa, Japan) accurate to \pm 0.02 mm and rounded to the nearest 0.1 mm (i.e., rounded up for measurements 0.06 and 0.08 and rounded down for 0.02 and 0.04). Wing length was measured using a standard butt-ended wing ruler (to the nearest 1.0 mm). The 5 morphological measurements taken for adults were: (1) head length from the tip of the maxillary unguis (upper nail of the bill) to the rear of the skull, (2) bill length from the maxillary unguis to the posterior extremity of the nares (nasal tubes), (3) vertical bill depth at the proximal base of the nares, (4) length of the tarsometatarsus (hereafter tarsus), and (5) wing length from the carpal joint to the end of the 10th primary feather. All birds were banded with an individually identifying Australian Bird and Bat Banding Scheme (ABBBS) stainless steel band. When birds were being handled during egg-laying they were sexed by cloacal examination (Serventy 1956; Boersma & Davies 1987). Birds with an obviously distended, oedematous cloaca (i.e., evidence of an oviduct stretched by laying an egg) were presumed to be female. Birds that were partnered with females were presumed to be male, as no same-sex pairs of breeding short-tailed

shearwaters have been recorded. Only those pairs which laid an egg were included in this study.

Statistical analysis

Statistical analysis was performed using SPSS (version 17.0: SPSS, Chicago, IL, USA). All variables were tested for their normality and homogeneity of variances before using appropriate tests. Principal Components Analysis (PCA) was used to characterise variability in body dimensions within the total sample. The 1st principal component (PC1) comprised head length, bill length, bill depth, wing length and tarsus length and is used as a single composite measure of body size. Differences between the sexes for each measurement were tested with a *t*-test. The sequential Bonferroni adjustment was used as multiple measures of the same individual were used ($P = 0.008$) (Sokal & Rohlf 1995). For all other tests the significance was set to $P < 0.05$.

Sexual dimorphism (SD) was calculated as a percentage between the sexes in each measurement as:

$$SD = \frac{(\bar{x}_m - \bar{x}_f)}{\bar{x}_m} \times 100$$

Where \bar{x}_m and \bar{x}_f were the mean values in males and females, respectively.

A DFA based on external morphometrics was performed after Dytham (2003). Body mass was not

Table 2. Descriptive statistics of the measurements of 390 adult sexed short-tailed shearwaters (\pm SD). Percentage of sexual dimorphism and level of significance between males and females according to the *t*-test in each variable is also shown.

	Males (<i>n</i> = 193)	Females (<i>n</i> = 197)	<i>t</i> _{2,388}	<i>P</i>	% dimorphism
Head length (mm)	83.4 (\pm 2.0)	81.3 (\pm 1.9)	10.50	<0.001	2.5
Bill length (mm)	32.7 (\pm 1.3)	31.6 (\pm 1.2)	8.24	<0.001	3.1
Bill depth (mm)	8.9 (\pm 0.4)	8.3 (\pm 0.4)	16.82	<0.001	7.5
Wing length (mm)	272.8 (\pm 6.3)	269.7 (\pm 5.9)	5.11	<0.001	1.1
Tarsus length (mm)	59.2 (\pm 1.5)	58.3 (\pm 1.6)	5.73	<0.001	1.5
Body mass (g)	632.4 (\pm 51.6)	599.8 (\pm 67.4)	5.16*	<0.001	5.1
PC1 scores	0.60 (\pm 0.80)	-0.59 (\pm 0.80)	14.57	<0.001	n.a.

*Mann-Whitney *U*-test**Table 3.** Accuracy of the discriminant function derived from measures of 390 short-tailed shearwaters. Frequencies (%) of classified birds with the original function and with the cross validation shown.

	Sex	Predicted sex	
		Male	Female
Original	Male	157 (81.3)	36 (18.7)
	Female	27 (13.7)	170 (86.3)
Cross validation	Male	156 (80.8)	37 (19.2)
	Female	28 (14.2)	169 (85.8)

included in the analysis because this can vary greatly according to the time since last food ingestion and stage of breeding. The reliability of the discriminant function was estimated by checking the predicted sex against the actual sex determined in the field. To test the reliability of the prediction a jack-knife procedure (cross validation) was performed, where each individual was classified using a function derived from the total sample minus the individual being classified.

Because a number of known pairs were sexed and measured, the degree to which males and females mated assortatively with respect to their body measurements were examined. To test for assortative mating, Pearson correlation coefficients (*r*) were calculated between pairs in all linear morphometric measurements, body mass and PC1 scores.

RESULTS

Morphometrics

In total, 390 adults were measured over the 3 years of the study: 178 in 2006/07, 177 in 2007/08 and 35 in 2008/09 (Table 1). Female body mass varied between years (Kruskal-Wallis $\chi^2 = 9.19$, *d.f.* = 2, *P* = 0.01) but these differences were not significant after Bonferroni adjustment. There were also differences in male body mass ($F_{2,190} = 6.95$, *P* = 0.001) and tarsus length ($F_{2,190} = 5.85$, *P* = 0.003) between years. *Post hoc* least significant difference (LSD) testing

(Fisher's LSD test) revealed that males in 2007/08 were significantly lighter than those in 2006/07 (mean difference: 23.2 g, *P* < 0.01) and 2008/09 (mean difference: 41.2 g, *P* < 0.01). Tarsus length of male adults were marginally longer in 2006/07 than those measured in 2007/08 (mean difference: 0.6 mm, *P* = 0.01) and 2008/09 (mean difference: 1.3 mm, *P* < 0.01). No other significant differences were found between sexes over the sampled years (Table 1).

Sexual dimorphism

All measurements except body mass met the assumptions of a 2-sample *t*-test according to the results of Levene's test for equality of variances. Thus, body mass was tested using a Mann-Whitney *U*-test which showed that males were significantly heavier than females (Table 2). For all other variables, males were larger than females in linear measurements, and PC1 scores (Table 2). The largest proportional differences were in bill depth (7.5%), body mass (5.1%) and bill length (3.1%). The degree of sexual size dimorphism was least in wing length (1.1%). All differences were highly significant (*P* < 0.001) between the sexes and remained significant after Bonferroni adjustment.

Discriminant function

The discriminant analysis was applied to 5 morphometric characters of 390 adult short-tailed

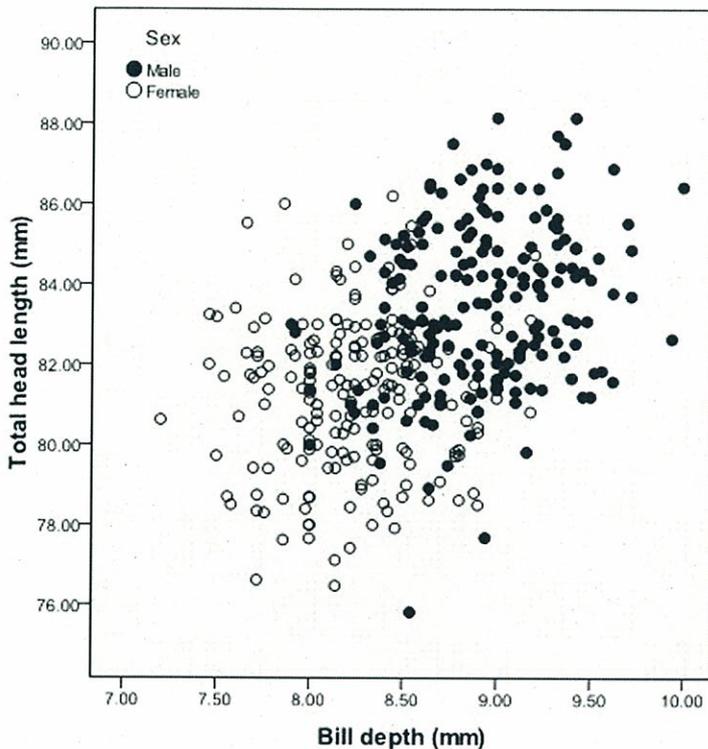


Fig. 2. Segregation of male and female short-tailed shearwaters corresponding to the most accurate variables used in the discriminant function model that included bill depth and total head length.

shearwaters (193 males and 197 females). Bill depth and head length were the most accurate variables for use in a discriminant function model, predicting sex with 83.8% accuracy (Table 3). The assumptions of the DFA were met as no significant differences between group covariance matrices or deviations from multivariate normality were found (Box $M = 1.44$, approximate $F = 0.48$, $P = 0.70$). Cross-validation classified adults marginally lower with 83.3% accuracy (Wilks' $\lambda = 0.553$, $\chi^2 = 243.52$, $P < 0.001$). The discriminant function (D) obtained was:

$$D = 0.21 (\text{head length}) + 2.138 (\text{bill depth}) - 35.616$$

When $D > 0$, the individual is classified as a male (mean 0.94 ± 1.03) and when < 0 , a female (mean -0.92 ± 0.97). Misclassification of some adults indicates a degree of overlap in the discriminant scores between the sexes resulting from a slight overlap in body size (Fig. 2). When only 1 variable, bill depth or total head length, was taken into account in the discriminant function, accuracy decreased to 82.1% and 69.7%, respectively.

To test the accuracy of a discriminant model developed by Einoder *et al.* (2008), I applied their model to the 390 known sexed birds used in this study. Of the 390 adults, only 72.5% were accurately allocated the correct sex using the Einoder *et al.* (2008)

model. This finding indicates some geographical size differences within the species.

Within-pairs, males were significantly heavier and larger than females in all linear variables tested but not based on their PC1 scores (paired t -test; Table 4). These differences were still highly significant after Bonferroni adjustment. The most dimorphic character, bill depth, had an average difference of $0.7 (\pm 0.5)$ mm between partners. In 92.4% of cases, males had a deeper bill than their female partners.

Tests for assortative mating

In pairs where both birds were measured, there was an opportunity to study assortative mating in their morphometric characters. A total of 171 pairs were used in the analysis. No significant correlation was found between partners in morphometric measurements (Table 5). Body mass and their PC1 scores were not significantly correlated within-pairs (Table 5).

DISCUSSION

Over the 3 years of this study the linear body measurements of short-tailed shearwaters caught each year did not change significantly with the exception of male tarsus length. Body mass, which was measured at the same time each year, also

Table 4. Magnitude of difference between male and female short-tailed shearwater measurements within the same pair. Total pairs $n = 171$.

