

**FORAGING STRATEGIES OF  
SOUTHERN ROYAL ALBATROSSES,  
*DIOMEDEA EPOMOPHORA*,  
CAMPBELL ISLAND  
DURING INCUBATION.**

---

A thesis submitted in partial fulfilment of the requirements

for the Degree of

Master of Applied Science

in

Animal Ecology

at

Lincoln University

---

by

Christina Troup

Lincoln University 2004



Southern Royal Albatross taking off from Campbell Island.

Abstract of a thesis submitted in partial fulfilment of the requirements for  
the Degree of Master of Applied Science

**Foraging strategies of Southern Royal Albatrosses, *Diomedea  
epomophora*, Campbell Island during incubation**

**Christina Troup**

Among the species of *Diomedea* albatrosses, diverse foraging strategies during breeding have been described, indicating species differences in foraging ecology and behaviour. Foraging strategies of Southern Royal Albatrosses, *Diomedea epomophora* (SRA) breeding on Campbell Island were studied in January – early February 1999 during the latter half of incubation. Movements and activity of ten birds were monitored using satellite transmitters and wet-dry activity recorders. Three birds from a pilot tracking study in February 1997 were also included in some analyses. Foraging strategies, zones used, factors influencing the duration of foraging trips, and the influence of wind conditions were investigated.

Foraging activity took place at sites with bathymetric characteristics associated with high productivity: outer shelf and shelf-break zones, with a concentration of activity on a shelf contour south of the Snares Islands. This is in contrast to Wandering (*D. exulans*) and Gibson's (*D. gibsoni*) albatrosses, typically deep oceanic foragers, but is similar to Northern Royal Albatross (*D. sanfordi*). The maximum distance of foraging trips from the colony was 1250 kilometres (mean  $584 \pm 351$ (SD)). This was closer than for incubating Wandering and Gibson's Albatrosses but more distant than for Northern Royal Albatross from the Otago Peninsula.

The mean duration of 77 foraging trips from 52 nests was 10.11 days for females and 8.76 for males (ns). Foraging trips became shorter as incubation progressed. Foraging trips were shorter, but not significantly so, when the median wind speed throughout the foraging trip was higher. No significant relationship was found between bird mass

and duration of foraging trips. The mean cumulative distance flown by the ten birds tracked in 1999 was 4262 km  $\pm$  1318 (SD).

Eight of the ten SRA employed a ‘commute, forage, commute’ foraging strategy, and the other two alternated short bouts of commuting and foraging. Commuting phases were characterised by rapid directional flight with a straight-line distance (range) of 180 km to 800 km between positions 24 hours apart. Foraging phases were characterised by a range of less than 180 km per 24 hour interval and frequent tight turns. Displacement rate between successive uplinks was significantly higher during commuting phases (28.6 kph  $\pm$  1.93 SE) than foraging phases (15.1 kph  $\pm$  1.4 SE). Wind strength and direction influenced the timing of the return commute to the colony. SRA covered greater distances at more favourable wind angles relative to flight track (broad reach and close reach) than in head, tail or direct side winds. Birds of low mass (< 8kg) made fewer landings in winds above 40 kph than in lighter winds, whereas heavier birds had a similar level of landing activity across all wind speed bands. One bird was delayed for several days by light winds, and another flew off course during strong winds. Two birds exploited the same window of wind conditions to return to the colony, each flying a similar course in both timing and route.

These results define the foraging strategies of SRA during incubation, and demonstrate the influence of wind conditions and other factors on the overall duration of foraging trips and on the timing of commuting and foraging phases.

### **Key words**

*Diomedea epomophora*, Southern Royal Albatross, foraging strategies; foraging behaviour, incubation, body weight, satellite tracking, wind, foraging trip duration.

## **Table of contents**

<b>Abstract</b>	<b>iii</b>
<b>Table of contents</b>	<b>v</b>
<b>List of figures</b>	<b>viii</b>
<b>List of tables</b>	<b>ix</b>
<b>Chapter 1 : General introduction</b>	<b>1</b>
<b>1.1. New Zealand’s place in global albatross diversity</b>	<b>1</b>
<b>1.2. Genus <i>Diomedea</i> – the Great Albatrosses</b>	<b>3</b>
<b>1.3. Southern Royal Albatross</b>	<b>4</b>
1.3.1. Ecology – overview	5
1.3.2. Breeding habitat	9
1.3.3. Foraging range / habitat	10
1.3.4. Breeding biology and life history traits	11
1.3.5. Conservation status and vulnerabilities	14
1.3.6. Ecological importance	16
<b>1.4. Studies of foraging strategies</b>	<b>18</b>
<b>1.5. Rationale for this study</b>	<b>22</b>
<b>1.6. Research goals and objectives</b>	<b>24</b>
<b>1.7. Study site</b>	<b>24</b>
<b>1.8. Thesis structure</b>	<b>26</b>
<b>References</b>	<b>28</b>
<b>Chapter 2 : Foraging zones of Southern Royal Albatrosses</b>	<b>35</b>
<b>2.1. Introduction</b>	<b>35</b>
<b>2.2. Methods</b>	<b>37</b>

<b>2.3. Statistical analyses</b>	<b>38</b>
<b>2.4. Results</b>	
2.4.1. Southern royal albatross foraging zones	38
2.4.2. Comparison among great albatrosses	43
<b>2.5. Discussion</b>	
2.5.1. Southern royal albatross foraging zones	43
2.5.2. Comparison among great albatrosses	46
<b>References</b>	<b>47</b>
<b>Chapter 3 : Aspects of foraging strategies</b>	<b>51</b>
<b>3.1. Introduction</b>	<b>51</b>
<b>3.2. Aims</b>	<b>55</b>
<b>3.3. Questions</b>	<b>55</b>
<b>3.4. Methods</b>	<b>56</b>
<b>3.5. Results</b>	<b>59</b>
<b>3.6. Discussion</b>	<b>64</b>
<b>References</b>	<b>67</b>
<b>Chapter 4 : Foraging trip patterns - commuting and foraging</b>	<b>70</b>
<b>4.1. Introduction</b>	<b>70</b>
<b>4.2. Questions</b>	<b>73</b>
<b>4.3. Methods</b>	<b>74</b>
<b>4.4. Results</b>	<b>77</b>
<b>4.5. Discussion</b>	<b>88</b>
<b>References</b>	<b>94</b>

<b>Chapter 5 : General Discussion</b>	<b>97</b>
<b>5.1. Introduction</b>	<b>97</b>
<b>5.2. Directions for further research</b>	<b>100</b>
<b>References</b>	<b>103</b>
<b>Acknowledgements</b>	<b>104</b>
<b>Appendices</b>	<b>105</b>

## List of figures

<b>Figure 1.1</b> : Southern Royal Albatross on nest	12
<b>Figure 1.2</b> : Incubation shift change	13
<b>Figure 1.3</b> : NZ archipelago and continental shelf	25
<b>Figure 1.4</b> : View of study study area on Campbell Island	25
<b>Figure 2.1</b> : Density plot of foraging tracks	41
<b>Figure 2.2</b> : Three individual foraging tracks	42
<b>Figure 3.1</b> : Foraging trip durations: equipped / not equipped	60
<b>Figure 3.2</b> : Foraging trip durations: individual tracked birds	61
<b>Figure 3.3</b> : Duration vs wind speed	62
<b>Figure 3.4</b> : Duration vs bird mass	62
<b>Figure 3.5</b> : Duration vs start date	63
<b>Figure 3.6</b> : Foraging shift change patterns	64
<b>Figure 4.1</b> : Defining ‘commute’ vs ‘forage’	75
<b>Figure 4.2 a-j</b> : Individual tracks, time on water, 24 hour range	79-84
<b>Figure 4.3</b> : Plot of synchronised return to Campbell	85
<b>Figure 4.4 a-c</b> : Relative wind direction vs speed and distance	87
<b>Figure 4.5</b> : Number of take-offs at range of wind speeds	88
<b>Figure 6.1</b> : Heart rates vs activity	106
<b>Figure 6.2</b> : Attachment of transmitter	107
<b>Figure 6.3</b> : Attachment of activity recorder	107

## **List of tables**

<b>Table 1 :</b> Trip duration, range and cumulative distance	39
<b>Table 2 :</b> Foraging parameters compared by species	41
<b>Table 3 :</b> Summary of foraging trip details for 10 SRA	106

## **Chapter 1 : General Introduction**

### **1.1 New Zealand's place in terms of global Albatross diversity**

The New Zealand region is the most important in the world for albatross (Diomedidae) family diversity (Robertson and Nunn 1997), and is similarly significant for the diversity of the wider petrel (Procellariiformes) order (Taylor 2000). Under the Robertson and Nunn revised taxonomy of the Diomedidae (Robertson and Nunn 1997), 13 out of the 24 species breed in New Zealand, and of these, nine are endemic breeders (Gales 1997). To put this in the global context, the next most diverse regions are the combined French administered Indian Ocean island groups of Crozet, Kerguelen and Amsterdam Islands (7 albatross species), and the combined British administered islands of the South Atlantic Ocean (Falkland Islands, South Georgia and Tristan da Cunha (also with 7 species) (Gales 1997). Based on figures collated and published by Gales, the combined breeding populations of all albatross species within the New Zealand jurisdiction is estimated at about 250,000 pairs breeding annually. As some of these species are biennial breeders, the absolute number of breeding pairs is considerably higher.

However, in terms of relative population sizes, there are instances elsewhere of larger breeding populations of single species than for the combined New Zealand breeding albatross species. For example in the Hawaiian archipelago, one site alone, Midway Atoll, has 427,500 breeding pairs of the annually breeding Laysan Albatross; and on the combined Falkland Islands, annually breeding Black-browed Albatrosses have been estimated at over half a million pairs (Gales 1997).

The other families of the order Procellariiformes are also well represented around New Zealand, with 31 of the 90 global species breeding in the New Zealand region, and a further five in New Zealand administered Antarctica (from Warham 1990).

Appropriate management of this rich component of our avifauna depends on an adequate understanding of the ecology and behaviour of each of these species. For example, individual species' foraging ecology, foraging strategies, foraging areas, foraging activity, foraging energetics and flight characteristics render them vulnerable in different ways to anthropogenic and other disturbances. It is also important to understand intraspecific differences between, for example, male and female birds, breeders and non-breeders, and experienced and inexperienced breeders. The most relevant knowledge is that which relates to stages of the life cycle where the species is the most constrained. Incubation and brooding were found to be the most demanding stages of the reproductive cycle in Wandering Albatrosses (Salamolard and Weimerskirch 1993), and this is expected to be the case for all albatross species; hence the importance of understanding the constraints that apply during these times. Once these various parameters are better understood for the species breeding within the New Zealand jurisdiction, any changes in breeding success, in other aspects of population dynamics, or changes in foraging patterns can more accurately be attributed to their cause, which is an important factor in appropriate management for their conservation.

## 1.2 Genus *Diomedea* – the Great Albatrosses

### Taxonomy / Phylogeny<sup>1</sup>

The term ‘great albatrosses’ refers to the group of albatross species that are substantially larger in size than all the others. From molecular evidence, Nunn and others have found the group to be phylogenetically distinctive enough to propose that the genus *Diomedea* (which formerly included all the albatrosses except the two Sooty Albatross species) should refer exclusively to this group (Nunn et al. 1996); (Robertson and Nunn 1997).

The Northern and Southern Royal Albatrosses are discussed below. The other Great Albatrosses include four that were until recently considered sub-species of *Diomedea exulans*, Wandering Albatross; Robertson and Nunn have proposed that these be reclassified as four species (Wandering Albatross *Diomedea exulans*, Tristan Albatross *D. dabbenena*, Antipodean Albatross *D. antipodensis*, and Gibson’s Albatross *D. gibsoni*) (Nunn et al. 1996). The latter two are endemic to New Zealand sub-antarctic islands, while the other two breed in the Indian and Atlantic Southern Ocean. The rarest of the Great Albatrosses is the recently discovered Amsterdam Albatross, *Diomedea amsterdamensis*, which is endemic to Amsterdam Island in the Indian Ocean. A survey of their breeding grounds in 1995 found only 13 breeding pairs (Gales 1997).

---

<sup>1</sup> For consistency, throughout this thesis the taxonomy proposed by Roberts and Nunn (1997) is followed. It is noted, however, that this taxonomy is still the subject of debate.