Character	Mean difference (\pm SD)	% male larger (n)	Paired t	P
Head length (mm)	2.0 (\pm 2.8)	79.5 (136)	9.4	<0.001
Bill length (mm)	1.0 (\pm 1.6)	72.5 (124)	8.1	<0.001
Bill depth (mm)	0.7 (\pm 0.5)	92.4 (158)	17.2	<0.001
Wing length (mm)	3.3 (\pm 9.1)	67.8 (116)	4.7	<0.001
Tarsus length (mm)	0.9 (\pm 2.3)	64.9 (111)	4.9	<0.001
Body mass (g)	25.9 (\pm 88.1)	64.3 (110)	3.8	<0.001
PC1	<0.00 (\pm 1.4)	53.2 (91)	<0.01	>0.05

Table 5. Correlation analyses of morphometrics of short-tailed shearwater pairs breeding on Great Dog I, Furneaux Group, Tasmania. Total pairs $n = 171$.

	Head length	Bill length	Bill depth	Wing length	Tarsus length	Body mass	PC1
r	-0.069	0.106	0.090	-0.097	0.002	-0.016	0.016
P	0.37	0.17	0.24	0.20	0.98	0.83	0.83

varied in males between years. Female body mass did fluctuate between years but was not found to be significant. These observations suggest annual variation in the body condition of male shearwaters at the Furneaux Group colonies. Aspects of the breeding biology, behaviour and adult body condition of seabirds can be an important indicator of marine food supply and the observed mass variation may indicate annual fluctuations in food availability on distant shearwater feeding grounds during the breeding season (Weimerskirch & Chérel 1998; Chérel *et al.* 2005).

Male short-tailed shearwaters captured on Great Dog I were, on average, significantly larger than females in all linear body measurements, body mass and their PC1 scores. These findings support previous studies of this species across their geographical range (Meathrel *et al.* 1993; Bull *et al.* 2005; Bradley & Meathrel 2006; Einoder *et al.* 2008). The differences between the sexes observed in this study have been reported in other studies of procellariids, such as Manx shearwater (*P. puffinus*) (Brooke 1990), Hutton's shearwater (*P. huttoni*) (Cuthbert & Davis 2002), Balearic shearwater (*P. mauretanicus*) (Genovart *et al.* 2003), pink-footed shearwater (*P. creatopus*) (Guicking *et al.* 2004), Cory's shearwater (*Calonectris diomedea*) (Lo Valvo 2001), Antarctic petrel (*Thalassoica antarctica*) (Lorentsen & Rov 1994), and Gould's petrel (*Pterodroma leucoptera*) (O'Dwyer *et al.* 2006) although the degree of sexual dimorphism varies considerably between these species. The degree of sexual size dimorphism presented in this study was between 1 - 7.5%, and a similar range was found

for Balearic shearwaters (0.3 - 8.3%; Genovart *et al.* 2003). However, this range is small given the degree of sexual dimorphism between northern giant petrels (*Marconectes halli*), with males being 20 - 25% heavier and from 5 - 16% larger than females in linear measurements (González-Solís 2004).

Short-tailed shearwaters could be sexed in 84% of cases using bill depth and total head length in a DFA. Validation methods suggested a more realistic estimate of the success rate for the function of 83%. Thus, using the DFA on other shearwaters from this study colony it would be expected that there would be an error in sexing of less than 2 in 10 times. This contradicts the findings of Meathrel *et al.* (1993) where it is suggested that sex for this species cannot be predicted based on structural size. My results show short-tailed shearwaters can be sexed with relatively high success using a DFA. However, the DFA produced can only be applied to the population used in this study. This suggests some geographical variation within the species and reinforces the need for researchers to obtain sex models from locally caught birds (Weidinger & van Franeker 1998; Guicking *et al.* 2004). Geographic variation may reflect some kind of ecomorphological adaptation to different environmental conditions (Spear & Ainley 1998; Guicking *et al.* 2004).

The success rate of the DFA model achieved in this study for short-tailed shearwaters is intermediate between that reported for many shearwater species (>90%; Lo Valvo 2001; Genovart *et al.* 2003; Guicking *et al.* 2004; Thalmann *et al.* 2007) and the success rate for petrels (59-86%, Weidinger

& van Franeker 1998; 73%, O'Dwyer *et al.* 2006). At a short-tailed shearwater colony in South Australia, 1500 km to the west of Great Dog I, Einoder *et al.* (2008) were able to predict sex 92% of the time, despite a low sample size ($n = 61$). Application of this sex model to another colony close by reduced its accuracy to 70–80% (Einoder *et al.* 2008). Although the results of a DFA are sensitive to sample size and other statistical attributes (Morrison 1984), much of the variation in success rate is most likely the result of variation in the relative degree of sexual size dimorphism (Chardine & Morris 1989).

The stepwise DFA used to determine the classification function chose bill depth, followed by total head length, indicating bill depth was the better discriminator of sex. The value of bill depth in determining sex in procellariids has been reported previously (Lo Valvo 2001; Genovart *et al.* 2003; Einoder *et al.* 2008). Used alone, bill depth successfully sexed 82% of short-tailed shearwaters in the sample. However, given the reduction of success rate it is recommended that both bill depth and total head length is used when sexing live short-tailed shearwaters in the Furneaux Group colonies. Sexual differences in procellariid bill morphology has been suggested to reflect sexual differences in foraging behaviour (González-Solís *et al.* 2000; González-Solís 2004). Furthermore, it is not known whether a sex difference in foraging behaviour exists in short-tailed shearwaters.

In almost all short-tailed shearwater pairs observed in this study, the male was larger. Similar results have been obtained by Meathrel *et al.* (1993) and Einoder *et al.* (2008) for short-tailed shearwaters. Differences in relative size of certain body parts, such as bill depth, within a pair may be a more reliable indicator of sex. Predicting sex within-pairs was achieved with a higher accuracy rate than the DFA when bill depth of both birds were analysed. Within-pair comparisons have substantially improved the accuracy of determining sex in seabirds with monomorphic plumage such as cape petrels (Weidinger & van Franeker 1998), common terns (*Sterna hirundo*), Arctic terns (*S. paradisaea*) (Fletcher & Hamer 2003), and brown noddies (Chardine & Morris 1989).

Short-tailed shearwaters from my study colony showed no assortative mating in either body mass or linear body measurements. These results contrast with those of Bradley & Meathrel (2006) and Einoder *et al.* (2008) who found positive assortative mating for bill depth, tarsus length and their body size index. Despite the fact that assortative mating has been shown to occur in brown noddies (Chardine & Morris 1989), Arctic terns (Fletcher & Hamer 2003) and other species, it seems that short-tailed shearwaters may mate randomly based on morphological traits. A lack

of assortative mating in short-tailed shearwaters based on size alone is perhaps not surprising given the structural similarity between males and females (the most dimorphic feature, bill depth, was only 7.5% larger in males). If assortative mating occurs in short-tailed shearwaters it may be based on traits other than structural size. For example, it has been suggested that assortative mating in short-tailed shearwaters may occur based on the number of years since they first bred (Wooller *et al.* 1990; Bradley *et al.* 1995), which has been found for northern giant petrels (González-Solís 2004) and some tern species (Nisbert *et al.* 1984; Bridge & Nisbert 2004).

In summary, sexual size dimorphism does occur in the short-tailed shearwater. The most dimorphic feature of the species is bill depth, and when combined with total head length, sex can be predicted with an 84% accuracy using a DFA model. Where measurements have been taken of both members of a pair accuracy increases to 92% based on a comparison of bill depth. When applying a discriminant function to other colonies of short-tailed shearwaters, it is recommended that investigators use measurements of their specific population due to geographic variation within the species. Size differences are also reflected within-pairs. In those pairs in which it may be difficult allocating gender, within-pair comparison of bill depth will assist in predicting sex. Assortative mating was not observed in this species despite the findings of Bradley & Meathrel (2006) and Einoder *et al.* (2008). Finally, it is recommended that a single observer should perform all morphological measurements to eliminate inter-observer differences as the degree of dimorphism in short-tailed shearwaters is small.

ACKNOWLEDGEMENTS

Support was received from the La Trobe University Postgraduate Write-up Award. I thank the many field assistants involved in this project over the 3 years, particularly Julia Mynott, Victoria McCartney and Felix De Natris. I thank the Newall family for providing access to Great Dog Island. Funding for this project was provided by the ANZ Trustees Foundation–Holsworth Wildlife Research Endowment. This research was conducted under La Trobe University animal ethics permit number AEC05-15-W and Tasmanian Department of Primary Industries, Parks, Water and Environment, Permit to Take Wildlife for Scientific Purposes: Permit numbers. F.A. 06494 (2006/07); F.A. 07166 (2007/08); F.A. 08145(2008/09).

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Predation of Short-tailed Shearwater Eggs on Great Dog Island, Tasmania

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Summary

Evidence of predation by Blotched Blue-tongue Lizards *Tiliqua nigrolutea* and Water-rats *Hydromys chrysogaster* on Short-tailed Shearwater *Ardenna tenuirostris* eggs was obtained during the 2006–07 breeding season on Great Dog Island, Tasmania. Overall, 120 burrows were monitored across the entire incubation period, with 8.3% of eggs being eaten. Predation occurred throughout the incubation period, with the highest numbers being taken during December. In 90% of cases, eggs were taken when left unattended in the burrow. These figures are minima, since Water-rats were also suspected of being the cause of egg predation between observation visits. Predation at this level may not significantly affect the island's population of Short-tailed Shearwaters.

Introduction

Understanding the key factors that influence seabird reproductive success, and therefore populations, is needed for effective management and conservation. Predation of seabirds, including their eggs and young, can be a driving force in regulating or causing declines in populations, particularly on offshore islands (Pierce 2002). Although colonially nesting seabirds on offshore islands are protected from many mainland predators, they offer a dense and predictable food supply to native and introduced predators (Meathrel & Klomp 1990; Wooller & Dunlop 1990). Most studies of the effects of predators on seabirds have focussed on introduced species, such as rats *Rattus* spp. (Kepler 1967; Fleet 1972; Grant *et al.* 1981; Booth 1995; Booth *et al.* 1996; Pierce 2002; Mulder *et al.* 2009; Towns 2009) and feral Cats *Felis catus* (Cooper *et al.* 1995; Twyford *et al.* 2000; Copson & Whinam 2001). Predation by native species has received far less attention, but nevertheless may have an impact on seabird populations, which are already under threat by anthropogenic factors (Millus *et al.* 2007).