Under the previous taxonomy, all the smaller albatrosses (commonly referred to as mollymawks) except the Sooty Albatross and the Light-mantled Sooty Albatross were also included in the genus *Diomedea*. But recent work on the phylogenetic relationships of Diomedeidae (Nunn et al. 1996) places the four geographically isolated northern Pacific albatrosses (of the proposed new genus *Phoebastria*) closer to the Great Albatrosses than are the mollymawks, and the reinstated genus name *Thalassarche* is given to the remainder of the former *Diomedea*. *Thalassarche* and the two Sooty Albatrosses, *Phoebetria fusca* and *P. palpebrata*, are shown as more closely related to each other than to *Diomedea* and *Phoebastria*. This finding is supported by Heidrich et al.(1995) and by Sibley and Alquist (1990) (cited in Kennedy and Page 2002).

### **1.3 Southern Royal Albatross**

The Southern Royal Albatross, *Diomedea epomophora* (SRA) breeds almost exclusively on Campbell Island (in the New Zealand sub-antarctic). It is the largest of the *Diomedea* (Tickell 2000). Until recently it was regarded as the southern (nominate) sub-species, *Diomedea epomophora epomophora*, of the Royal Albatross *Diomedea epomophora*, the other sub-species being *Diomedea e. sandfordi*, the Northern Royal Albatross (NRA). Robertson and Nunn's proposed reclassification separates these into two species, *Diomedea epomophora* (SRA) and *Diomedea sandfordi* (NRA) (Robertson and Nunn 1997). Both are endemic to New Zealand, the former breeding mainly on Campbell Island and the latter on the Chatham Islands and the Otago Peninsula.

### 1.3.1 Ecology – overview

Albatrosses, like all petrels, are marine in every respect except for the need to come ashore to breed or for pre-breeding social activity. All the albatross species feed at sea, roost at sea, and even moult at sea. All have the ability to fly hundreds or thousands of kilometres to food resources, and most travel considerable distances even during breeding periods when constrained by the requirement to return to the nest.

Albatross flight consists of gliding on outstretched wings, with little flapping, least of all in the largest albatross species (Tickell 2000). Using a combination of techniques referred to as dynamic soaring and slope soaring (Warham 1990), the great albatrosses search on the wing, covering large distances in search of prey patches or individual prey items. Dynamic soaring requires windy conditions, and albatrosses can be almost becalmed or at least reduced to very low flight speed in the absence of wind (Salamolard and Weimerskirch 1993). Flapping flight is restricted as albatrosses have a shoulder locking tendon which prevents elevation of the wing above the horizontal – hence is used only for short periods at low wind speeds (Pennycuik 1982). SRA on average have the highest wing loading (a logarithmic function of body mass to wing area) of the great albatrosses (Tickell 2000) , and could be expected to be amongst species most susceptible to becalming.

The range of feeding behaviours varies to some extent between albatross species. Surface seizing of prey or scavenging are common to all, but some of the smaller albatrosses of the genera *Thalassarche* and *Phoebastria* also dive for prey, with

pursuit-diving (swimming underwater to chase prey) also found (Prince et al. 1994). Prince et al. recorded diving depths of 6 m for Grey-headed Albatross, *Thalassarche chrysostoma* (GHA), and 12.4m for Light-mantled Sooty Albatross *Phoebastria palpebrata* (LMSA). Prince also notes an observation reported by Voisin (1981) of a Wandering Albatross (WA) diving to 2m and swimming underwater; however this is thought to be a rare occurrence, given the buoyancy of the species. Buoyancy in the great albatrosses comes from high levels of stored fat and from air sacs around key internal organs as well as air cavities in vertebrae and wing bones (Tickell 2000). Royal Albatrosses are also thought to be surface feeders primarily or exclusively; however the possibility of occasional shallow diving behaviour has not been investigated to date.

SRA diet studied during chick rearing (Imber 1999) was found to consist largely of Cephalopoda. This included adult squid, with one inshore breeding species (*Moroteuthopsis ingens*) estimated to form 44% of total biomass intake; an unexpected finding was that adult octopus are consumed, albeit in small numbers. Fish, crustacea and salps were also included. A feature of the diet of SRA (as for NRA) was the absence of oceanic species and of Antarctic species that are commonly found in WA diets. The indications from this dietary evidence are that SRA differ from WA by being primarily continental shelf and shelf-break feeders. Observations at sea tend to confirm this evidence. Non-breeding SRA and NRA are observed on other continental shelf areas as well as New Zealand; many of them feeding off the west and east coasts of southern South America and around the Falkland Islands, and others off eastern and southern Australia (Marchant and Higgins 1990). In effect there is some degree of resource partitioning between SRA breeders and non-breeders (East

and West hemispheres); and between WA (out from the shelf break, except for during the early stages of chick-rearing) and SRA (from the shelf-break in over the shelf). In WA breeding on Crozet Island there is also a clear pattern of foraging zone partitioning between males and females (Weimerskirch et al. 1997) that will be discussed further in Chapter 3.

In suitable conditions, the dynamic soaring flight of albatrosses (and some other large petrels) enables greater distances to be covered than does the most efficient swimming possible, and the greatest distances within the constraints of breeding of all birds, with minimal expenditure of energy. However, dependence on it exposes them to the variability of wind conditions (both wind direction and wind speed) that adds an extra layer of complexity and uncertainty to be incorporated in the evolution of optimal foraging strategies. This could explain the stretched out time frame for chick rearing compared to other groups of birds, which allows some flexibility in terms of frequency of chick provisioning. In effect, the cost of the enormous distances is paid in time rather than in energy.

Albatrosses need to operate flexibly in response to a number of environmental variables. These variables are driven by different processes and are mostly out of phase with each other; some fluctuate on regular cycles, some to more erratic but loosely structured patterns, and yet others with no apparent pattern. These variables are discussed below:

**Bathymetry** (changes over evolutionary time with continental drift – eg progressive opening of the Southern Ocean)

**Oceanographic features** including currents, upwellings, gyres, boundaries between water bodies; continental drift gives rise to changes on long time scale, and climate driven changes in ocean circulation patterns occur on medium time scale.

These two sets of features influence patterns of prey abundance and distribution.

**Patterns of prey distribution & abundance** - these vary according to nutrient availability, plankton transport and sea surface temperature. Other possible contributing factors include anthropogenic changes due to fishing activity, bioaccumulating toxins and pollutants such as heavy metals, and nutrient discharge - affecting any level of the food web.

**Sea surface conditions** – affecting upthrust for wave-soaring flight, and the visibility of prey at the surface of the water. This factor can vary on a time scale of hours.

**Surface weather** – day by day / hour by hour variations in wind direction and strength - the SRA's “ transport system”, variable with some degree of predictability (underlying patterns of passage of highs, lows, fronts).

**Seasonal climate** – seasonal changes in prevailing wind direction and strength, changes in incidence of lows and fronts through the year.

**Variations in climate** driven by regular and irregular cycles and trends, eg ENSO cycles (2 to 9 year cycle); the Antarctic circumpolar wave (~ 4 year cycle) (White and Peterson 1996); Pacific decadal oscillation (20 to 30 year phase), etc.

**Global scale climate change** (ice ages, global warming, solar fluctuations). While the variations in and out of ice ages may happen at a rate to which species can adapt, adaptation to more abrupt changes as may occur with global warming may not be possible.

Daily **solar and lunar cycles** give rise to tidal effects, and to light / dark / moonlight cycles which have visibility implications for foraging birds as well as navigational

guidance implications. Some prey species respond to solar and lunar cycles in ways that alter their availability to foraging birds.

Most of these factors may impact on both distribution and abundance of prey and on SRA's ability to locate and access prey.

### **1.3.2 Breeding habitat**

Of the total breeding population of SRA, almost all (99%) breed on Campbell Island, an isolated sub-Antarctic island of 114 km<sup>2</sup> at latitude 52°30'S, longitude 169°15'E. The island was farmed for a period from 1894, and the last of the stock was removed in 1992. Enderby Island (Auckland Islands group), where most of the remainder of SRA nests are found, has a similar history.

On Campbell Island, SRA nest in the tussock herbfields above the scrub-line on sheltered aspects over most of the island. Nests are usually spaced such that birds are not in direct view of each other, and are often sheltered by clumps of tussock. The average density of nests is 30 per ha. (Tickell 2000).

Well adapted to an aquatic life, the great albatrosses including SRA cannot move rapidly on land. Their large wings require open ground for landing, and steep ground with a head wind for take-off. Walking is laboured. On Campbell Island, to take off into flight, birds leaving the nest must clamber uphill, and, depending on the nest's location, sometimes take as long as an hour (with frequent rests) to reach the nearest ridge-top over cliffs facing to windward. From other sites they go to an elevated and unobstructed area resembling a runway where they can run into the wind to get

airborne. Landing and take-off on land are apparently avoided in calm conditions. When wind speeds increase there is a noticeable increase in the amount of landing and taking off, both by breeding birds and by sub-adults attending the colony.

Most of the lower slopes of the island, other than where there are sheer cliffs, have dense vegetation, primarily *Dracophyllum* spp., which is almost impenetrable, hence is not available for nest sites.

In 1953 Campbell Island was designated a Fauna and Flora Reserve, and more recently a Nature Reserve. The New Zealand Department of Conservation (DoC) is required to manage Nature Reserves for 'the protection and preservation in perpetuity of the indigenous fauna and flora as far as possible in a natural state' (Reserves Act 1997). All visitors require a permit, and Campbell Island Nature Reserve currently has a restriction of 600 tourist visitor permits per year. In 1999 Campbell Island was listed a World Heritage Site along with other significant sub-antarctic islands under New Zealand's administration.

### **1.3.3 Foraging range / habitat**

In his study of the diet of SRA, Imber (1999) showed that the main foods fed to chicks are squid and marine carrion. Imber's finding that SRA mostly forage at steep shelf edges indicates a likely relationship with upwelling currents that concentrate nutrients near the sea surface. This pattern differs from the closely related WA (*Diomedea exulans*), which in the Indian Ocean was found to be a more pelagic forager at the same stage of the breeding cycle (Weimerskirch et al., 1993). In the

current study, all of the ten tracked SRA remained north of the Antarctic front and south of the sub-tropical front, although both boundaries were visited.

#### **1.3.4 Breeding biology and life history traits**

All of the great albatrosses exhibit traits identified with k-selection, being long lived and with a slow rate of reproduction. SRA may live to 50 years or more; one banded NRA was known to be breeding at age > 61 (Robertson 1997). The earliest known age of first breeding in NRA is 6 years for males and 7 for females, and the most common age is around 10 years; earlier ages within the range may be associated with periods of population decline (Tickell 2000). The range is less well documented for SRA but is given as 6-12 in Childerhouse et al. (2003). As for the other great albatrosses, SRA are biennial breeders, although failure early in one season can result in a breeding attempt the following year (Warham 1990). All the great albatrosses are primarily monogamous, and at least one season is spent in establishing the pair bond before breeding (Marchant and Higgins 1990). This investment in pair bonding may play an important part in the commitment each bird makes in maintaining the incubation, brooding and chick rearing relay.

A single egg is laid in a wide low conical nest made of earth and vegetation. Laying takes place in November – December, peaking in first week of December, which is up to 3 weeks later than for NRA at Taiaroa Head (Waugh et al. 1997). In SRA the peak hatching period is from 14 – 20 February after a mean incubation period of 78.5 days which is similar to NRA incubation length (Waugh et al. 1997). Brooding plus guard stages last approximately 40 days (Marchant and Higgins 1990). As with other

pelagic seabirds, chick growth is slow (Stearns 1992). Fledglings go to sea between early October and early December (Tickell 2000).



**Fig. 1.1** Southern Royal Albatross on nest

Between laying and hatching, each bird of the pair takes shifts incubating the egg while the other goes to sea to forage. The length of each shift was expected to be within the range of 5 – 14 days, based on a pilot study conducted by Weimerskirch and Waugh in 1997 (*pers. com.*) and unpublished records of P. Moore (N.Z. Department of Conservation). The risk of egg predation by skuas (*Catharacta skua*) is extremely high, so the incubating bird does not have the opportunity to leave the nest, even momentarily. During its shift on the nest the bird consumes stored energy. In other procellariiformes, loss of body mass below a critical level has been shown to result in desertion of the nest (Weimerskirch 1999). However, SRA, as the largest of

the procellariiformes, is likely to have a greater buffer zone between the expected nest shift duration and the time at which the critical body mass triggering desertion is reached compared to smaller species. Co-ordination of nest duties in such a way that both birds are able to maintain adequate condition is none-the-less an important aspect of successful breeding (Weimerskirch 1999).



**Fig. 1.2** A female SRA begins a new incubation shift and the male (right) is about to climb to a take-off site to begin a foraging trip at sea.

Salamolard estimated that incubation and the guard stage are the most demanding phases of the breeding cycle in WA (Salamolard and Weimerskirch 1993), and shows that most breeding failures occur between laying and hatching. Records from Campbell Island for SRA during the 1960s indicate that of all breeding failures, half occurred during incubation and over a quarter during the guard stage (Waugh et al. 1997). During these stages either one of the pair is constantly on the nest, hence for

approximately half the time is unable to forage. Therefore, in the course of each trip, the foraging bird needs to replenish its reserves to cover the energetic cost for the period of the trip as well as lay down reserves for the next nesting shift to cover its own basic metabolic requirements and any additional energetic costs of incubation. This requires the bird to have well developed foraging skills. WA begin breeding after a long period of “adolescence” (at around age 8) as do SRA, and first year attempts frequently end in failure (Weimerskirch 1992). Although WA reach their full adult skeletal dimensions before this age, Weimerskirch proposes that they must reach a mass threshold of >7.5 kg before succeeding at breeding. It may be that mass is simply an indicator of foraging efficiency (i.e. ability to access resources with minimal energetic cost). Greater mass should also be an advantage by increasing birds’ ability to sustain long nesting shifts.

### **1.3.5 Conservation status and vulnerabilities**

Almost all SRA breed on Campbell Island, 800 km south of Stewart Island, and the remainder on the Auckland Islands, an island group 400 km to the north-west of Campbell Island. A 1996 survey of the breeding population found 7,800 pairs on Campbell Island and 72 on the Auckland Islands (Gales 1997). As the birds breed biennially (unless unsuccessful), this figure is likely to be at least half the total breeding population. Gales (ibid) gives an estimate of 13,000 breeding pairs, and maybe 50,000 individuals. The population appears to be increasing, but that may be an artefact of improved census techniques with successive surveys (P. Moore, Department of Conservation, pers. comm.). A significant increase was noted in the period preceding the 1980's, as the population recovered from earlier predation by

sealers, and from breeding habitat modification by burning and grazing while the island was farmed from 1894 to 1970 (Gales 1997).

SRA are classified as Vulnerable on the 2003 IUCN Red List of Threatened Species, in the following category of criteria version 3.1, 2001 (IUCN 2003):

D. Population very small or restricted in the form of either of the following:

2. Population with a very restricted area of occupancy (typically less than 20 km<sup>2</sup>) or number of locations (typically five or fewer) such that it is prone to the effects of human activities or stochastic events within a very short time period in an uncertain future, and is thus capable of becoming Critically Endangered or even Extinct in a very short time period.

The accompanying citation states:

This species qualifies as Vulnerable because it has a very small range, breeding on four islands, though largely confined to just one, with a fifth mainland subpopulation comprising only hybrid birds.

Population trends are assumed to be stable.

As this citation indicates, SRA's primary vulnerability arises from the concentration of the nearly all of the breeding population on one island. Because of this, they are vulnerable to a number of potential environmental risks on that island, including widespread fire and introduced predators or disease pathogens. NRA breeding at Chatham Island colonies suffered heavy losses during a severe storm in 1985, which also destroyed large areas of nesting habitat resulting in negative impacts on productivity over a number of years (Robertson 1997). Changes in vegetation cover in response to warming could also affect SRA, as they nest in tussock herbfields above the scrub-line over most of the island. Encroachment of dense scrubby *Dracophylum* species upslope into the tussock herbfields would reduce the area available for nesting

and access. SRA require open ground for landing because of their large wings and lack of ability to manoeuvre. They also need unencumbered access to steep ground with a head wind for take-off, in some cases up to an hour's uphill climb through tussock from a nest site.

Beyond the island, factors that could impact on SRA include changes in wind regime that reduce the ability to reach foraging grounds economically. SRA cannot take off from the water in calm conditions, and, as gliders, require strong winds to commute between the breeding area and foraging grounds. Environmental changes leading to reduced abundance of key prey species within range of the breeding site would also be detrimental. Increase in sea surface temperature is thought to be the reason for the 94% decline of Southern Rockhopper Penguins (*Eudyptes chrysocome filholi*) breeding on Campbell Island over 43 years (Cunningham & Moore, 1994), while a 57% decline of Northern Rockhopper Penguins (*Eudyptes c. moseleyi*) on Amsterdam Island from 1971 to 1993 was correlated with a localised decline in sea surface temperature (Guinard et al. 1998). Pollution, such as chemical contamination or hydrocarbon spill, could have a detrimental impact if it were to occur at a site frequented by a large number of breeding birds, either in key foraging zones or close to the island where most birds spend time sitting on the water on departure and return from foraging flights (own unpublished data). SRA are known to be caught on longlines and in trawling operations, although accidental bycatch impacts appear to be lesser for SRA than for many other albatross and petrel species. Robertson reports a total of 13 recorded accidental catches of SRA by fishing vessels with observers within the New Zealand sector in the six seasons from 1996 to 2002 (Robertson et al. 2004). This does not reflect the total number caught, as not all vessels carry observers;

but it implies a lower rate than for the most bycatch-impacted albatross species (for example 91 Antipodean Albatrosses and 34 Gibson's Albatrosses for the same period (ibid). There are also records of SRA being caught on longlines in the South Atlantic Ocean, the Indian Ocean and the Australian Fishing Zone (Gales, 1998). There is no indication that competition from fisheries for prey (in particular for certain species of squid) is currently an issue for SRA.

SRAs' life history, physiology and ecology tend towards the outer extremes of bird biology on a number of parameters, which could make them vulnerable to ecological and environmental changes. Their large body mass (means: females 7.7kg, males 10.3kg, (Tickell 2000), the largest of the albatross species by a small margin, requires relatively high energy inputs. Their wings, spanning over 3 m, are ideally adapted to gliding, but of little use in windless conditions given the large distances they need to cover. Other, smaller gliders such as the White-chinned Petrel (*Procellaria aequinoctialis*) are able to cover similar distances at similar or greater speeds (Catard and Weimerskirch 1999), gaining comparable foraging potential for a lower energy investment than the SRA. The SRAs' large mass makes take-off from the water in lighter winds more energy demanding, and this could increase their vulnerability to any climate change in the direction of longer periods of calm conditions at the latitude of their breeding and foraging grounds, or seasonal changes in overall windiness. Incubation may be the stage of breeding where the adults are most vulnerable to sub-optimal conditions in terms of food availability and in terms of wind conditions for access to foraging grounds.

As SRA is a slow breeding species, raising a maximum of one chick per pair every two years and commencing breeding at a late age, population recovery from impacts would take a long time; and even small decreases in breeding success could accumulate into an slow population decline.

### **1.3.6 Ecological importance**

Seabirds are an important component of the Southern Ocean ecosystem, with large numbers using the New Zealand sector of the Southern Ocean. As top predators and scavengers, albatrosses are conspicuous indicators of environmental change because of their rapid response to changes such as the variable position of the polar front and to fluctuations in localised abundance of marine resources that occur in response to biotic and abiotic influences.

## **1.4 Studies of foraging strategies**

Studies of seabird foraging strategies are useful not only for our understanding of individual species' needs, but also for monitoring key aspects of the marine ecosystem. Since the advent of miniaturised satellite tracking technology and the pioneering of its use to track large seabirds, it has been possible to gain new insights into the foraging strategies of a number of species. Studies of foraging strategies of top marine predators such as SRA are also an important complement to studies of demographic trends, of diet, energetics, of chick rearing and provisioning and of body condition of adults and chicks, as well as studies of

productivity and prey availability at key foraging sites (Baduini and Hyrenbach 2003).

First, foraging strategy studies provide important information about the species' key foraging zones at specific stages of breeding and life cycles. The first successful study of foraging strategies of seabirds using satellite telemetry were of WA weighing 10 – 12 kg, using transmitters weighing 180g (Weimerskirch et al. 1993). As the size and weight of platform Terminal Transmitters (PTTs) reduced, smaller flying seabirds such as Black-browed Albatrosses (Weimerskirch 1997), Light-mantled Sooty Albatrosses (Weimerskirch and Robertson 1994) and White-chinned Petrels (Catard and Weimerskirch 1999) were studied, as well as non-flying seabirds such as the King Penguin (Jouventin et al. 1994). More recently, 20g PTTs were deployed on Northern Fulmars weighing 745 – 985 g (Weimerskirch et al. 2001).

Weimerskirch (1998) has studied the foraging strategies of WA and five other albatross species in the Indian Ocean and the way these strategies determine each species' relationship with commercial fisheries. A number of typical foraging strategies employed to different extents by the six albatross species at different stages of the breeding season were identified: short and long commuting trips to a shelf edge or frontal zone; linear (oceanic or along a shelf edge) searching trips and looping (oceanic) searching trips. The differences between species reflect differences in the way each species exploits the marine environment of the Southern Ocean, including differences in the prey taken.

Second, a number of studies have used knowledge of species' foraging strategies to examine areas of overlap with fishing activity: Cherel and Weimerskirch investigated interactions between seabirds and longline vessels fishing for Patagonian toothfish in Kerguelen Island waters the aim of introducing practices to reduce seabird mortality (Cherel and Weimerskirch 1996) using a combination of at-sea observations and satellite tracking data; and Weimerskirch used satellite tracking to investigate foraging strategies of six species of Indian Ocean albatrosses and their relationships with fisheries across a wider zone (Weimerskirch 1997). White-chinned Petrels, the species most frequently caught accidentally by longline fishing methods, were found to be at risk in their foraging grounds during incubation which range from the tropics to the Antarctic (Weimerskirch et al. 1999). Nicholls et al. examined time spent by non-breeding WA in the exclusive economic zones of Southern Oceans nations to highlight the implications for national responsibilities for conservation (Nicholls et al. 2000). Tuck et al. developed a model using the trends in space and time of longline fishing effort in the Southern Ocean in relation to spatial and temporal foraging by WA to predict the implications for accidental bycatch of WA males, females and juveniles from two different populations under a range of scenarios (Tuck et al. 2001), (Tuck et al. 2003). Recently Robertson et al. summarised all the known distributions of New Zealand breeding seabird species around the world, based on tracking studies and at-sea observations, and the distributions of fisheries known to catch seabirds, to identify the potential risks and enable mitigation measures to be promoted (Robertson et al. 2003).

Third, studies of foraging strategies of top predators are also important for understanding marine ecosystems and even for monitoring abiotic environmental factors. Trivelpiece et al. investigated the potential use of Adélie and Chinstrap penguins as monitors of the Southern Ocean Marine ecosystem (Trivelpiece et al. 1990); Cherel also investigated the value of seabirds as indicators of marine resources in a study of Black-browed Albatrosses feeding on ommastrephid squids in Kerguelen waters (Cherel and Weimerskirch 1995). Handrich et al. used breeding penguins as indicators of marine resources (Handrich et al. 1995). Furness and Camphuysen also looked at seabirds as monitors of the marine environment in relation to fish stocks and oil or other pollution (Furness and Camphuysen 1997). More recently Wilson et al. have summarised studies across 14 species of seabird to assess their use for measuring marine environmental variables from both a practical and an ethical perspective (Wilson et al. 2002).

Fourth, monitoring changes in foraging zones from year to year, particularly when used in tandem with diet, chick rearing, breeding success and long-term demographic studies can give important information about top predators' response to climate variability, which also provides an indication of variations in productivity at lower trophic levels. Culik et al. investigated changes in foraging strategies of Humboldt Penguins in response to stages of the El Niño Southern Oscillation (ENSO) cycle (Culik et al. 2000). Other studies have also revealed substantial variation in breeding success correlating with climatic variation, across a number of years and for a range of species according to their foraging habitat. Inchausti et al. investigated the breeding performance of eight species of seabirds in the Crozet and the Kerguelen sectors of the Southern Ocean and found that their

response to warmer or cooler sea surface temperatures in relation to oceanographic anomalies such as the Antarctic Circumpolar Wave depended on each species' foraging habitat at key times in relation to breeding (Inchausti et al. 2003).