Water-rats *Hydromys chrysogaster* and Blotched Blue-tongue Lizards *Tiliqua nigrolutea* are two native species common on islands in the Furneaux Group, north-eastern Tasmania (Brothers *et al.* 2001; Harris *et al.* 2001), but there is scant knowledge regarding their ecology on these islands. Population size and density estimates are not known for either species. Both species are generally considered omnivorous, having a varied diet of plants, seeds, terrestrial invertebrates (Wilson & Swan 2003) and, at least for the Water-rat, marine arthropods scavenged along the intertidal zone (Menkhorst & Knight 2004). Seabird eggs, young and adults may also contribute to their diet, but the importance of this contribution is unknown (Serventy *et al.* 1971).

The Short-tailed Shearwater *Ardenna tenuirostris* is a medium-sized (~600 g) procellariiform seabird that breeds on islands and headlands of south-eastern Australia (Marchant & Higgins 1990), and the Furneaux Group supports the largest breeding population of Shearwaters in the world (Skira 1991). It is abundant, with estimates of 23 million breeding adults worldwide, all of which perform a trans-

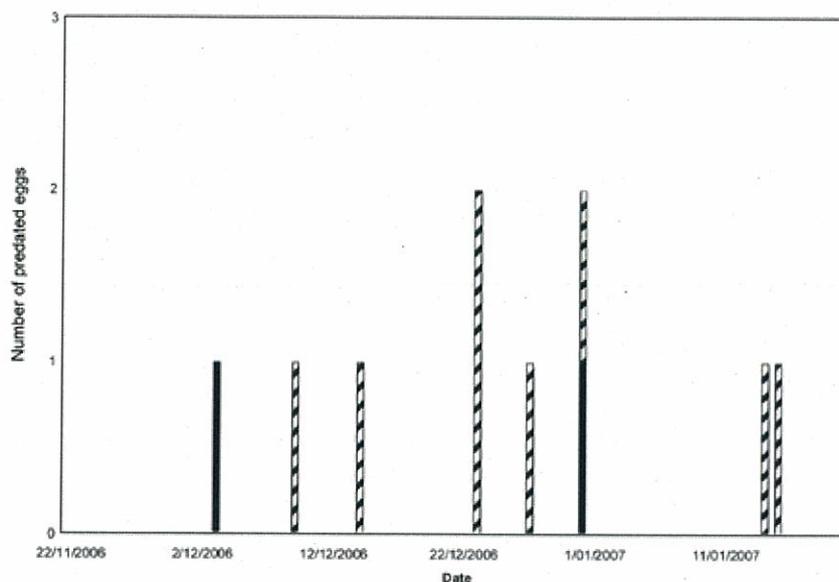


Figure 1. Bar graph indicating the number of eggs taken and date of Water-rat (hatched bars) and Blotched Blue-tongue Lizard (solid black bars) predation on Short-tailed Shearwater eggs. Eggs were laid 22–27 November 2006, and all eggs had hatched by 20 January 2007.

equatorial migration to the northern Pacific (Serventy *et al.* 1971; Skira 1991). Laying is highly synchronous, with ~85% of eggs laid between 24 and 28 November (Serventy 1956, 1963, 1967). Incubation lasts for ~53 days, and hatching occurs in mid to late January (Serventy 1967). This study reports on loss of Shearwater eggs caused by Water-rats and Blotched Blue-tongue Lizards during the 2006–07 breeding season.

Methods

The breeding biology of Short-tailed Shearwaters was assessed on Great Dog Island (377 ha), Furneaux Group, Tasmania (40°15'S, 148°15'E) from November 2006 to the end of January 2007 (MJC unpubl. data). The island supports Tasmania's third-largest colony of Shearwaters, with an estimated 952 000 burrows (Skira & Brothers 1988; Skira *et al.* 1996). Regular checks on 120 of the burrows were made throughout the incubation period, ranging from daily to weekly inspections, as part of an experimental study on disturbance (MJC unpubl. data). Where possible, observations were made of loss of eggs and the probable cause. Predation of young chicks was not investigated.

Eggs destroyed by predation were easily recognised. Typically, eggs eaten by Water-rats were identified by jagged edges of the shell (Plate 14), and numerous small pieces of shell, as described for rats *Rattus* spp. (Imber 1984; Booth 1995; Booth *et al.* 1996). Eggs taken by Blue-tongue Lizards showed evidence of the shell having been crushed along the longitudinal axis of the egg (Plate 15), as described by Meathrel & Klomp (1990); these eggs were often found inside the burrow-chamber.

Results

Egg-laying commenced on 22 November 2006, with the first evidence of

predation occurring on 3 December (Figure 1). The egg was found relatively intact inside the nest-chamber but displayed significant damage along the longitudinal axis (Plate 15). Hence, it was deemed to be the first of two eggs (1.7%) eaten by a Blotched Blue-tongue Lizard over the course of the incubation period.

Predation by Water-rats accounted for 6.7% of eggs monitored: the first egg was eaten on 9 December 2006, the next on 14 December, and four between 23 and 31 December. A further two eggs were eaten towards the end of incubation in mid January. Eggs eaten by Water-rats were usually found either inside the nest-chamber or close to the entrance of the burrow, and the shell always had a distinctive jagged edge (Plate 14). In 75% of cases, smaller pieces of eggshell were also observed outside the burrow. Water-rats were also suspected of being responsible for the disappearance of at least some of the eggs (5%) that disappeared between observation visits.

In total, 10 eggs (8.3%) were eaten over the incubation period (Figure 1), and 90% of these had been left unattended by the incubating adult the night before predation. Peak predation occurred over a 9-day period up to and including 31 December, when 50% of the observed eggs eaten were taken, with 80% of these taken by Water-rats. In some cases, eggs were lost between observation visits, so that all values for loss of eggs are likely to be underestimates.

Gulls were observed eating eggs outside the colony, but it is unclear whether they took eggs from shallow burrows or scavenged eggs brought to the surface by other predators. None of the 120 eggs monitored here was seen to be consumed by Pacific *Larus pacificus* or Silver *Chroicocephalus novaehollandiae* Gulls.

Discussion

Approximately 8% of Short-tailed Shearwater eggs laid on Great Dog Island in 2006–07 were lost to predators. Water-rats appeared to take the majority and predation occurred throughout incubation. It is suspected that eggs were taken during the night, when Water-rats are most active (pers. obs.). Increased predation by Water-rats during the middle of the incubation period may indicate that Water-rats learned to exploit a new and abundant food source as other food items became scarce. Grant *et al.* (1981) suggested that the removal and eating of petrel eggs is a learned behaviour by Black Rats *Rattus rattus* on Midway Atoll in the Pacific Ocean. An alternative view is that Water-rats switched their diet to a more abundant prey item (Kjellander & Nordström 2003). Prey switching is frequency-dependent predation, where the predator preferentially consumes the most common type of prey (Allen 1988). Imber (1984) found that rat *Rattus* spp. predation of gadfly petrel *Pterodroma* spp. eggs increased as incubation progressed. Water-rats may not be learning to prey on eggs *per se* but instead learning that eggs are a more profitable food resource to exploit. However, as peak predation was in the middle of incubation and not observed at the end, as the observed pattern of predation is not consistent with prey switching alone, but may have been from an interaction between prey switching and the behaviour of incubating Shearwaters. Absence of incubating adults, whereby the egg is temporarily abandoned, is common in many procellariiform seabirds (Warham 1990), and such behaviour may increase the vulnerability of eggs to predation (Walls 1978; Imber 1984).

In this study, Blotched Blue-tongue Lizards played only a minor role in egg loss, ~1.7% of eggs monitored. This is surprising since reptiles are known to consume significant numbers of seabird eggs elsewhere on offshore islands (Walls 1978;



Typical damage to Short-tailed Shearwater egg incurred by a Water-rat *Hydromys chrysogaster*. Note the sharp, jagged edges of the shell.

Plate 14

Photo: Mark J. Carey



A Short-tailed Shearwater egg crushed along the longitudinal axis, characteristic of Blotched Blue-tongue Lizard *Tiliqua nigrolutea* predation

Plate 15

Photo: Mark J. Carey

Meathrel & Klomp 1990; Wooller & Dunlop 1990). Both Wooller & Dunlop (1990) and Meathrel & Klomp (1990) demonstrated that King's Skinks *Egernia kingii* take large numbers of Silver Gull and Little Penguin *Eudyptula minor* eggs on Carnac and Penguin Islands in Western Australia. Walls (1978) reported that Tuataras *Sphenodon punctatus* take 15% of eggs laid by Fairy Prions *Pachyptila turtur* in New Zealand. Whether eggs make up a significant proportion of the King's Skink diet is unclear, but Wooller & Dunlop (1990) suggested that the high density of skinks on Carnac Island may be because of the protracted breeding season of the gulls (eggs are present for up to 9 months of the year). On Great Dog Island, Short-

tailed Shearwaters provide a shorter glut of eggs, between the end of November and mid January, so their eggs may merely supplement the Blue-tongue Lizards' diet with a protein-rich food source. Density of Blue-tongue Lizards on Great Dog Island is not known, and the observed minor role in shearwater egg predation may be related to a low density of these lizards.