## **1.5 Rationale for this study**

Studies of the SRA to date have focussed on breeding biology (beginning with (Sorensen 1950; Sorensen 1954); population monitoring (Moore et al. 1995) and diet fed to chicks (Imber 1999). A study of SRA foraging strategies during incubation is valuable because it enables us to document and describe the foraging habitat type and specific zones used by SRA. By using newly available technologies, it extends our knowledge of a species whose natural history and ecology have been difficult to study because of the amount of time it spends at sea and its dependence on marine resources. For the first time we can determine where breeding SRA forage during incubation, and how they respond to variations in conditions such as wind direction and strength to reach foraging grounds and to carry out surface activity associated with feeding.

This study also increases our understanding of critical factors for breeding success, such as the location and accessibility of food resources in relation to the breeding ground, which will enable us to anticipate the impacts on the species of change in their environment and ecosystem such as localised changes in marine resources (for example as a result of changes in sea temperature or currents), localised contamination such as from oil spills or toxic algal blooms, or the effects of

changed wind patterns associated with climate change in altering the costs to the birds of reaching key foraging zones.

As baseline information is established, top predators such as SRA can be studied as indicators of ecosystem-level changes (Cherel and Weimerskirch 1995) and of resources (Ancel et al. 1992): for example, changes in foraging zones and / or changes in the duration of shifts at sea could indicate changes in abundance or location of prey species or other aspects of marine ecology, or of winds used to reach foraging grounds.

Information from this research facilitates predictions of the species' interactions with commercial fisheries in relation to competition for prey species, and in relation to the risk of accidental bycatch by long-line fishing vessels (which has caused serious population declines in some procellariiform species).

This knowledge can inform conservation policies, including monitoring and management of human activities such as fishing in key foraging zones.

The study is conducted in collaboration with Henri Weimerskirch, Centre d'Études Biologiques de Chizé (CEBC), Centre Nationale de Recherche Scientifique (CNRS), France. Instruments, satellite time and meteorological data were supplied by the CEBC.

## **1.6 Research goals and objectives**

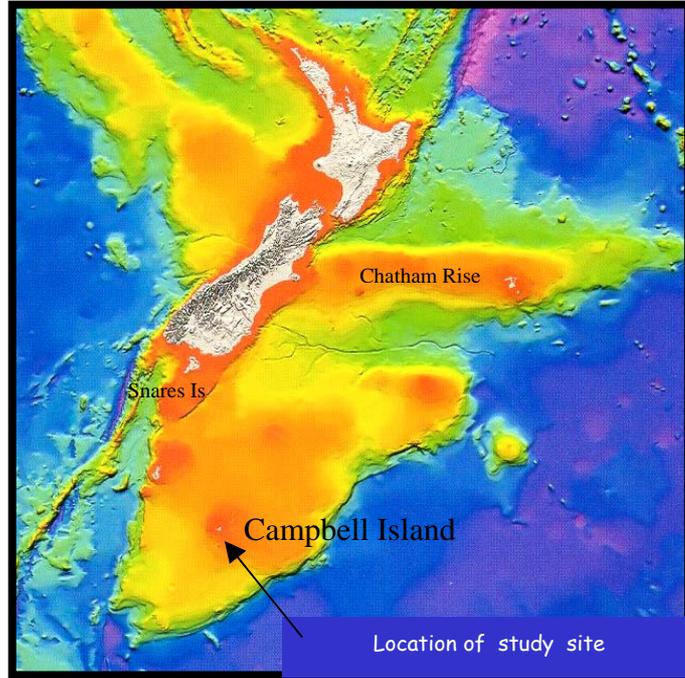
This study aims to investigate and describe the foraging strategies and foraging zones of Campbell Island Southern Royal Albatrosses during incubation. It will increase our understanding of parameters that could act as constraints on the birds' ability to forage effectively and return to the nest for incubation duties within a time frame that is sustainable by both birds of an incubating pair.

The specific objectives of this study are to establish:

- where breeding SRA forage during incubation, and how this compares with the foraging habitat of other great albatross species
- the duration of foraging trips, and factors that may contribute to variation in foraging trip duration
- the foraging strategies employed by SRA, comparisons with other albatross species, and intraspecific differences such as by sex or body mass
- how SRA use the wind to reach foraging grounds
- structure of foraging trips: time allocated to different phases and activities

## **1.7 Study site**

The study was conducted on Campbell Island, 700km to the south of the South Island of New Zealand (Fig 1.1). The study area of 52 nests was in the Col area close to the centre of the island (Fig. 1.2).



**Fig. 1.3** The New Zealand archipelago showing the continental shelf and slope. Campbell Island is towards the south of the Campbell Plateau. Blue areas are deep oceanic waters.



**Fig. 1.4** View of the study area on Campbell Island. The 52 nests monitored were within the encircled area (referred to as the Col area).

## 1.8 Thesis structure

This thesis is divided into five chapters.

Chapter One is a general introduction, providing biological background and geographic context for the current study in terms of the Southern Royal Albatross' place within the order Procellariiformes, its habitat requirements both at sea and at its breeding site, and its highly specialised adaptations to a distinctive environment. The population status and vulnerabilities are discussed, and the aims of this research are

**Fig. 1.4** View of the study area on Campbell Island. The 52 nests monitored were within the area marked by an oval (referred to as the Col area).  
outlined.

Chapter Two discusses the findings of the satellite tracking study in terms of where the birds foraged and the bathymetric and oceanographic characteristics of its foraging zones. It compares the foraging strategy of SRA with those of three other species of great albatross and the implications for SRA feeding ecology. This chapter was published in *The Condor* (August 2002: Volume 104, 3, pp.662 – 667) under the joint authorship of Susan Waugh, myself (Christina Troup), Dominique Filippi and Henri Weimerskirch. Susan Waugh and Henri Weimerskirch initiated the project and undertook satellite tracking of three incubating SRAs during in January – February 1997; I undertook the tracking of a further 10 SRAs during January-February 1999 with the assistance of Antoine Catard, and I prepared and integrated

tracking and activity data with a number of environmental variables using a software package written by Dominique Filippi for this purpose. Susan Waugh drafted the paper with significant input from myself and Henri Weimerskirch and further software and technical assistance of D. Filippi.

Chapter Three takes a more detailed look at the parameters of time and distance in SRA's foraging flights during incubation and seeks to understand key factors that control the duration of trips.

Chapter Four examines the foraging strategies utilised by the study birds in terms of phases and modes. Continuing with the investigation into SRA's use of the wind considered in Chapter 3, it examines the role of wind speed and direction for the activities of flight and the timing of phases of the trips. It considers differences between birds by sex and by weight as a way of seeking to understand the parameters within which SRA are constrained, particularly in respect of variations in wind speed.

Chapter Five takes the form of an overall discussion of the results, and further questions warranting investigation.

## References

- Ancel, A., G. L. Kooyman, P. J. Ponganis, G.-P. Gendner, J. Lignon, X. Mestre, N. Huin, P. H. Thorson, P. Robisson, and Y. Le Maho. 1992. Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature* **360**:336-338.
- Baduini, C., and K. D. Hyrenbach. 2003. Biogeography of Procellariiform foraging strategies: does ocean productivity influence provisioning? *Marine Ornithology* **31**:101-112.
- Catard, A., and H. Weimerskirch. 1999. Satellite tracking of White-chinned Petrel and comparison with other Procellariiformes. Pages 3008 - 3023 in N. Adams and R. Slotow, editors. 22nd Ornithological Congress. University of Natal, Durban, Durban, South Africa.
- Cherel, Y., and H. Weimerskirch. 1995. Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. *Marine Ecology Progress Series* **129**:295-300.
- Cherel, Y., and H. Weimerskirch. 1996. Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. *Biological Conservation* **75**:63-70.
- Childerhouse, S., C. J. R. Robertson, W. Hockley, and N. Gibbs. 2003. Royal albatross (*Diomedea epomophora*) on Enderby Island, Auckland Islands. Electronic copy DOC Science Internal Series 144, Department of Conservation, Wellington.

- Croxall, J. P., and P. A. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society* **14**:103 - 131.
- Culik, B., J. Hennicke, and T. Martin. 2000. Humboldt penguins outmanoeuvring El Nino. *The Journal of Experimental Biology* **203**:2311 - 2322.
- Furness, R. W., and C. J. Camphuysen. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* **54**:726-737.
- Gales, R. 1997. Albatross populations: status and threats. Pages 20 - 45 in G. G. Robertson, R, editor. *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton.
- Guinard, E., H. Weimerskirch, and P. Jouventin. 1998. Population changes and demography of the Northern Rockhopper Penguin on Amsterdam and Saint Paul Islands. *Colonial Waterbirds* **21**:222-228.
- Handrich, Y., G.-P. Gendner, and Y. Le Maho. 1995. Breeding penguins as indicators of marine resources: a study with minimal human disturbance. Pages 73-79 in P. Dann, I. Norman, and P. Reilly, editors. *The Penguins*. Surrey Beatty & Sons.
- Imber, M. J. 1999. Diet and Feeding Ecology of the Royal Albatross *Diomedea epomophora* - King of the Shelf Break and Inner Slope. *Emu* **99**:200-211.
- Inchausti, P., C. Guinet, M. Koudil, J. P. Durbec, C. Barbraud, H. Weimerskirch, Y. Cherel, and P. Jouventin. 2003. Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of*

Avian Biology **34**:170-176.

IUCN. 2003. 2003 IUCN Red List of Threatened Species. <[www.redlist.org](http://www.redlist.org)>. *in*.

Jouventin, P., D. Capdeville, F. Cuenot-Chaillet, and C. Boiteau. 1994.

Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. Marine Ecology Progress Series **106**:11-19.

Kennedy, M., and R. D. M. Page. 2002. Seabird supertrees: Combining partial estimates of procellariiform phylogeny. The Auk **119**:88-108.

Marchant, S., and P. J. Higgins, editors. 1990. Handbook of Australian, New Zealand and Antarctic Birds. Volume 1: Ratites to Ducks, 1 edition. Oxford University Press, Melbourne.

Moore, P. J., S. M. Waugh, C. West, and G. Mitchell. 1995. Preliminary results of a Southern Royal Albatross *Diomedea epomophora epomophora* census, Campbell Island, 12 January - 10 February 1995. Science and Research Series No 100 Department of Conservation, Wellington.

Murray, M. D., D. G. Nicholls, E. Butcher, and P. J. Moors. 2002. How Wandering Albatrosses use weather systems to fly long distances. 1. An analytical method and its application to flights in the Tasman Sea. Emu **102**:377-385.

Nicholls, D. G., M. D. Murray, E. C. Butcher, and P. J. Moors. 2000. Time spent in exclusive economic zones of Southern Oceans by non-breeding wandering albatrosses (*Diomedea* spp.): Implications for national responsibilities for conservation. Emu **100**:318 - 323.

- Nicholls, D. G., C. J. R. Robertson, P. A. Prince, M. D. Murray, K. J. Walker, and G. P. Elliott. 2002. Foraging niches of three *Diomedea* albatrosses. *Marine Ecology-Progress Series* **231**:269-277.
- Nunn, G. B., J. Cooper, P. Jouventin, C. J. R. Robertson, and G. G. Robertson. 1996. Evolutionary relationships among extant albatrosses (Procellariiformes: Diomedidae) established from complete cytochrome-b gene sequences. *The Auk* **4**:784-801.
- Pennycuik, C. J. 1982. The flight of petrels and albatrosses (procellariiformes), observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society of London* **B300**:75-106.
- Pinaud, D., and H. Weimerskirch. 2002. Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* **99**:141-150.
- Prince, P. A., N. Huin, and H. Weimerskirch. 1994. Diving depths of albatrosses. *Antarctic Science* **6**:353-354.
- Reinke, K., E. C. Butcher, C. J. Russell, D. G. Nicholls, and M. D. Murray. 1998. Understanding the flight movements of a non-breeding wandering albatross, *Diomedea exulans gibsoni*, using a geographic information system. *Australian Journal of Zoology* **46**:171-181.
- Robertson, C. J. R. 1997. Factors influencing the breeding performance of the Northern Royal Albatross. Pages 99-104 *in* G. Robertson and R. Gales, editors. *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton.

Robertson, C. J. R., E. A. Bell, and P. Scofield. 2004. Autopsy report for seabirds killed and returned from New Zealand fisheries, 1 October 2001 to 30 September 2002. DoC Science Internal Series 155, Department of Conservation, Wellington.

Robertson, C. J. R., E. A. Bell, N. Sinclair, and B. D. Bell. 2003. Distribution of seabirds from New Zealand that overlap with fisheries worldwide. *Science for Conservation* 233, Department of Conservation, Wellington.

Robertson, C. J. R., and G. B. Nunn. 1997. Towards a new taxonomy for albatrosses. Pages 13 - 19 *in* G. Robertson and R. Gales, editors. *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton.

Salamolard, M., and H. Weimerskirch. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Functional Ecology* 7:643-652.

Sorensen, J. H. 1950. The Royal Albatross. Pages 1-39 *in* Cape Expedition Series, Bulletin No. 2. Department of Scientific and Industrial Research, Wellington.

Sorensen, J. H. 1954. *Notornis* 6:25-27.

Spruzen, F., and E. Woehler. 2002. The influence of synoptic weather patterns on the at-sea behaviour of three species of albatross. *Polar Biology* 25:296 - 302.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.

- Taylor, G. A. 2000. Action plan for seabird conservation in New Zealand. Part A, Threatened seabirds. Department of Conservation, Biodiversity Recovery Unit, Wellington, New Zealand.
- Tickell, W. L. N. 2000. Albatrosses. Yale University Press, New Haven and London.
- Trivelpiece, W. Z., S. G. Trivelpiece, G. R. Geupel, J. Kjelson, and N. J. Volkman. 1990. Adélie and Chinstrap penguins: their potential as monitors of the Southern Ocean Marine ecosystem. *Antarctic Ecosystems. Ecological Change and Conservation*:191-202.
- Tuck, G. N., T. Polacheck, and C. M. Bulman. 2003. Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation* **114**:1-27.
- Tuck, G. N., T. Polacheck, J. P. Croxall, and H. Weimerskirch. 2001. Modelling the impact of fishery by-catches on albatross populations. *Journal of Applied Ecology* **38**:1182 - 1196.
- Warham, J. 1990. The Petrels: their ecology and breeding systems. Academic Press.
- Waugh, S. M., P. M. Sagar, and D. Paull. 1997. Laying Dates, Breeding Success and Annual Breeding of Southern Royal Albatrosses *Diomedea epomophora epomophora* at Campbell Island during 1964-69. *Emu* **97**:194-199.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**:464-473.

- Weimerskirch, H. 1997. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. Pages 168-179 in G. Robertson and R. Gales, editors. Albatross Biology and Conservation. Surrey Beatty & Sons, Chipping Norton.
- Weimerskirch, H. 1999. The role of body condition in breeding and foraging decisions in albatrosses and petrels. in N. J. Adams and R. H. Slotow, editors. 22nd International Ornithological Congress. Bird Life South Africa, Durban.
- Weimerskirch, H., A. Catard, P. A. Prince, Y. Cherel, and J. P. Croxall. 1999. Foraging white-chinned petrels *Procellaria aequinoctialis* at risk: from the tropics to Antarctica. Biological Conservation **87**:273-275.
- Weimerskirch, H., O. Chastel, C. Y., H. J.-A., and T. Tveraa. 2001. Nest attendance and foraging movements of northern fulmars rearing chicks at Bjornoya Barents Sea. Polar Biology **24**:83-88.
- Weimerskirch, H., Y. Cherel, F. Cuenot-Chaillet, and V. Ridoux. 1997. Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology **78**:2051-2063.
- Weimerskirch, H., and G. Robertson. 1994. Satellite tracking of light-mantled sooty albatrosses. Polar Biology **14**:123-126.
- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. The Auk **110**:325-342.

White, W. B., and R.G. Peterson. 1996. An Antarctic circumpolar wave in surface pressure, temperature and sea-ice extent. *Nature* **380**:699-702.

Wilson, R. P., D. Gremillet, J. Syder, M. A. M. Kierspel, S. Garthe, H.

Weimerskirch, C. Schafer-Neth, J. A. Scolaro, C. A. Bost, J. Plotz, and D.

Nel. 2002. Remote-sensing systems and seabirds: their use, abuse and

potential for measuring marine environmental variables. *Marine Ecology-*

*Progress Series* **228**:241-261.

## Chapter 2: Foraging zones of Southern Royal Albatrosses

*The Condor*, Aug 2002; Susan Waugh<sup>1</sup>, Christina Troup<sup>2</sup>, Dominique Filippi<sup>3</sup> and Henri Weimerskirch<sup>4</sup>

<sup>1</sup>Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

<sup>2</sup>Ecology and Entomology, P.O. Box 84, Lincoln University, New Zealand

<sup>3</sup>CEA-LSCE, 91190 Gif-sur-Yvette, France

<sup>4</sup>CNRS-CEBC, 79360 Villiers-en-Bois, France

Copyright Cooper Ornithological Society Aug 2002

---

### Abstract

Southern Royal Albatrosses (*Diomedea epomophora*) were satellite-tracked from Campbell Island during the incubation period in 1997 and 1999. Their foraging activity was restricted to shelf and shelf-break areas within 1250km of their breeding site. Foraging activity by 8 of the 14 individuals tracked was concentrated at a zone near the Snares Islands, on the Campbell Plateau. Southern and Northern Royal Albatrosses (*D. sanfordi*) foraged on average nearer their breeding site than two other species of great albatrosses (Gibson's [*D. gibsoni*], and Wandering [*D. exulans*] Albatrosses) studied during the incubation period.

Key words: continental shelf, *Diomedea epomophora*, foraging, resources, satellite tracking, Southern Royal Albatross.

---

## 2.1 Introduction

The distribution of resources in the marine environment leads to particular problems for foraging higher predators. Physical and biological factors lead to high variability in prey abundance (Murphy et al. 1988, Hunt 1991, Rodhouse et al. 1996).

Hydrographic features such as sea-ice, ocean fronts, eddies, and upwellings may lead to prey aggregations at mesoscales, while prey schooling behaviors, or predator-prey interactions, and wind-driven Langmuir cells are thought to concentrate prey into dense patches at finer scales (Hunt 1991). Albatrosses in the Southern Ocean epitomize foraging specialization in this difficult environment, using energy-efficient soaring flight to cover great distances in search of sparsely distributed prey (Arnould et al. 1996, Weimerskirch et al. 2000).

Recent technical developments in the study of behavior of large, wide-ranging procellariiform birds, such as satellite telemetry (Jouventin and Weimerskirch 1990) and the use of activity recorders, allow us to examine their behavior using spatial analyses (Wood et al. 2000). Indeed, the need to take into account spatial components of ecological data has been strongly emphasized recently (Tilman and Kareiva 1997, Selmi and Boulinier 2001, Yoccoz et al. 2001). Bird-activity density analyses enable us to take into account information about seabird behavior in relation to physical, biological, and anthropogenic factors in the marine environment (Berrow et al. 2000, Gremillet et al. 2000, Wood et al. 2000).

In this paper we apply quantitative analytical tools to determine the characteristics of the feeding habitat of Southern Royal Albatrosses (*Diomedea epomophora*) foraging during two breeding seasons in New Zealand. We compare foraging characteristics of this species with published reports of three other greater albatross species: Northern Royal Albatross (*D. sanfordi*) and Gibson's Albatross (*D. gibsoni*), which were

studied using satellite telemetry in New Zealand, and Wandering Albatross (*D. exulans*), which was studied at the Crozet Islands. Formerly these four species were considered to be only two distinct taxa, Wandering and Royal Albatrosses, but we follow the taxonomy proposed by Robertson and Nunn (1997).

## 2.2 Methods

Southern Royal Albatrosses were satellite-tracked at Campbell Island (52°33'S, 169°09'E) during incubation. Four birds were tracked during 6-15 February 1997 and 10 birds during 12 January-11 February 1999. Transmitters were attached to the back feathers of incubating birds using surgical-grade (Tesa) tape and removed after one foraging trip. Locations were received through the ARGOS system (Argos, CSL, Toulouse, France). Data were classified into 6 classes of decreasing accuracy and quality: Class 3: (error radius of 150m), 2 (350m), 1 (1km), 0, A and B (accuracy to be determined by the user). The threshold for rejection of low-quality satellite locations was a flight speed of  $>90 \text{ km hr}^{-1}$  between successive uplinks. Trip durations were calculated from a combination of satellite locations and observations of birds leaving or returning to their nests.

Data were treated using a custom software package ("Diomedea," D. Filippi, unpubl. Program; see Weimerskirch et al. 2000 for details and other examples of its use).

The system estimates the mean speed of travel between successive satellite locations at 1 min or greater intervals, allowing environmental databases to be linked to locational estimates. The pattern of activity of individuals can then be analyzed in relation to the environment they are exploiting. In this study we chose to examine bathymetric data (Integrated Global Ocean Services System, unpubl. data) in

relation to bird foraging movements. Further, we generated a matrix of density of bird activity (time spent per unit area) and integrated this with the bathymetric data using Matlab 5 (Mathworks Inc. 1996).

Data for comparison of trip parameters between albatrosses of different species were obtained from publications, and maximum ranges were estimated for Northern Royal Albatross to the nearest 10 min of longitude and latitude from published maps (Nicholls et al. 1994). As there are considerable differences in foraging ranges and strategies between periods of the breeding season for this group of birds (Weimerskirch et al. 1993, Stahl and Sagar 2000a, 2000b), we restricted our comparison to trips followed during the incubation period.

### **2.3 Statistical analyses**

Due to high variances in the foraging parameters measured, nonparametric statistics were used to test between-group differences in foraging parameters (Mann-Whitney U-tests for two-sample tests, Kruskal-Wallis tests for four-way comparisons of means; Sokal and Rohlf 1995, SAS Institute 2001). There were no differences between results from these and parametric tests (two-sample t-test, ANOVA). Statistical tests were carried out using SAS Y.8 (SAS Institute 2001), with  $P < 0.05$ . Values reported are means  $\pm$  SD.

## **2.4 Results**

### **2.4.1 Southern royal albatross foraging zones**

The characteristics of the flights of 14 Southern Royal Albatrosses satellite tracked from Campbell Island are shown in Table 1. There were no significant differences in foraging parameters between years except for maximum range (trip duration 1997 =

6.9 ± 4.2 days, 1999 = 11.7 ± 3.6 days.  $U = 6.0$ ,  $P = 0.1$ ; maximum range 1997 = 187 ± 54 km, 1999 = 703 ± 351 km,  $U < 0.01$ ,  $P < 0.01$ ; distance traveled 1997 = 2707 ± 1721 km, 1999 = 4004 ± 1554 km,  $U = 7.0$ ,  $P = 0.02$ ). Differences in maximum range could be explained by the slightly later period of study during the first season. We chose to pool all results between years (Table 2).

TABLE 1. Characteristics of 14 Southern Royal Albatross foraging trips followed by satellite telemetry, indicating the time spent at sea (trip duration), the maximum distance from the colony attained by each bird (maximum range), and the distance traveled by each bird along its trip (cumulative distance traveled). The first two digits of each bird number indicate the year of study. For bird 97-3, the transmitter stopped functioning after 3.5 days at sea; thus minimum distances only are given.

Bird No.	Trip duration (days)	Maximum range (km)	Cumulative distance traveled (km)
97-1	8.8	223	4289
97-2	9.9	213	2959
97-3	3.5+	107+	1394+
97-4	2.1	125	875
99-1	16.0	1259	6589
99-2	15.2	773	5497
99-3	9.6	493	3487
99-4	6.8	343	2835
99-5	15.9	1214	6051
99-6	9.0	506	3302
99-7	16.3	517	3250
99-8	12.8	638	3338
99-9	8.8	768	4263
99-10	9.9	512	5323

All 14 Southern Royal Albatrosses tracked used the Campbell Plateau during their foraging trips, either as a thoroughfare or as a foraging site in itself. A single zone was very intensively prospected, south of the Snares Islands, in a wide band from the west to the centre of the plateau (Fig. 1). This zone (hereafter referred to as the Snares Islands hotspot) lies along the inner shelf-break at a depth of 200 m. A second feature of the foraging strategy of the tracked birds was the intensive activity in the vicinity of steep bathymetric gradients (1000-3000 m depth). For example, peaks of bird activity were concentrated on the continental shelf slope to the southeast of Campbell Plateau (used by two birds), along the Chatham Rise (two birds), off the Otago Peninsula (three birds), and at the Puysegur Trough off the southwest corner of New Zealand (one bird). While one or a few individuals used these diverse zones, eight birds, including birds from both years of study, frequented the Snares Islands hotspot. The tracks of three individuals are shown in Figure 2.