The only other potential predators of seabird eggs on Great Dog Island are Tiger *Notechis ater* and Copperhead *Austrelaps superbus* Snakes; although predation by snakes was not observed in this study, young shearwater chicks are important in the snakes' diet throughout the Furneaux Group (Serventy *et al.* 1971; Brothers *et al.* 2001). Feral Cats are also present on the island but would probably not consume eggs, although they take many young and adult birds (Brothers *et al.* 2001; MJC pers. obs.). Whether Shearwater chicks form an important part of the diets of the Water-rat and Blue-tongue Lizard remains unclear. As adult Shearwaters are at sea during the day, chicks are highly vulnerable to predation, particularly during the first few weeks. In other procellariid seabirds, predation by rats and reptiles just after the chick-guard stage is the most damaging to populations (Walls 1978; Imber 1984). This, combined with egg predation, may affect an island's population, particularly if already declining from anthropogenic factors (Millus *et al.* 2007), although this remains to be investigated on Great Dog Island. Other seabirds such as Silver and Pacific Gulls, White-faced Storm-Petrels *Pelagodroma marina* and Little Penguins also breed on this island but in considerably smaller numbers than Shearwaters (Brothers *et al.* 2001). Whether Water-rats and Blue-tongue Lizards also prey on their eggs and young is unknown, and requires further investigation: this would be particularly timely, given the relatively small population on Great Dog Island of White-faced Storm-Petrels, which are vulnerable to local extinction from predation by feral Cats (Brothers *et al.* 2001).

Acknowledgements

I thank all field staff involved in this project, particularly the La Trobe University Marine Ornithology Group: Felix De Natris, Victoria McCartney and Julia Mynott. I also thank the Newall family for granting access to Great Dog Island over the past 6 years. ANZ Trustees Foundation – Holsworth Wildlife Research Foundation kindly provided financial assistance to this project. This research was conducted under La Trobe University animal ethics permit AEC05-15-W and Tasmanian Department of Primary Industries & Water permit FA 08145. I am grateful to Kerry-Jayne Wilson and Dean Portelli, whose comments significantly improved the manuscript.

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A new method for the long-term attachment of data-loggers to shearwaters (Procellariidae)

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Abstract. Recent advances in tracking technology (i.e. smaller and lighter devices) have enabled long deployments, of up to 12 months or more, on shearwaters (Procellariidae). These deployments have been successfully used to examine migration patterns, wintering sites and non-breeding ranges as well as at-sea activity. Hence, an effective method for the long-term deployment of tracking devices that is able to withstand UV radiation, saltwater immersion and terrestrial abrasion while reducing any adverse effects of the attachment of the logger to the bird is needed. Here, a method for attaching global location-sensing (GLS) data-loggers to Short-tailed Shearwaters (*Ardenna tenuirostris*) on a modified aluminium band is described. GLS loggers were attached for 12 months from the 2007–08 austral summer and 74% of geolocated birds returned the following season compared with a slightly higher rate of 82.5% for birds with no loggers attached. Body mass between birds with and without loggers was not significantly different in the short or long term. No adverse injuries to the birds were observed. We believe the application of this method with its high rate of return can be applied to all species of shearwater and will not only assist researchers in future tracking studies but help minimise any adverse effects the logger has on the birds' behaviour.

Additional keywords: *Ardenna*, banding, geolocation, investigator disturbance, logger attachment, Procellariiformes, seabirds, Short-tailed Shearwaters, tracking.

Introduction

With a growing interest in seabird ecology and at-sea behaviour, there has been a considerable increase in tracking studies in recent years owing to advances in remote sensing devices (for a review see Burger and Shaffer 2008). In the past, most studies have been fairly short in their duration (weeks or months), but recent advances in global location-sensing (GLS) loggers, or geolocators, have facilitated longer deployments (12–18 months) (Afanasyev 2004; Croxall *et al.* 2005; Phillips *et al.* 2006). These technological advances have expanded our knowledge of the ecology and behaviour of procellariiform seabirds considerably, particularly with regard to migration patterns and distant foraging locations, non-breeding distribution and the overlap of their range with long-line fisheries (Iguar *et al.* 2005; Phillips *et al.* 2006, 2007; Shaffer *et al.* 2006, 2009; Phalan *et al.* 2007; Guilford *et al.* 2009; Catry *et al.* 2009). This information is vital for conservation efforts.

While there are clear benefits from tracking seabirds, concern has been raised about the effect of the devices themselves on the reproductive and foraging behaviour of the birds as the extra mass of the data-logger, as well as the method and location of attachment, may affect flight, diving and foraging ability (Wilson *et al.* 1986; Söhle *et al.* 2000; Phillips *et al.* 2003; Söhle 2003; Iguar *et al.* 2005; Carey 2009), particularly if the tracking device is greater than 3% of a bird's total body mass (Phillips *et al.* 2003). Recently, leg-mounted GLS devices have been deployed on a variety of procellariiform seabirds

such as Grey-headed Albatrosses (*Thalassarche chrystostoma*) (Croxall *et al.* 2005), White-chinned Petrels (*Procellaria aequinoctialis*) (Phillips *et al.* 2006), Sooty Shearwaters (*Ardenna griseus*) (Shaffer *et al.* 2006, 2009), Manx Shearwaters (*Puffinus puffinus*) (Guilford *et al.* 2009), Streaked Shearwaters (*Calonectris leucomelas*) (Takahashi *et al.* 2008; Yamamoto *et al.* 2008) and Cory's Shearwaters (*C. diomedea*) (Iguar *et al.* 2005; González-Solis *et al.* 2007) for up to 18 months with little apparent effect on feeding ecology or demographic parameters. However, in some cases there were low return rates (Table 1). In these studies, light-level geolocators were attached to plastic or Darvic bands placed on the bird's leg. The advantages of Darvic bands are their mass, ease of attachment and relatively long durability with little reported effects on the bird's tarsometatarsus. However, one of the distinguishing features of shearwater morphology is these birds' laterally compressed (streamlined) tarsometatarsi (hereafter tarsus), which are believed to lessen resistance to water while pursuing prey (Wood 1993). Unless modified to fit the shearwater tarsus, attachment of a round Darvic band to a compressed tarsus may be hazardous to the bird as any movement over the toes or rotating around the tarsus could cause injury. In addition, using a round Darvic band increases the risk of shading of the light sensor if the sensor faces inward towards the bird, because that can affect the quality of light data (Afanasyev 2004). Darvic bands can be reshaped by heating them, then moulding them to fit the shape of the tarsus (S. A. Shaffer and D. Drynan, pers. comm.). However, this can make the plastic band friable (D. Drynan, Australian Bird and Bat Banding Schemes

Table 1. Comparison of mean total mass of band and geollogger, length of deployments, and rates of return of procellariform GLS studies
NR, not reported

Species	<i>n</i>	Mean total mass band + geollogger	Percentage of body mass	Approximate length of deployment of geollogger	Total rate of return (%)	Source
White-chinned Petrel (<i>Procellaria aequinoctialis</i>)	35	10.5 g	<1%	Mean 366 days (range 226–664 days)	31%	Phillips <i>et al.</i> (2006)
Sooty Shearwater (<i>Ardenna griseus</i>)	33	11 g	1.40%	Mean 262 ± 23 days (s.d.)	60%	Shaffer <i>et al.</i> (2006), Adams <i>et al.</i> (2009)
Short-tailed Shearwater (<i>A. tenuirostris</i>)	28	6 g	<1.5%	0–30 days	100%	Shaffer <i>et al.</i> (2009)
Cory's Shearwater (<i>Calonectris diomedea</i>)	27	5.4 g	0.7–1%	1 year	74%	This study
	40	12 g	1.5–2%	1 year	60–65%	Igual <i>et al.</i> (2005)
	52	10 g	NR	1 year	42%	González-Solis <i>et al.</i> (2007)
Streaked Shearwater (<i>C. leucomelas</i>)	11	7 g	1.30%	290 days	36%	Takahashi <i>et al.</i> (2008)
	48	7 g	1.2–1.5%	1 year	79.2%	Yamamoto <i>et al.</i> (2008)
Manx Shearwater (<i>Puffinus puffinus</i>)	12	2.5 g	NR (0.6% for a 400-g adult)	11 months	100%	Guilford <i>et al.</i> (2009)
Cook's Petrel (<i>Pterodroma cookii</i>)	10	3 g	1.5%	14 days (<i>n</i> = 8 birds), 1 year (<i>n</i> = 2)	80% (after 2 weeks)	Rayner <i>et al.</i> (2008)

(ABBBS), pers. comm.) and could lead to the loss of some devices.

In this paper, we describe the development of a modified band used for long-term attachment of geolocators to Short-tailed Shearwaters (*Ardenna tenuirostris*). The aim was to produce a modified band that would adequately fit a shearwater's compressed tarsus, was of low mass and low resistance, and had longevity in relation to the environment in which it would need to perform, therefore maximising retrieval rates.

Methods

Development of bands

After reviewing the attachment methods from several shearwater and petrel GLS tracking studies (Igual *et al.* 2005; Phillips *et al.* 2006; Shaffer *et al.* 2006; González-Solis *et al.* 2007; Rayner *et al.* 2008; Takahashi *et al.* 2008), we developed a band similar in size and shape to that of the ABBBS size-16 shearwater band. ABBBS stainless steel bands were designed specifically to match the shape of the legs of shearwaters (Lowe 1989) by being compressed laterally. This was important to ensure that the band did not rotate while attached to the leg, thereby, as required by our research permits, reducing the potential to cause abrasion. After trialling stainless steel bands as a possibility, we found it too difficult to 'close' the band on artificial shearwater legs. Instead, marine grade aluminium was chosen. Aluminium is lightweight and malleable, and thus possesses two of the qualities needed for the new band to be functional. Using measurements of size-16 shearwater

bands as a guide (diameter 10.5 × 4.3 mm, length (height) 7 mm; ABBBS), these new bands were cut to size and tested in the laboratory on several artificial legs. As a result, the bands were made longer (25 mm) to assist with mounting and stabilising the logger. The internal diameter of the closed band was also made slightly wider (11 × 6 mm) to ensure that there was no rubbing on the tarsus. Three 2-mm holes were drilled on either side of the band to allow sand and other debris to flush once the bird returned to sea (Fig. 1a). The edges of the band and the cable-tie holes were smoothed with a fine-tooth file to further reduce the risk of abrasion.

Next, a means of attaching the geollogger to the band was assessed. We found from other studies that one of the most commonly-cited ways to attach the geollogger to the plastic Darvic bands was to use weather resistant, nylon cable-ties. We trialled a 2.3-mm wide UV-resistant cable-tie (from RS Components Ltd, Melbourne, see <http://www.rsaustralia.com>). To attach the geollogger to the aluminium band, two 2.2-mm holes were drilled 7 mm apart into the flat side of the band. One cable-tie was then fed through the holes ready for attachment of the geollogger (Fig. 1a). Mean total mass of the band, including cable-tie, was 3.6 g (±0.02 s.e.m., *n* = 62). All means below are given ± standard error of the mean.

Field testing and deployment

Several bands were again tested on artificial Short-tailed Shearwater legs before deployment. This allowed the bander (M. J. Carey) to practice closing the band and attaching the geollogger to the band. It also helped ensure that there was no rubbing between the leg and the band. In all cases the band

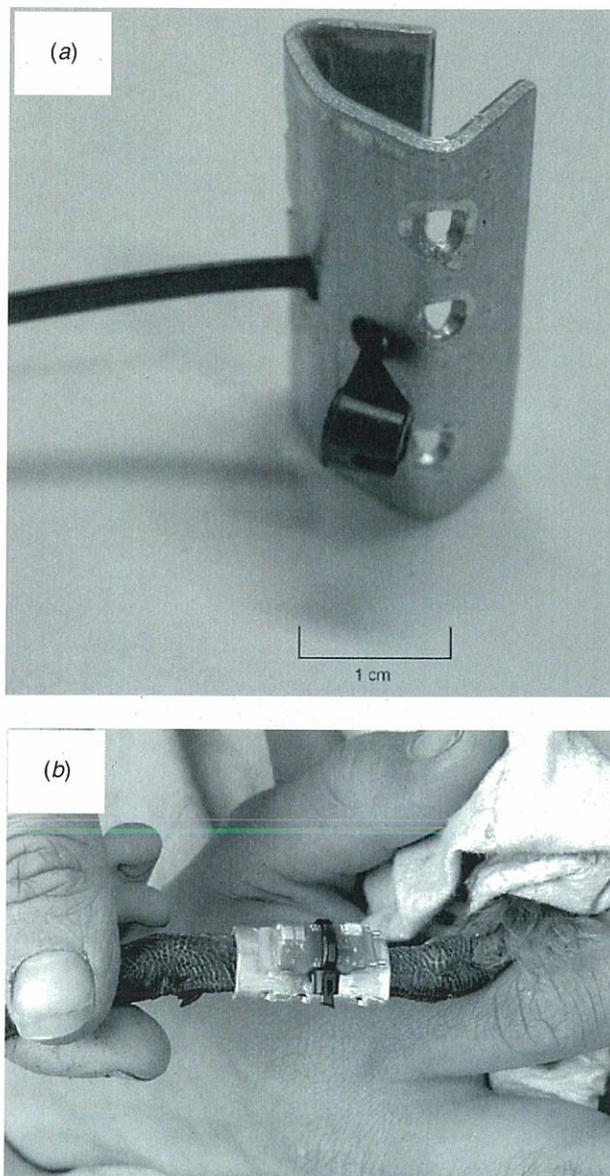


Fig. 1. Photographs of (a) a modified band ready for deployment on a shearwater (note the cable-tie has already been attached) and (b) band with geollogger attached on the tarsus of a Short-tailed Shearwater. The trailing end of the cable-tie has been removed.

moved freely up and down the artificial leg and could not rotate around the leg.

During December 2007, 27 geolocator loggers were attached to adult Short-tailed Shearwaters (13 males, 14 females) breeding on Great Dog Island, Furneaux Group, Tasmania ($40^{\circ}15'S$, $148^{\circ}15'E$). Each adult was removed from its burrow by hand and placed in a calico bag. The birds were then weighed with Pesola scales ($1\text{ kg} \pm 10\text{ g}$) and measured. All birds had been previously banded with ABBBS bands as part of a long-term study on recruitment (Meathrel and Carey 2007). Each new

band was placed on the bird's left leg. First, the band was closed around the tarsus with the UV cable-tie already threaded through the two holes. Then the geollogger (MK13, British Antarctic Survey, Cambridge, UK), embedded in transparent resin and weighing 1.8 g, was placed in position on the band and the cable-tie tightened around the geollogger. Pre-attachment of the geollogger was not possible as it would interfere with the band being closed around the tarsus. A cable-tie tool (RS Components Ltd) was used to tighten the tie further, and the trailing end of the cable-tie was removed at the clasp with pliers (Fig. 1b). This procedure took ~ 5 min. Finally, the band was checked to ensure that it could freely move up and down the tarsus. In all cases the band moved freely and showed no signs of abrasion. Adults were then placed back in their burrows.

Total mass of the band plus the mass of the geollogger was 5.4 g (± 0.02 , $n = 27$) and represented a range of 0.7–1% of adult body mass and 1.3% of the lightest body mass previously measured ($410 \pm 10\text{ g}$, adult female, 24 September 1989) (C. E. Meathrel, unpubl. data). These figures are comparable to weights of geolocgers used in other studies of procellariiform seabirds (Table 1) and fall well below the recommended 3% additional weight for flying seabirds (Phillips *et al.* 2003).

Assessing short-term impacts

In this study, birds were left for 2–3 weeks after attachment of the band before they were re-caught and assessed for any injuries. Only male birds were handled during this time because female birds are more susceptible to abandonment of the nest (Warham 1990; M. J. Carey, unpubl. data). Males had just returned from sea and were beginning their second incubation shift. Birds were caught by hand, weighed with a Pesola scale and assessed for any abrasion or discoloration where the geollogger was attached. For a comparison, 20 birds without geolocgers within the same colony were also caught and weighed to assess any short-term effects on body mass.

Recovery and removal of geolocgers

During the subsequent breeding season, in November and December 2008, marked burrows from the previous season were inspected during laying and early incubation. Burrows within a 10-m radius of these marked burrows were also inspected in case adults had moved burrows. A 10-m radius was chosen as a search area because adult Short-tailed Shearwaters have strong fidelity to their nesting site and rarely move more than 3 m from their original burrow (Serventy and Curry 1984; Skira 1991).

The adults that had returned were first placed into a calico bag. They were then weighed and the geollogger removed. To remove the bands, first the UV cable-tie was cut and the geollogger was removed. Then two sets of circlip pliers were inserted either end of the band gripping the two butt-ends. Pressure was carefully applied to prise open the band until the circlip pliers could be inserted between the butt-ends of the band. Once this could be achieved pressure was applied which opened the band and it was removed. This procedure took less than 7 min and was achieved by two people – one to hold and steady the bird, the other to remove the band.

All birds were then assessed for injury, if any, caused by the band or its subsequent removal. Geologger-bands were examined for growth of goose barnacles (*Lepas* spp.) noted by Phillips *et al.* (2007), and for other marine organisms. Since Short-tailed Shearwaters are burrow nesting, bands were also examined for evidence of abrasion caused by digging.

To determine any effects of the band on return body mass of equipped adults an additional 20 birds without geologgers were weighed for comparison purposes. Further to this, in order to determine the effects of the bands on rates of adult returns, 40 birds that were banded as part of another study were used as a control group. These adults were a part of the same colony and were banded in November and December 2007. These adults were handled only once at laying or early incubation. Their burrows and a 10-m radius were again inspected in November and December 2008.

Results

Short-term effects

All 13 males were caught after two weeks and there were no differences in body mass between equipped and 20 randomly selected adults without geologgers (equipped males 566.2 ± 15.8 g, $n = 13$; non-equipped males 592.0 ± 12.9 g, $n = 20$; $t_{31} = 1.29$, $P > 0.2$). Power analysis revealed that for a power ($1 - \beta$ error probability) of 0.95 the minimum detectable difference between the means was ~ 67 g (R. V. Lenth, 2006–09, Java Applets for Power and Sample Size, see <http://www.stat.uiowa.edu/~rlenth/Power>, accessed 1 September 2009). This indicates that we would have needed a difference of at least 67 g in the means to detect a significant difference between the two groups. Given that we could not detect a 12% change in body mass the data should be considered cautiously as it could not reveal a change of that magnitude. No abrasions or injuries were observed during this time, and no sand or soil had accumulated inside the modified band.

Band recovery and assessment

During November and December 2008, 20 geologgers, or 74% of those fitted, were recovered from adult birds (10 males, 10 females). Despite searching all burrows within a 10-m radius of the marked burrows, none of the remaining seven birds equipped with geolocators could be found. Results from another study in the same colony of birds without geologgers returning to breed between 2007 and 2008 indicated a return rate of 82.5% (i.e. 33 of 40 banded in 2007 returned in 2008), which is comparable to the return rate of equipped birds. All returned birds fitted with geolocators were of the same mass, compared with birds without geologgers (equipped adults 652 ± 13.6 g, $n = 20$; non-equipped adults 632 ± 12.9 g, $n = 20$; $t_{38} = 1.04$, $P > 0.3$). Power analysis revealed that for a power of 0.95 the minimum detectable difference between the means was ~ 64 g (following Lenth 2006–09). Given this, the dataset was inadequate to detect a 10% change in body mass.

Apart from two birds that had minor callusing on their legs (a 10×10 -mm area of flaking skin on the inside of the leg), the others showed no sign of abrasion or injuries. No goose barnacles, other marine organisms, were found on the bands. In

90% of cases, bands showed some evidence of scratching over the surface. However, the abrasions did not threaten the integrity of the band or attachment design.

Discussion

Compared with other GLS studies of shearwaters (Table 1) the retrieval rate of 74% of equipped birds in this study exceeded the retrieval rate in all studies except for those on Manx (Guilford *et al.* 2009) and Streaked (Yamamoto *et al.* 2008) Shearwaters. In those studies, 100% and 79% respectively were recaptured with a geologger at their breeding colony after one year. In this study, return rates between birds with and without geologgers were comparable, which has been found in similar studies (Iguar *et al.* 2005; Takahashi *et al.* 2008). There are a variety of reasons for the absence of our control and study birds in the colony including their intermittent breeding behaviour, where 14% of each sex may skip breeding during any given year depending on environmental conditions, and a further 15% of males and 13% of females can be present but not associated with an egg in any given year (Bradley *et al.* 2000). Natural attrition also claims 7–11% of birds between the ages of 6–15 years (Bradley *et al.* 1989). It is also possible that we failed to find the birds at the colony or that some birds that skipped breeding the season following geolocator deployment did return to the colony but were not captured because they returned and left during the night (fieldwork was only conducted during the day as required by our research permits).