We divided the area used by the birds into four zones depending on the bathymetry, and calculated the time spent by birds in each. These zones correspond to (1) the inner continental shelf (<200 m depth), a zone dominated by swimming predators (e.g., seals and sea-lions, penguins, shags); (2) the continental shelf (200-300 m depth), a zone that is more productive than open ocean waters; (3) lower shelf-slope waters (800-1500 m depth), where the bathymetric gradient descends rapidly, a zone which may be associated with mixing and nutrient upwelling; (4) deep oceanic waters (1500-6000 m depth) in which foraging resources are generally scarce (Schneider 1997). For the 14 birds tracked, inner shelf waters received little attention ( $14 \pm 12\%$  of bird time), while foraging activity was centered over continental shelf waters ( $59 \pm 21\%$ ) or lower shelf-slope waters ( $21 \pm 22\%$ ). Deeper waters were rarely used ( $5 \pm 6\%$ ).

TABLE 2. Comparison of mean  $\pm$  SD foraging parameters for four species of greater albatrosses.

Site	Albatross species	Year(s)	<i>n</i>	Trip duration (days)	Maximum range from colony (km)	Cumulative distance traveled
Campbell Island <sup>a</sup>	Southern Royal Albatross	1997 1999	13	10.8 $\pm$ 4.1	584 $\pm$ 351	4004 $\pm$ 1554
Otago Peninsula <sup>b</sup>	Northern Royal Albatross	1993	3	3.9 $\pm$ 1.9	145 $\pm$ 69	-
Crozet Island <sup>c</sup>	Wandering Albatross	1992 1994	10	10.2 $\pm$ 8.4	1456 $\pm$ 1059	5739 $\pm$ 4781
Auckland Islands <sup>d</sup>	Gibson's Albatross	1994	3	12.1 $\pm$ 1.1	1275 $\pm$ 211	4538 $\pm$ 922

<sup>a</sup> This study; <sup>b</sup> Nicholls et al. 1994; <sup>c</sup> Weimerskirch et al. 1994, Weimerskirch, Wilson, and Lys 1997; <sup>d</sup> Walker et al. 1995.

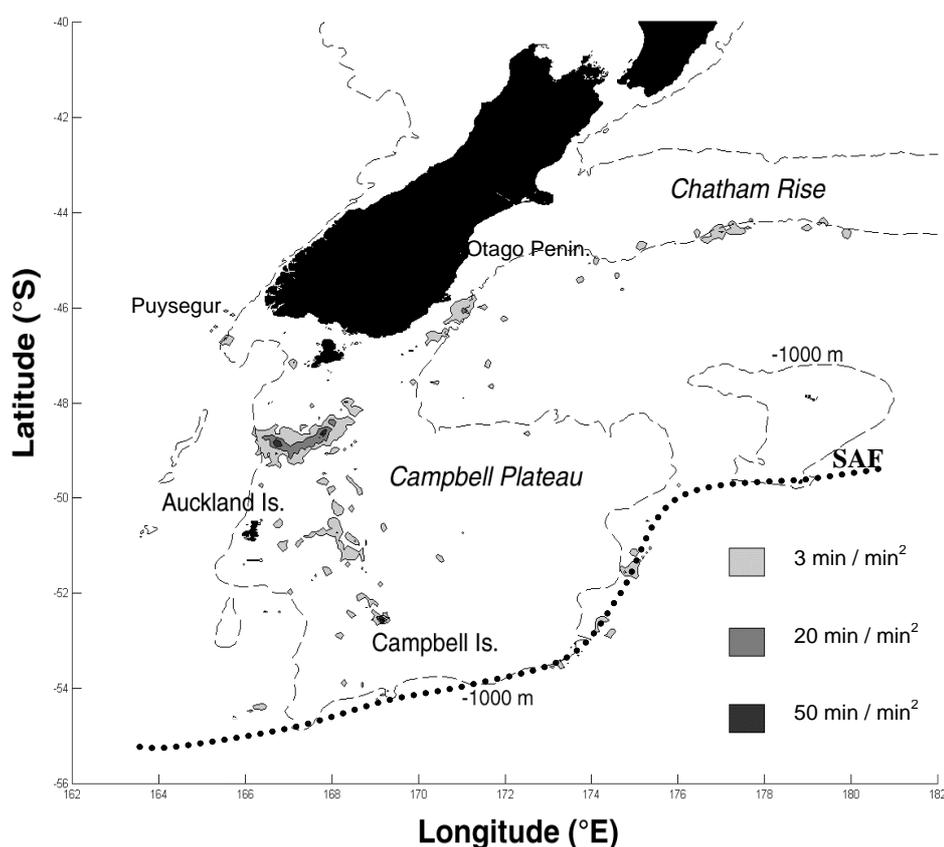


FIGURE 1. Density plot of 14 Southern Royal Albatross tracks, showing use of waters over the Campbell Plateau and other bathymetric features. The lower shelf break (1000 m deep, dashed), coast (solid), and approximate position of the Sub-Antarctic Front (SAF; as indicated by the 8°C sea-surface temperature isotherm, dotted) are shown. Density is indicated in minutes of bird time per unit area (minute latitude X minute longitude). One degree of latitude represents 109 km.

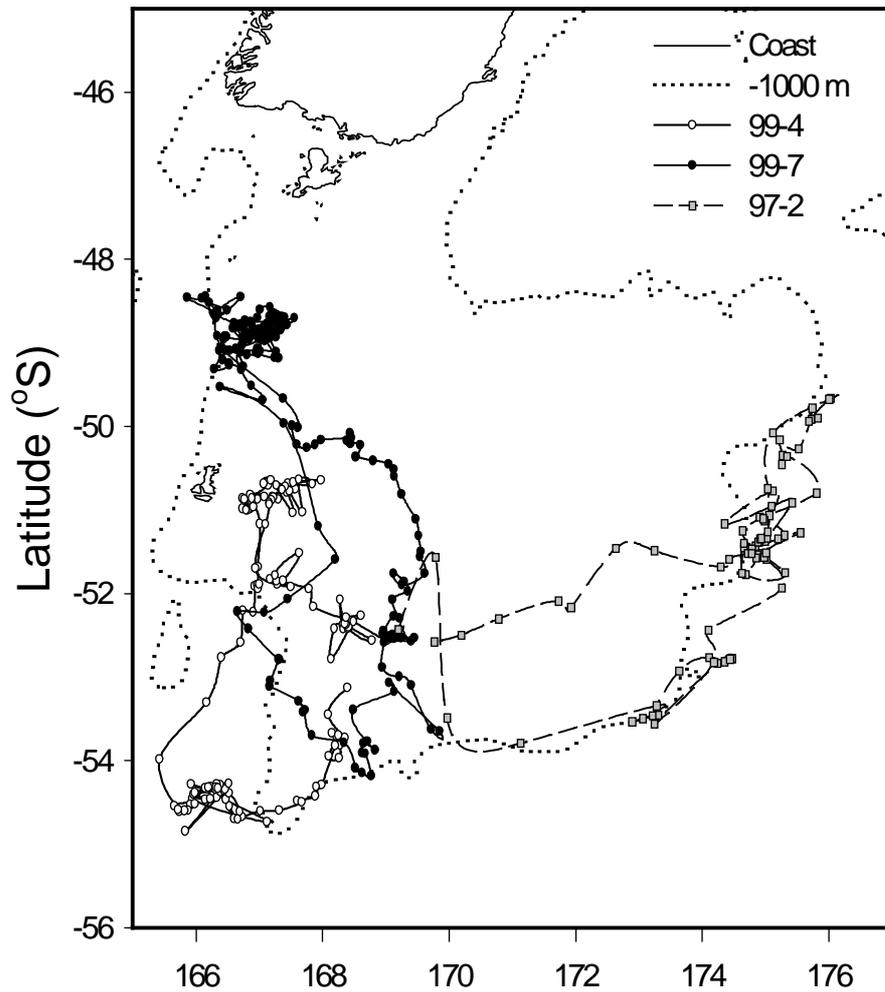


FIGURE 2. Three individual tracks from foraging trips using the southern (individual 99-4, unfilled circles) and southeastern shelf breaks of the Campbell Plateau (individual 97-2, gray squares) and Snares Islands hotspot (individual 99-7, filled circles). Symbols represent satellite fixes, which occurred at irregular intervals. The coastline (solid) and 1000m isobath (dashed) are shown. One degree of latitude represents 109 km.

## **2.4.2 Comparison among great albatrosses**

We compared foraging trip parameters for great albatrosses followed by satellite telemetry at four sites (Table 2). Data were available for Wandering Albatrosses (Crozet Islands 1992,  $n = 5$ , Weimerskirch et al. 1994; and 1994,  $n = 5$ , Weimerskirch, Wilson, and Lys 1997) Gibson's Albatross, (Auckland Islands, 1994,  $n = 4$ , Walker et al. 1995) and for Northern Royal Albatross (Otago Peninsula,  $n = 4$ , 1993, Nicholls et al. 1994).

There were no significant between-year differences in the foraging parameters for Wandering Albatrosses tracked from the Crozet Islands; thus these samples were pooled (trip duration 1992 =  $5.4 \pm 3.2$  days, 1994 =  $15.0 \pm 9.6$  days,  $U = 4.0$ ,  $P = 0.09$ ; maximum range 1992 =  $1196 \pm 763$  km, 1994 =  $1717 \pm 1331$  km,  $U = 12.0$ ,  $P = 1.0$ ; distance traveled 1992  $2868 \pm 2364$  km, 1994 =  $6695 \pm 4696$  km,  $U = 5.0$ ,  $P = 1.0$ ).

There were significant differences between species in all foraging parameters (duration  $H_3 = 7.6$ ,  $P = 0.05$ , maximum range  $H_3 = 15.1$ ,  $P < 0.01$ ; distance traveled  $H_3 = 10.5$ ,  $P = 0.01$ ; Table 2). In particular, Northern Royal Albatross carried out short foraging trips of limited range, while Wandering and Gibson's Albatrosses performed trips with greater maximum range than did the Southern or Northern Royal Albatrosses.

## **2.5 Discussion**

### **2.5.1 Southern royal albatross foraging zones**

The study revealed a characteristic foraging pattern for Southern Royal Albatross, that of a shelf- and shelf break feeding species which, despite foraging trips of moderate duration, does not venture far from its breeding site. Southern Royal Albatrosses used

the continental plateau extensively, with one hotspot south of the Snares Islands. Further, they seemed to concentrate their foraging effort over shelf-breaks. They may use sites with upwelling and eddies associated with the concurrence of oceanic fronts and the submarine relief, a feature common in the foraging strategies of many marine top predators (Rodhouse et al. 1996, Veit et al. 1993). In the two study periods, the KC isotherm passed along the southwestern edge of the Campbell Plateau (Integrated Global Ocean Services System, unpubl. data), indicating that the Sub-Antarctic Front was located in this zone (Heath 1981, Belkin and Gordon 1996). A concurrent study of Black-browed and Greyheaded Albatrosses (*Thalassarche melanophrys* and *T. chrysostoma*) also nesting at Campbell Island showed some overlap between these species and Southern Royal Albatross in their usage of the Campbell Plateau, but both *Thalassarche* species also made extensive use of the oceanic waters to the east and south of the plateau (Waugh et al. 1999). Segregation of foraging habitat relative to water depth has been well documented in marine birds, and is thought to be related to differences in primary productivity over shelf or deep-water environments (Schneider 1997).

Several of the areas prospected by Southern Royal Albatrosses were also used extensively by Buller's Albatrosses (*T. bulleri*) satellite-tracked from the Snares and Solander Islands (Stahl and Sagar 2000a, 2000b). The main area of overlap with Southern Royal Albatross was along the continental shelf edge off the Otago Peninsula and Chatham Rise. Buller's Albatrosses nest in winter; thus the periods of study do not allow us to examine between-species interactions over the same foraging zones using the current data set.