Reasons behind low return rate in other studies are not clear. However, some researchers did have difficulty locating burrows in the following season (Phillips *et al.* 2006). The large variation between the return rates of two studies on Streaked Shearwaters may simply reflect the nest-site fidelity or nesting behaviour of the species (Takahashi *et al.* 2008; Yamamoto *et al.* 2008). None of the other researchers suggested that their attachment method contributed to the low return rates, although this is a possibility. In their study, Guilford *et al.* (2009) modified the plastic band to fit the tarsus of Manx Shearwaters but the researchers do not suggest that this was the reason for their 100% return rate. However, low recovery rates (30–40%) do not necessarily mean that the attachment methods were problematic, if the natural recapture rates were low (see Takahashi *et al.* 2008). Similarly, the high recovery rates of some studies (70–80%) do not necessarily mean that attachment methods were effective if the natural return rates were even higher. Future studies would benefit from comparing rates of return of adults without geologgers, and not simply assessing body mass upon return. Power analyses in these types of studies are also helpful given the low sample sizes of most GLS studies. In this study, we were unable to detect a $< 10\%$ change in body mass. For a bird that relies on distant foraging grounds this could be ecologically significant, particularly during the incubation period.

For long-term deployments of tracking devices to be successful, they require an adequate attachment method capable of surviving a sufficient amount of time for data to be collected while also being able to withstand the harsh environmental conditions seabirds experience on land and at sea. Our results indicate that the use of a modified metal band

to attach GLS loggers on shearwaters was an adequate solution for long-term tracking studies. Apart from flaking skin observed on two adults, which was also reported by Shaffer *et al.* (2006) in Sooty Shearwaters, this method revealed no obvious negative effects on Short-tailed Shearwaters and we recommend its use on other species of shearwater of similar size to help maximise return rates. For smaller, more sensitive, species such as storm-petrels (Hydrobatidae) and some smaller *Puffinus* shearwaters, further investigation is needed into the effects of the attachment of geologgers on reproductive success, rates of return, chick quality, and survival. The possible physiological effects of attachment of geologgers and the associated effects of handling by researchers have also received little attention (Carey 2009; but see Navarro *et al.* 2008). This may require minor modifications to each band to suit particular species, and we highly recommend extensive laboratory and field testing before any deployment.

Acknowledgements

We thank Aldonga Engineering, Barry Baker (Agreement on the Conservation of Albatross and Petrel Advisory Committee), David Drynan (ABBBS) and Geoff Dandie (Australian and New Zealand Council for the Care of Animals in Research and Teaching) for their technical advice. We also thank Scott Shaffer, Richard Phillips, Peter Hodum and Bruce Robertson for their contributions and discussion regarding this research. Warren Paul provided statistical assistance with power analysis. We are indebted to Dennis Black, Felix De Natris, Sophie Kennedy, Victoria McCartney, Danni Smith, Terry Karis, Laura Savige and Michael North for their assistance with fieldwork. We thank and acknowledge Laura Savige for providing photos of the bands and shearwater legs in the field. This manuscript was also improved by thoughtful comments by Robert Trevethan and three anonymous reviewers. ANZ Trustees Foundation – Holsworth Wildlife Research Foundation kindly provided financial assistance. This research was conducted under La Trobe University animal ethics permit (number AEC05–15-W) and Tasmanian Department of Primary Industries and Water permit (number FA 08145) (both to C. E. Meathrel).

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Manuscript received 2 July 2009, accepted 21 October 2009

The effects of investigator disturbance on procellariiform seabirds: a review

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Keywords disturbance; petrels; seabird behaviour; breeding; impact; investigator disturbance; Procellariiformes

Abstract Despite long-held concerns about the effects of researchers on breeding birds, few studies have focused on the impact of investigators on Procellariiformes. In this review, we summarise published investigations concerning the effects of investigators on physiology, behaviour, reproductive success, offspring quality, and population trends of procellariiform seabirds. Many of the smaller procellariid taxa, such as storm-petrels (Hydrobatidae, and some shearwater *Puffinus* species) are particularly sensitive to handling during the incubation period, resulting in lowered reproductive success, burrow shifts, and increased divorce between pairs. However, repeated handling of chicks does not seem to have a discernible effect on chick quality. In larger procellariiforms, the presence of researchers within the breeding colony is associated with significant increases in heart rates. Therefore, researchers seeking unbiased estimates of demographic and ecological parameters of birds should be encouraged to measure their own impact and report the findings in the literature, even if they detect no adverse effects of investigator disturbance. Techniques should be developed that ensure the accurate recording of birds' natural behaviour while minimising the impact of investigator disturbance. If investigators are willing to study disturbance problems, it should be possible to reduce biases caused by their activities.

INTRODUCTION

Ideally, in ecological studies of wildlife, researchers strive to obtain data that represent animals' normal behaviour by reducing stress to the organism during the research process (Götmark 1992). In doing so, researchers believe they observe their subjects under natural conditions and do not bias their results. However, these beliefs may not be well founded, and they should be examined.

Carney & Sydeman (1999) recognised "investigator disturbance" simply as all activities affecting individual birds or nests (marking nests, trapping, banding, and handling of adults and their young) (Götmark 1992; Carney & Sydeman 1999). Nisbet (2000, p. 313) defined disturbance as "... any human activity that changes the behaviour or physiology of one or more individuals within a breeding colony of waterbirds". He drew a distinction between "research procedures" (e.g., banding, trapping, and taking blood) and "investigator intrusions" (e.g., counting nests or walking through the nesting area for population monitoring).

Some studies of breeding waterbirds, including gulls, penguins, boobies, gannets, and cormorants, emphasise the dangers of disturbance to colonially breeding seabirds (see reviews by Götmark 1992; Carney & Sydeman 1999; Nisbet 2000). Human-induced effects include the predation of eggs and young, the desertion of nests, and behavioural changes of adult birds (see Götmark 1992). Visiting the nests of Atlantic puffins (*Fratercula arctica*) by researchers, and handling of least auklets (*Aethia pusilla*), reduced breeding success by 38 and 30% respectively (Piatt et al. 1990; Rodway et al. 1996). Tufted puffins (*F. cirrhata*) disturbed by investigators temporarily deserted their eggs for longer periods of time than undisturbed birds (Pierce & Simons 1986). Activities in this colony reduced

fledging success from 94% in undisturbed areas to 18% in the heavily disturbed areas (Pierce & Simons 1986). Penguins may suffer some negative effects on physiology, behaviour, and breeding success (Wilson et al. 1989, 1991; Giese 1996; Regel & Pütz 1997; Walker et al. 2008); in some gull and tern species, handling of adult or young, and checking nest contents, has significantly reduced the reproductive success (Gillett et al. 1975; Robert & Ralph 1975; Brubeck et al. 1981; Fetterolf 1983; Nisbet 2000). By contrast, other studies found no negative impact, or even positive outcomes associated with the presence of humans (Hill & Rosier 1989; King et al. 1992; King 1993; Brown & Morris 1994; Dunlop & Jenkins 1994; Nisbet 2000).

Procellariiformes (albatrosses, shearwaters, and petrels) are particularly long-lived seabirds, some with declining populations (Warham 1990; Baker et al. 2002). Populations may be decreasing because their island breeding habitat is being lost or degraded due to human development or disturbance (Brothers & Harris 1999; Taylor 2000; Micol & Jouventin 2001; Le Corre et al. 2002; Keitt et al. 2003; Priddel et al. 2006); because predators have been introduced to their breeding islands (Simons 1985; Cooper et al. 1995; Booth et al. 1996; Gaze 2000; Taylor 2000; Twyford et al. 2000; Copson & Whinam 2001; Cuthbert 2004; Martínez-Gómez & Jacobsen 2004; Schulz et al. 2005; de León et al. 2006; Igual et al. 2006); or because of mortality associated with long-line fishing (Baker et al. 2002; Baker & Wise 2005; Ryan et al. 2006; Sullivan et al. 2006). Investigator disturbance that reduces reproductive success in already-stressed populations might not only hasten these population declines but might also interfere with the accurate assessment of demographic parameters (Blackmer et al. 2004).

This paper provides a review of the current literature relating to investigator disturbance on procellariiform seabirds from Australia, New Zealand, Antarctica, North America, South America, and Europe. While most previous studies of investigator disturbance have measured only the effects on hatching success (Götmark 1992), others include the physiological condition (e.g., elevated hormone levels), behaviour (e.g., chick provisioning), survival, and future reproductive performance. Unfortunately, few such studies report the effect of investigator disturbance on procellariiform seabirds. Therefore, this paper summarises papers dealing with the effects of investigator disturbance (as opposed to human disturbance more generally) on physiology, behaviour, reproductive success, offspring quality,

and population trends of procellariiform seabirds. Techniques to manage and/or lessen the impact of investigator disturbance, and directions for future research, are also discussed.

METHODS

To locate appropriate literature, the keywords “investigator” and “researcher” were combined with “disturbance” or “impact” and with “seabirds”, “Procellariiformes”, “shearwaters”, “muttonbirds”, “petrels”, and “albatrosses” into MetaLib®, a multiple database search engine that accesses Biological Abstracts, CAB Abstracts, and Web of Science. As a result, 136 relevant publications were obtained, 28 of which directly referred to investigator disturbance in Procellariiformes (Table 1). Additional material such as journal articles, books, and book chapters already in the author’s possession were also used (Table 1).

RESULTS

Short-term effects of handling adult birds

Generally, researchers consider the effects of their actions as insignificant and not worth reporting in the literature, but some results suggest an unacknowledged negative effect on procellariiform seabird behaviour and reproduction. For example, handling of storm-petrels during the incubation period has been associated with permanent abandonment of breeding attempts (Allan 1962; Morse & Buchheister 1979; Warham 1990; Huntington et al. 1996). Boersma et al. (1980) found that daily handling of fork-tailed storm-petrels (*Oceanodroma furcata*) caused a significant number of adults to desert their nests, and even a slight disturbance by researchers caused a reduction in hatching success (58% from nests checked daily, compared with 84% for nests visited only four times late in the incubation period). Marks & Leasure (1992) found that adult Tristram’s storm-petrels (*O. tristrami*) readily abandon their eggs when disturbed by handling and nest visits. Of the 22 nests that failed during incubation, 55% failed between the first and second visits and 23% between the second and third visits; only 33% of eggs hatched, and overall breeding success rate was 18%.

In one of the few studies to quantify the frequency of investigator disturbance and its effects on reproduction, Blackmer et al. (2004) found that handling Leach’s storm-petrels (*O. leucorhoa*),

whether daily or weekly, significantly reduced hatching success compared with a control group that were not handled. By the subsequent breeding season, divorce was common between unsuccessful, disturbed pairs, and 37% more disturbed pairs than control pairs deserted the nesting burrows that they had used in the previous year (Blackmer et al. 2004). In this case, investigator disturbance may have had a long-term negative effect on the birds' lifetime reproductive success, as changes in pair bonding and nest site fidelity are known to affect reproductive output (Boersma et al. 1980; Wooller et al. 1989, 1990; Wooller & Bradley 1996). These findings complement those of Richdale (1963), who had previously noted that disturbance of nesting sooty shearwaters (*Puffinus griseus*) caused burrow shifts and divorces between pairs the following season, and even increased the likelihood that immature birds would emigrate from their natal colony.

Long-term effects of handling adult birds

Long-term research programs on seabird ecology are rare (Bradley et al. 1991; Wooller et al. 1992). In particular, the impact of handling adults during

the breeding period and over a number of breeding seasons is not well known for most procellariiform seabirds. Furthermore, although population estimates and demographic data are vitally important to conservation efforts, the reliability of these data is unknown. In one study on Fisher Island in Bass Strait, Serventy & Curry (1984) documented a case of investigator disturbance, and suggested that handling short-tailed shearwaters (*P. tenuirostris*) at night resulted in a decline in the number of occupied breeding burrows by 71% during the first 25 years. Serventy & Curry (1984) suggested that night patrols by investigators reduced attendance of immature and prospecting birds, and caused them to abandon Fisher Island as a potential future breeding site and relocate on nearby Little Green Island to breed. Not only had investigator disturbance reduced potential recruits into the population, but it also increased burrow desertion, decreased breeding success, decreased recruitment of young birds and delayed the start of some birds breeding (Serventy & Curry 1984). The implication is that the well-known Fisher Island study (see Bradley et al. 1991, and references therein), does not correctly describe either the short-tailed

Table 1 Parameters measured to detect effects of investigator disturbance on procellariiform seabirds.

Parameters	Species	Source
Reproductive success	Fork-tailed storm-petrels; Tristram's storm-petrel; Leach's storm-petrel; Madeiran storm-petrel; Gould's petrel; little shearwater; sooty shearwaters; short-tailed shearwater; Cory's shearwater; northern fulmar; southern giant petrel; wandering albatross; laysan albatross; black-browed albatross; grey-headed albatross; antipodean albatross; waved albatrosses; light-mantled sooty albatrosses	Allen 1962; Richdale 1963; Morse & Buchheister 1979; Boersma et al. 1980; Sinclair 1981; Serventy & Curry 1984; Warham 1990; Marks & Leasure 1992; Weimerskirch & Robertson 1994; Booth et al. 1996; Anderson et al. 1998; Burger & Gochfeld 1999; Cooper et al. 2001; Phillips et al. 2003; Söhle 2003; Blackmer et al. 2004; Wheeler et al. 2009
Breeding population	Leach's storm-petrel; short-tailed shearwater; northern fulmar; southern giant petrel; wandering albatross	Ollason & Dunnet 1978, 1980; Serventy & Curry 1984; Croxall et al. 1990; Warham 1990; Huntington et al. 1996; Micol & Jouventin 2001; Nel et al. 2002; Woehler et al. 2003; Pfteiffer & Peter 2004
Chick growth and survival	Short-tailed shearwater; sooty shearwater; Gould's petrel; Pycroft's petrel; wandering albatross	Saffer et al. 2000; Söhle 2003; Gangloff & Wilson 2004; O'Dwyer et al. 2006; Wheeler et al. 2009
Physiological parameters	Wandering albatross; northern giant petrel	Weimerskirch et al. 2002; de Villiers et al. 2006
Feeding ecology	White-chinned petrels; westland petrels; short-tailed shearwater; pink-footed shearwater; Cory's shearwater; wandering albatross; black-browed albatross; grey-headed albatross; Campbell Island albatrosses	Weimerskirch et al. 1992; Weimerskirch & Robertson 1994; Arnould et al. 1996; Anderson et al. 1998; Berrow et al. 2000; Catard et al. 2000; Klomp & Schultz 2000; Waugh et al. 2000; Freeman et al. 2001; Guicking et al. 2001; Igual et al. 2003; Phillips et al. 2003

shearwaters' natural "undisturbed" behaviour or their population trends on Fisher Island. In another long-term study, Ollason & Dunnet (1978, 1980) reported that handling of adult fulmars (*Fulmaris glacialis*) caused an increase of breeding failures of around 10% and also reduced the likelihood of the birds returning to breed in the subsequent year. In both long-term studies, prospector and young breeders were particularly affected by investigator handling, and that in turn affected recruitment.

Other long-term studies report that monitoring and banding birds during incubation reduced the hatching success of Leach's storm-petrels (Huntington et al. 1996), but not that of Southern Hemisphere albatrosses (Croxall et al. 1990; Baker et al. 2002).

Handling of chicks

Few studies have investigated whether handling young seabird chicks interferes with growth rates or survival (Götmark 1992). Investigator handling of incubating adult birds might also affect the quantity and frequency of food brought back by parents to their chicks, and that may influence subsequent chick growth and survival (Warham 1990), but evidence is scarce. On Great Dog Island, Tasmania, Saffer et al. (2000) reported no discernible effects from low (handled 3–6 times during the study), medium (handled 18–20 times), or high (handled 136 times) levels of investigator handling on short-tailed shearwater chick growth rates, although this study included no true "control" group (i.e., chicks that were never handled). Similarly, handling of adult Gould's petrels (*Pterodroma leucoptera*) every 7–10 days during the incubation stage did not appear to affect chick growth rates or survival (O'Dwyer et al. 2006), suggesting that parental provisioning rates, though not measured, were normal despite handling during the incubation stage.

Handling of young may elicit defensive responses (e.g., regurgitating stomach contents, in particular proventricular oil, as an anti-predator mechanism or a response to handling (Quillfeldt & Peter 2000)), generate physiological changes (e.g., increased heart rate and energy expenditure), and ultimately affect growth rate and peak body mass. The regurgitation of stomach contents by many petrel species when handled (but not great shearwater (*P. gravis*) chicks: Cuthbert 2005) could have growth implications as the chick loses a meal (or part meal) each time this occurs. Neither Saffer et al. (2000) nor O'Dwyer et al. (2006) made any attempt to quantify whether growth rate was affected by regurgitation of stomach

contents associated with handling. For some highly pelagic species, whose chicks are fed infrequently, such losses could be serious, particularly in the early stages of chick development. Gangloff & Wilson (2004) investigated chick provisioning and growth in Pycroft's petrel (*P. pycrofti*) and found that control chicks were significantly heavier than "study" chicks during the latter part of the chicks' development. The authors concluded that disturbance due to daily handling of chicks may have affected the study birds, but acknowledged that there may have also been an age difference between the two groups.

Effects on physiology

Only two studies have explored the impact of researcher disturbance on the heart rate and associated metabolic rate of incubating albatrosses and petrels. Weimerskirch et al. (2002) found that heart rates of wandering albatrosses (*Diomedea exulans*) doubled upon initial detection of human presence, and increased further on handling. The response lasted for up to 3 h, suggesting that energy expenditure was increased as a result of the disturbance. Males reacted more strongly to handling than did females, but females took longer to recover after handling (Weimerskirch et al. 2002).

The increased energy expenditure associated with approach and handling, and the prolonged recovery period after handling, could have potentially serious consequences, particularly if birds are handled several times and/or for prolonged periods of time (Weimerskirch et al. 2002). Wheeler et al. (2009) tested the effects of disturbance frequency and approach distance on 148 brooding/guarding wandering albatrosses at Marion Island. Frequency of approach did not influence short-term behavioural responses, but did affect chick survival significantly. The birds that were approached most frequently (twice a day, for 3 consecutive days) at a distance of 2 m had the highest percentage of nest failures (Wheeler et al. 2009). Wandering albatrosses did not habituate to short- or long-term disturbance (as did Laysan albatrosses (*Phoebastria immutabilis*) (Burger & Gochfeld 1999) so though not reflected in their behaviour, the sensitivity of these birds to disturbance may have induced physiological changes, so heart rate may have been a better indicator of stress than was direct observation (Ely et al. 1999; Weimerskirch et al. 2002; Wheeler et al. 2009).

In northern giant petrels (*Macronectes halli*), de Villiers et al. (2006) used heart rate to measure response to human approach and subsequent nest manipulation. The birds' heart rate increased upon

detection of a researcher 40 m away, and continued to increase until the human was 5 m away. The maximum increase over the resting heart rate in response to a natural disturbance was 97%, while the response to human approach was 204%. As in wandering albatrosses, a likely consequence of the considerable increase in heart rate following investigator disturbance was an increase in energy expenditure (Weimerskirch et al. 2002). The sensitivity of southern giant petrels (*M. giganteus*) to human disturbance at their breeding sites has caused a decline in some populations (Woehler et al. 2003; Pfeiffer & Peter 2004), and breeding success at sites used for extensive research is lower than in other colonies of this species (Cooper et al. 2001). The disappearance of this species from around the research station on Marion Island is also thought to be the result of human activity (Nel et al. 2002).

The above findings have implications not only for researchers studying these birds but also for the growing ecotourism market. Guidelines specifying the minimum distance to which tourists can safely approach nesting birds are essential to protect seabird populations (Pfeiffer & Peter 2004; de Villiers et al. 2006). Above-ground nesting seabirds can habituate to the presence of humans (Burger & Gochfeld 1999), but their breeding biology needs to be closely monitored to ensure that they suffer no long-term negative consequences.

Heart rate and metabolism are not the only physiological effects of disturbance on birds. Variation in stress-related hormones such as corticosterone in response to investigator or tourist disturbance have been researched across seabird taxa, particularly in penguins (for a review, see Walker et al. 2008), but not so in any procellariiforms.