The use of the shelf-break as a principal feeding area for Southern Royal Albatrosses has previously been inferred from dietary analysis, where oceanic squid species were

conspicuously absent (Imber 1999). Southern Royal Albatrosses rely on a relatively narrow range of prey, taking squid from only five families compared to 27 families for Wandering Albatross (Cherel and Klages 1997).

In addition to noting which zones are most frequented by a population or some smaller sample of birds, it is of interest to examine how they use their environment. In particular, operating in an energy-efficient manner is important for birds that travel over large distances in search of sparsely or patchily distributed prey. One strategy used by procellariiform seabirds to maximize prey-capture rates and minimize energy spent in locomotion is to make long looping flights, covering vast distances to maximize encounter rates with sparse prey, and thus attain predictable prey yields (Weimerskirch, Wilson, and Lys 1997). Fauchald et al. (2000) showed that Common Murres (*Uria aalge*) use the hierarchical patch structure of their principal prey, capelin (*Mallotus villosus*), to guide them to areas of high prey density, as prey patches are predictable in neither time nor location. In contrast to these two patterns, optimal energy acquisition in the foraging environment of the Campbell Plateau may favor the visitation of known locations, regardless of the energetic costs of commuting between these areas and the breeding site. This pattern of activity has already been shown for Black-browed Albatrosses feeding at the Kerguelen Islands (Weimerskirch, Mougey, and Hindermeier 1997). The foraging patterns of Southern Royal Albatross show a strong link to physical attributes in the marine environment, suggesting that location, and not prey density, orients their mesoscale foraging search toward particular zones. The cues that albatrosses use to identify these areas and locate profitable prey patches within them are unknown. It may be that at finer scales prey-patch tracking also occurs, as for murres exploiting bands of capelin (Fauchald et al. 2000).

### **2.5.2 Comparison among great albatrosses**

In comparison with the other great albatrosses, both Southern Royal Albatrosses satellite tracked from Campbell Island (this study) and Northern Royal Albatrosses from Otago Peninsula (Nicholls et al. 1994) restricted their foraging to shelf areas or shelf-breaks, at relative proximity to their breeding sites. This is in spite of similar trip durations for Southern Royal Albatross, Wandering Albatross and Gibson's Albatross. The two Royal Albatross species appear to have foraging characteristics most similar to those described for Wandering Albatrosses from South Georgia, which clustered near the 1000 m isobath and made extensive use of the coastal shelf-slope and Patagonian Shelf (Prince et al. 1997). This pattern of behavior contrasts with that of Wandering Albatrosses from the Crozet Islands (Weimerskirch et al. 1994, Weimerskirch 1997, Weimerskirch, Wilson, and Lys 1997), and Gibson's Albatross (Walker et al. 1995) which feed more frequently over oceanic waters and forage significantly farther from their nests than do Royal Albatrosses during the incubation phase. The contrasting strategies of Gibson's Albatross and Southern Royal Albatross from Campbell Island suggest that the former species may be excluded from feeding over shelf waters, as they do not frequent the Snares Islands hotspot, despite its proximity to their Auckland Islands breeding site.

We wish to thank the Department of Conservation and the National Institute of Water and Atmospheric Research for their assistance with the program. Antoine Catard, Peter Moore and others made invaluable efforts in the field. The program was funded by the Conservation Services Levy, the France-New Zealand Cultural Agreement, and the Centre National de la Recherche Scientifique. We thank two anonymous reviewers for their comments to improve the manuscript.

## References

- Arnould, J. P. Y., D.R. Briggs, J. P. Croxall, P. A. Prince, and A.G. Wood. 1996. The foraging behaviour and energetics of Wandering Albatrosses brooding chicks. *Antarctic Science* 8:229-236.
- Belkin, I. M., and A. L. Gordon. 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. *Journal of Geophysical Research* 101: 3675-3696.
- Berrow, S., A. G. Wood, and P. A. Prince. 2000. Foraging location and range of White-chinned Petrels *Procellaria aequinoctialis* breeding in the South Atlantic. *Journal of Avian Biology* 31:303-311.
- Cherel, Y., and N. Klages. 1997. A review of the food of albatrosses, p. 113-136. In G. Robertson and R. Gales (Eds.), *Albatross biology and conservation*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Fauchald, P., K. E. Erikstad, and H. Skarsfjord. 2000. Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology* 81:773-783.
- Gremillet, D., R. P Wilson, S. Wanless, and T Chater. 2000. Black-browed Albatrosses, international fisheries and the Patagonian Shelf. *Marine Ecology Progress Series* 195:269-280.
- Heath, R. A. 1981. Oceanic fronts around southern New Zealand. *Deep-Sea Research* 28A:547-560.
- Hunt, G. L., Jr. 1991. Occurrence of polar seabirds at sea in relation to prey concentrations and oceanographic factors. *Polar Research* 10:553-559.
- Imber, M. J. 1999. Diet and feeding ecology of the Royal Albatross *Diomedea epomophora* - king of the shelf break and inner slope. *Emu* 99:200-211.

- Mathworks Inc. 1996. Using Matlab Version 5. Matlab the language of technical computing. The Mathworks Inc., Natick, MA.
- Murphy, E. J., D. J. Morris, J. L. Watkins, and J. Priddle. 1988. Scales of interactions between Antarctic krill and the environment, p. 120-130. In D. Sahrhage (Ed.), Antarctic ocean and resources availability. Springer-Verlag, Berlin.
- Nicholls, D. G., M. D. Murray, and C. J. R. Robertson. 1994. Oceanic flights of the Northern Royal Albatross *Diomedea epomophora sanfordi* using satellite telemetry. *Corella* 18:50-52.
- Prince, P. A., J. P. Croxall, P. N. Trathan, and A. G. Wood. 1997. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries, p. 137-167. In G. Robertson and R. Gales [Eds.], Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, Australia.
- Robertson, C. J. R., and G. B. Nunn. 1997. Towards a new taxonomy for albatrosses, p. 13-19. In G. Robertson and R. Gales [Eds.], Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, Australia.
- Rodhouse, P. G., P. A. Prince, P. N. Trathan, E. M. C. Hatfield, J. L. Watkins, D. G. Bone, E. J. Murphy, and M. G. White. 1996. Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions. *Marine Ecology Progress Series* 136:37-50.
- Sas Institute. 2001. The SAS System. Version 8e. SAS Institute Inc., Cary, NC.
- Schneider, D. C. 1997. Habitat selection by marine birds in relation to water depth. *Ibis* 139:175-177.
- Selmi, S., and T. Boulinier. 2001. Ecological biogeography of Southern Ocean islands: the importance of considering spatial issues. *American Naturalist* 158:426-437.

- Sokal, R. R., and F J. Rohlf. 1995. Biometry. 3rd ed. Freeman, New York.
- Stahl, J. C., and P M. Sagar. 2000a. Foraging strategies of southern Buller's Albatrosses *Diomedea b. bulleri* breeding on the Snares, New Zealand. Journal of the Royal Society of New Zealand 30: 299-318.
- Stahl, J. C., and P. M. Sagar. 2000b. Foraging strategies and migration of southern Buller's Albatrosses *Diomedea b. bulleri* breeding on the Solander Is, New Zealand. Journal of the Royal Society of New Zealand 30:319-334.
- Tilman, D., and P. Kareiva. 1997. Spatial ecology. The role of space in population dynamics and interspecific interactions. Monographs in Population Biology 30. Princeton University Press, Princeton, NJ.
- Veit, R. R., E. D. Silverman, and I. Everson. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. Journal of Animal Ecology 62:551-564.
- Walker, K., G. Elliott, D. Nicholls, D. Murray, and P. Dilks. 1995. Satellite tracking of Wandering Albatross (*Diomedea exulans*) from the Auckland Islands: preliminary results. Notornis 42: 127-137.
- Waugh, S. M., H. Weimerskirch, Y. Cherel, U. Shankar, P. A. Prince, and P. M. Sagar. 1999. Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. Marine Ecology Progress Series 177:243-254.
- Weimerskirch, H. 1997. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries, p. 168-179. In G. Robertson and R. Gales [EDS.], Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, Australia.

- Weimerskirch, H., T Guionnet, J. Martin, S. A. Shaffer, and D. P Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London Series B* 267:1869-1874.
- Weimerskirch, H., C. P Doncaster, and R. Cuenotchaillet. 1994. Pelagic seabirds and the marine environment: foraging patterns of Wandering Albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London Series B* 255:91-97.
- Weimerskirch, H., T Mougey, and X. Hindermeier. 1997. Foraging and provisioning strategies of Black-browed Albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8:635-643.
- Weimerskirch, H., M. Salamolard, F Sarrazin, and P. Jouventin. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk* 110:325-342.
- Weimerskirch, H., R. P. Wilson, and P. Lys. 1997. Activity pattern of foraging in the Wandering Albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series* 151: 245-254.
- Wood, A. G., B. Naft-Daenzer, P.A. Prince, and J. P. Croxall. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: application of kernel estimation to albatross locations. *Journal of Avian Biology* 31:278-286.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446-453.

## **Chapter 3: Factors influencing the duration of Southern Royal Albatross foraging trips during incubation**

### **3.1 Introduction**

The distance flown from the colony to access prey and the duration of each foraging trip may be mediated by a cluster of factors, including:

- wind direction and strength (discussed in more detail in Chapter 4)
- ability to anticipate the location of prey (see Chpt. 2)
- ability to detect prey
- variations in prey abundance and degree of concentration (see Chpt. 2)
- interactions with other foraging birds – (eg competitive exclusion)
- differences in an individual bird's ability to navigate out from and back to the island and to fly a set course in a range of wind conditions
- the amount of food a bird can digest and metabolise or store in a given time period may also be a factor where prey abundance is not limiting
- the need to recover from the different demands of breeding, including egg production in females and nest site preparation in males
- differences in wing loading between lighter and heavier individuals.

During incubation, in the course of each trip to sea the foraging bird needs to cover the energy costs for the current trip, as well as lay down reserves for the next nesting shift to cover its own basic metabolic requirements and any additional energetic costs of incubation while fasting. However, the length of absence from the nest for foraging impacts directly on the incubating partner who is unable to feed or rehydrate during

this time, and needs to operate at a metabolic rate whereby it can maintain the egg at the appropriate temperature at relatively cool ambient temperatures. Estimates of the energetic cost of incubation in seabirds range from 1.2 to 1.6 times basal metabolic rate (Tinbergen and Williams 2002); and relatively low ambient temperatures on Campbell Island (January 1999 mean daily temperature: 9.3°C; NZMS) may place additional energy demands on incubating birds. Breeding success is dependent on the foraging bird returning before the incubating mate abandons the egg. Weimerskirch et al. (1995) and others suggest that in petrels desertion will occur if the incubating bird's mass decreases to a threshold that endangers its chances of survival (sacrificing the current offspring in favour of potential future offspring). However, of all the petrels the great albatrosses have the largest mass, which may provide them with a buffer relative to smaller petrels, some of which engage in foraging trips of comparable or greater duration and distance. For example a maximum foraging range of 3495km from the colony and a trip of 17.5 days duration were recorded for individual White-chinned Petrels *Procellaria aequinoctialis* from Crozet Island during incubation, with a mean maximum range of 2165km and mean duration of 14 days for 7 birds (mean mass 1.37 kg); mean maximum range of 1720km and mean trip duration of 14 days for 5 Light Mantled Sooty Albatrosses *Phoebetria palpebrata* (mean mass 5kg) (Catard and Weimerskirch 1999); and mean maximum range of 1456km and mean foraging trip duration of 10.2 days for 10 Wandering Albatrosses *Diomedea exulans* from Crozet Island (mean mass 9.6kg) (Weimerskirch et al. 1997). These comparisons show that there is not a positive correlation between body mass and foraging range or duration between the species.

The duration of foraging trips during incubation has been found to shorten as hatching approaches in a number of albatross and other seabird species (W.A.(*exulans*): Weimerskirch et al. 1993; Tickell 2000); reasons for this have been discussed in detail in Deeming (2002).