Effects of satellite telemetry and data loggers

Over the last 20 years advances in tracking technology greatly advanced some areas of research, for example in satellite and geolocation studies of albatrosses and larger petrels (Falk & Møller 1995; González-Solís et al. 2000; Phillips et al. 2003 for a review). In addition, recent improvements in the size and weight of devices to be carried by shearwaters and storm-petrels (Igual et al. 2005; Burger & Shaffer 2008), have given researchers more information about foraging locations, breeding and wintering ranges, migratory directions and pathways, and important staging points used by these birds (Burger & Shaffer 2008). These tracking devices have provided extremely important information about the lifestyles and habits of these seabirds,

particularly on the overlap between fisheries and their foraging ranges—matters of great concern to research scientists and conservationists (Baker et al. 2002).

While acknowledging these advances, researchers must also recognise that tracking devices may themselves have an effect on the birds' behaviour, reproductive success, and survival. The size, weight, location, and method of attachment have all been raised as possible problems affecting flight, swimming, and diving efficiencies (Wilson et al. 1986; Phillips et al. 2003). Length of deployment on a bird may also affect its behaviour, body condition, and reproductive success (Igual et al. 2005).

Empirical evidence documenting these potential problems is mixed. Imitation satellite transmitters attached to sooty shearwaters decreased colony attendance and affected adult body mass, but it did not affect chick condition (Söhle et al. 2000; Söhle 2003). Data loggers had only slight short-term negative effects on the body condition of equipped Cory's shearwaters (*Calonectris diomedea*), and none on their demographic parameters or feeding ecology (Igual et al. 2005). Black-browed and grey-headed albatrosses (*Thalassarche melanophris* and *T. chrysostoma* respectively) with and without satellite transmitters were not different in trip duration, meal mass, breeding success, or rate of return in the next season (Phillips et al. 2003).

In other studies, extended trip duration and nest desertion were observed if transmitter loads were greater than 3% of adult body mass (Falk & Møller 1995; Klomp & Schultz 2000; Freeman et al. 2001; Phillips et al. 2003). Use of satellite transmitters has been associated with significantly longer foraging trips during the chick rearing stages in grey-headed albatrosses (Vaugh et al. 2000), Campbell Island albatrosses (*T. impavida*) (Vaugh et al. 2000), white-chinned petrels (*Procellaria aequinoctialis*) (Berrow et al. 2000; Catard et al. 2000), westland petrels (*P. westlandica*) (Freeman et al. 2001), pink-footed (*P. creatopus*) (Guicking et al. 2001), and sooty shearwaters (Söhle et al. 2000), but not in wandering albatrosses (Weimerskirch et al. 1992; Arnould et al. 1996), black-browed albatrosses (Phillips et al. 2003), or short-tailed shearwaters (Klomp & Schultz 2000). Attachment of satellite tags had no effect on reproductive success of waved albatrosses (*Phoebastria irrorata*) (Anderson et al. 1998) or light-mantled sooty albatrosses (*P. palpebrata*) (Weimerskirch & Robertson 1994). The attachment of harnesses caused a 100% failure of the breeding attempts by northern fulmars (Falk &

Møller 1995), and breeding failure was also observed in antipodean albatrosses (*D. antipodensis*) (Nicholls et al. 2002), but not in wandering albatrosses (Weimerskirch et al. 1992). All the northern fulmar pairs abandoned their nests for unknown reasons, but Falk & Møller (1995) believed that capture procedures, energetic constraints, or the attachment of the harness were responsible rather than impaired flight performance.

DISCUSSION

Important considerations and issues for researchers

Over the past several decades, a number of studies have indicated that research activities such as monitoring nest attendance, banding, and handling of birds during incubation reduce the reproductive success of some petrel species (Warham 1990). Yet, in their otherwise comprehensive review concerning the conservation and management of albatrosses and petrels, Baker et al. (2002) failed to acknowledge the potential impact of scientific investigations on vulnerable seabird populations. Given that little is known about the effects of investigator disturbance on most procellariiforms, documentation of any disturbance effects caused by researchers may be crucial for designing future research programmes, particularly those that are intended to advance conservation efforts. Most studies make no mention of these effects, but that does not mean they are not operating. Therefore, it is imperative that researchers studying these birds understand how their research affects their study animals, and take precautions to mitigate any adverse effects, when threatened species or small populations are involved.

A code of research procedures is needed for researchers working on procellariiform seabirds, including promotion of best practice methods for research requiring invasive procedures and repeated disturbance. The guidelines could be similar to those already protecting vulnerable seabird populations at some of the sub-Antarctic research stations.

Handling birds, their eggs, and their young is often essential for behavioural and ecological studies. Researchers need to capture birds at the nest, in the burrow, in the air, and at sea for many reasons including banding, sexing, obtaining morphometrics, and taking blood. Possible ways to limit the impact of such work include reducing both the number of times a bird is handled throughout the breeding season,

and the amount of time taken on each occasion. Compared with other bird species (Götmark 1992), some species of procellariiforms (or one gender) may be more or less susceptible to handling at different stages of their breeding season (early or late incubation, chick guarding, and chick rearing). While it is encouraging to know that handling chicks from some populations does not appear to have a discernible effect on chick growth, this cannot be assumed for all species. Future studies of chick feeding frequency, meal size, and chick growth must include a control group in order to document the consequences of regurgitation of proventricular oil by either parents or chicks for chick growth, health, peak body weights, or fledging weights. This issue has received little attention in the literature, yet has potentially serious consequences.

Some shearwater and albatross species can tolerate a degree of human disturbance, or are able to habituate to the presence of humans (Serventy et al. 1971; Burger & Gochfeld 1999), but storm-petrels are very easily disturbed at the nest, for reasons that remain unclear. One clue is that, for the larger albatrosses and petrels, single disturbance events may have little effect over the breeding season, but multiple disturbances within a season causing depletion of energy reserves becomes a more serious problem for them (Weimerskirch et al. 2002). For smaller species of petrel, the stress caused by investigator handling may have greater impact because their energy stores are smaller, with a fixed mass threshold, so birds may abandon their nests earlier if not relieved by their partner (Chaurand & Weimerskirch 1994). The otherwise unexpected loss of stored energy by smaller petrels when handled, particularly those handled several times, may explain why these species are more vulnerable to handling by investigators than are larger petrels. This suggestion, however, has yet to be thoroughly tested in the field.

Marks & Leasure (1992) have suggested that the interference to a burrow entrance and its internal structure caused by reaching into the burrow to check its contents may be perceived by the incubating adult as a signal that the burrow may be about to collapse. Likewise, creating "trap doors", a common practice to view or obtain easy access to the nesting chamber in burrows of nesting petrels, might increase the frequency of nest abandonment (Sinclair 1981). Then, the use of remote monitoring systems and burrowscopes should be encouraged, at least in studies where handling is not necessary and where the accuracy and practicality of using a burrowscope

in rough terrain and inclement weather are not serious issues (Jones et al. 2003; Schulz et al. 2005). If trap doors must be used, they should be constructed outside the breeding season to avoid disturbance to the burrow, and researchers should be mindful that, although the time of day of inspection may not have an effect on the birds' reproductive success, the frequency of inspection does (Blackmer et al. 2004). Innovations should also be encouraged. For example, the use of an artificial nesting habitat by Gould's petrels has had no reportable adverse effects on reproduction or survival, and has even been used to establish a new breeding colony as a safeguard against extinction (Priddel et al. 2006). Gould's petrels and Madeiran storm-petrels (*O. castro*) nesting in artificial burrows have both recorded a higher annual breeding success than those using natural nest sites (Bolton et al. 2004; Priddel et al. 2006).

Directions for future research

Clearly, more research on the effects of investigators on procellariiform seabirds is necessary. The effect of handling is well established for several populations, but for most species, many questions remain. For example, at what distance from the nest, at what frequency, at what stage of the breeding season, and for how long will particular species of birds accept investigator disturbance before negative consequences begin? Very few studies have been able to quantify disturbance adequately, and this gap in our knowledge offers opportunities for further research, possibly in conjunction with existing or new projects.

Answering some of these questions is likely to benefit a variety of bird species, as well as providing practical information for scientists and managers. Both may be particularly important for limiting the impact of the growing ecotourism industry in the sub-Antarctic islands and Antarctica. Managers of these areas must enforce strong precautionary guidelines to protect breeding seabirds against human disturbance, and to ensure minimal or no impacts from visits by researchers and tourists.

Measuring the effects of investigator disturbance will require studies of physiology, behaviour, and breeding biology as well as parallel studies of other known variables that affect bird populations, such as predation and food availability. Appropriate methods should be used in these studies, and more attention needs to focus on minimising the unwanted effects associated with attempts to collect accurate data. The publication of these studies should be widely

advocated, even if no negative outcomes are found. Ethics committees and government agencies should also promote research concerning disturbance, and encourage best practice methods in order to minimise any negative outcomes arising from research on the species being studied.

CONCLUSIONS

This review has summarised some important issues. There are too few studies detailing the effects of investigators on most procellariiform seabirds, particularly quantifying investigator disturbance (Götmark 1992; but see Blackmer et al. 2004). The value of measuring investigator disturbance, and mitigating investigator impact especially on threatened species, cannot be underestimated. Götmark (1992) has pointed out that variation in investigator visitation rates can mislead comparisons between studies of species unless the data can be corrected for the influence of investigator disturbance. Researchers need to be more aware of this when designing research programmes. Finally, research on the effects of investigator disturbance on nesting birds might not have a high priority among researchers or funding agencies, but it should be easy to combine the exploration of these effects with both short- and long-term studies of other aspects of avian ecology or behaviour. Researchers willing to study problems caused by investigator disturbance improve our knowledge and correct for biases caused by our activities.

ACKNOWLEDGMENTS

I thank Peter Pridmore for suggesting that I prepare this review, and for his encouragement along the way. I would particularly like to express my gratitude to Robert Trevethan whose comments greatly improved earlier versions of this manuscript. This manuscript was also improved by thoughtful comments from Karen Tymms, Catherine Meathrel, Phil Suter, Bruce Robertson, Kerry-Jayne Wilson, Carolyn King, and an anonymous reviewer. Funding for this research was kindly provided by ANZ Trustees Foundation—Holsworth Wildlife Research Endowment.

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