Differences between the sexes in foraging trip duration and ranges have been investigated in considerable detail for WA breeding on Crozet Island (Weimerskirch 1995) and for those breeding on Bird Island, South Georgia (Berrow and Croxall 2001). Female WA from Crozet Is. tend to forage in subtropical zones to the north of the colony, where wind speed is generally lower than in males' foraging zones towards the Antarctic. Foraging duration was significantly greater in female WA from Bird Island, South Georgia than in males during chick rearing in 1997 (Berrow and Croxall 2001). From preliminary studies, male and female Bullers Albatrosses also appear to have different foraging strategies (Sagar and Weimerskirch 1996). Sexual size and mass dimorphism is pronounced in WA and SRA (Tickell 2000) and this may influence the foraging strategies of each sex (Salamolard and Weimerskirch 1993, Shaffer et al. 2001).

The effect of size differences between smaller females and larger males are magnified by the relationship between mass (cubed function) to wing area (squared function) as a contribution to wing loading is such that large proportional increases in wing area would be needed to compensate for relatively small proportional increases in mass to maintain comparable wing loading. In fact, wing area differences between males and females (6.8% greater area in male WA) are not nearly enough to compensate for

their difference in body mass (20% higher in males), hence wing loading is 12% greater in males than females (Shaffer et al. 2001). Greater mass and higher wing loading may be an aid to foraging efficiently in strong wind conditions because of greater penetration and momentum, and conversely a disadvantage in light winds because of reduced lift. Differences between male and female birds' use of the wind according to their weight might be expected in SRA, as mean male mass (10.3kg) is higher than females (7.68kg) (Tickell 2000); a greater difference than their wing area could compensate for (SRA wing lengths 698mm and 666mm respectively (Tickell 2000); wing areas not known).

The demands on breeding birds are substantially greater than for non breeders, which in contrast are able to allocate most of their time to searching for prey. Non breeders can stay with or follow concentrations of prey, as they have no need to travel the hundreds or thousands of kilometres between breeding sites and foraging areas; and they don't have to fast for incubation shifts of up to 16 days at a time. WA do not begin breeding until around age 8 and first year attempts frequently end in failure (Weimerskirch 1992). Although WA reach their full adult skeletal dimensions before this age, Weimerskirch (ibid) proposes that they must reach a mass threshold of 7.5kg before successful breeding can be achieved. Adequate mass may be a prerequisite for successful foraging within the constraints of breeding; or it could simply be that birds that are able to forage efficiently enough to breed successfully have superior mass as a result of that ability. Greater mass should also be an advantage by increasing a bird's ability to sustain long nesting shifts.

### 3.2 Aim

**To investigate factors influencing foraging trip duration in Southern Royal Albatrosses during incubation.**

This chapter investigates parameters that may have influenced the foraging trip durations of the ten SRA studied in January – early February 1999.

### 3.3 Questions

- 1 Does foraging trip duration and range during incubation differ between the sexes in SRA as found in some other species (particularly those exhibiting significant size dimorphism); and if so, do these differences reflect other differences in foraging strategies between the sexes? (as for Crozet Island WA; Weimerskirch 1997.)
- 2 Is there a difference in foraging trip duration between birds equipped with instruments and birds without instruments? Longer durations for equipped birds have been reported in smaller petrels such as Sooty Shearwaters (*Puffinus griseus*) (Sohle et al. 2000). However, Phillips et al. (2003) suggest that this is most likely to occur where the instrument loads exceed 3% of the bird's mass, which is not the case in this study.
- 3 Will higher wind speed throughout the foraging trip reduce foraging trip duration? Flight speed was found to be lower at wind speeds below 15 knots (approx. 30 kph) in WA (Salamolard and Weimerskirch 1993), hence would be expected to increase the time required travelling to and from the colony and for locating prey.

- 4 Is there a relationship between bird mass and foraging trip duration? (Greater body mass could be an advantage in strong winds due to greater momentum or penetration, but a disadvantage in light winds due to a higher wing loading than for lighter birds with a similar wing area; Shaffer et al. 2001.)
- 5 Does foraging trip duration decrease as hatching approaches, as in other albatross species and other pelagic-foraging seabirds? (Chiaradia and Kerry 1999); (Weimerskirch et al. 1993)
- 6 Does the number of birds that return to the colony from their foraging shift increase when mean daily wind speed recorded on Campbell Island is higher, as would be expected if birds select windier conditions to commute back to the colony?

### **3.4 Methods**

The duration of foraging trips was recorded for birds at 52 nests by direct observation of nest attendance. Nest attendance was monitored in the study area between 10 January and 2 February 1999, corresponding to the second half of incubation (incubation begins early December and ends mid February on the majority of nests; Waugh et al. 1997). Each nest was identified with a numbered pole (previously put in place by Peter Moore, D.o.C.) that could be read from a distance of 5 m or more using binoculars. At the start of the monitoring period the bird in attendance at each nest was marked on the neck with a band of colour from a spray can of non-toxic stock marking paint to enable us to distinguish between each individual of the pair. Each nest was visited daily at approximately the same time as the previous day and the bird in attendance (marked / unmarked) was recorded. As foraging trips are expected to be

at least four days in duration there would be little risk of missing a double change-over within the time period of one day.

Sex was recorded according to prior determination made on the basis of bill length and plumage by previous researchers and documented with band numbers (NZ Banding Office records, D.o.C.); and confirmed in each case by our assessment based on plumage and relative size between both birds of each pair. As sexual dimorphism in both these characteristics is greater in SRAs than in most of the other albatross species, this method is expected to give a reliable indication of sex. Differences between males and females in foraging trip duration were investigated.

Satellite transmitters were used to determine the distances travelled and other aspects of foraging strategies during foraging trips undertaken by ten SRAs during the second half of incubation (between Jan 10 and Feb 7) in 1999. The transmitters were resin coated Telonics and Microwave Platform Terminal Transmitters (PTTs) with short whip aerials and weighed 20g. The units were attached using Tesa surgical tape to dorsal feathers, as described in Chapter 2. Each of the birds was fitted with its transmitter shortly after being relieved from incubation duties by the partner returning from a foraging trip, allowing the recording of a full foraging trip for the departing bird, and retrieval of the transmitter on the bird's subsequent return to the nest.

Transmitters were set to transmit every 90 seconds. Battery life exceeded the expected maximum period of use (up to two deployments per transmitter for foraging trips of a of >14 days each). Locations were received through the ARGOS system (Argos CSL, Toulouse, France). Data were classified into 6 classes of decreasing accuracy (as in Chapter 2). The threshold for rejection of low-quality satellite locations was a flight

speed in excess of 90 km per hour between successive uplinks after subtracting the time the bird had spent on the water during that time interval (calculated from data supplied by the wet-dry activity recorder described below).

A miniature wet-dry activity data logger (mass 11 g, Francis Scientific Instruments, Caxton, UK) was attached to each of the ten SRAs with transmitters to record their landing activity and time spent on the water and in the air, sampled at 15 second intervals. Data loggers were cylindrical in shape and attached to a Davik band on the tarsus using Tesa fabric adhesive tape. Full immersion of both ends of the logger in salt water was required to record a 'wet' reading. Five of the birds equipped with PTTs and activity recorders were also fitted with Polar heart rate monitors and recorders. Foraging trip duration was compared with those without instruments.

The mass of each of the ten equipped birds was recorded before departure, and influence of mass on foraging trip duration was investigated. For analyses where birds were grouped by mass, the 'heavy' group birds were those >9kg, (4 birds, of which all of the 3 males and one heavy female; range 9.75kg to 10.66kg); and the 'light' group (6 females, range 7.29kg to 8.61 kg). They were grouped by mass rather than by sex because differences in the parameters investigated are likely to be due to mass differences, and in this sample one heavy female was closer in mass to the males than to the other females.

As well as providing the bird's location at each uplink, the satellite records enabled calculations of each bird's furthest distance from the colony, its cumulative distance flown, and the amount of time the bird was on the water or in the air. Combined

satellite positions and wet/dry activity data were integrated with environmental data local to the bird's position. Data integrated included wind strength, which was examined for possible influence on foraging trip duration. The data integration was performed using the purpose-built "Diomedea" software package (D. Filippi, unpublished programme; further details in Weimerskirch et al. 2000).

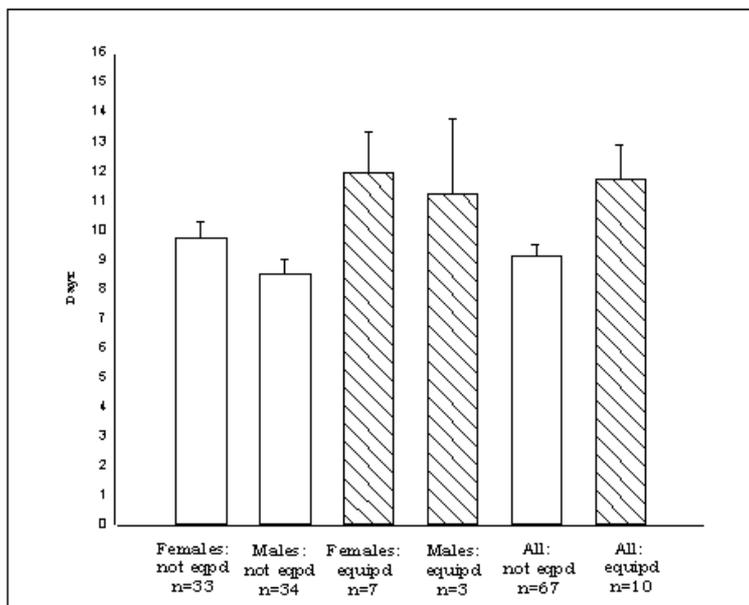
The relationship between stage of incubation and foraging trip duration was investigated for the total of 72 trips completed by birds nesting in the study area. Incubation stage was based on trip start date; as hatching in this species is relatively synchronous (median date 18 February, range 6 February – 6 March with 58 % eggs (n=85) hatching during the week of 14 to 20 February in 1969 - Waugh et al. 1997), trip start date was used as a substitute for proximity to hatching as actual hatching dates for each nest could not be obtained. To reduce the inherent bias towards over-recording short trips (because of termination of monitoring before hatching), trips incomplete at the end of the monitoring period were not included if the days to date did not exceed the mean length of all complete trips, and the three that exceeded the mean trip duration were given a return date of the day following the end of monitoring as a minimum estimate.

### **3.5 Results**

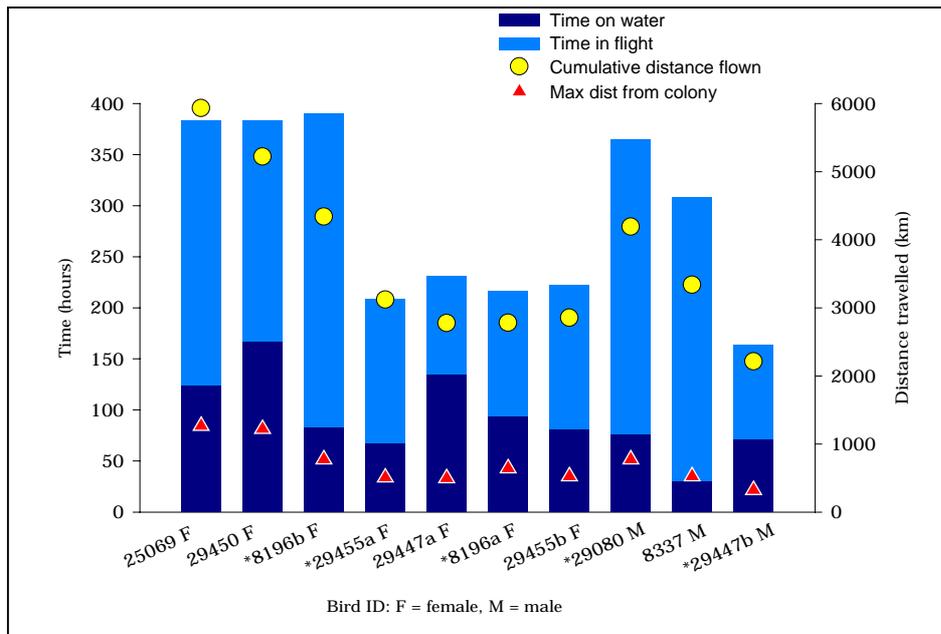
1. Durations of the 77 trips from 52 nests (including 3 incomplete trips that exceeded mean trip duration) ranged from 4 to 16 days. The mean duration of all female trips (10.11 days) was longer than for all males (8.76 days)(Fig.3.1), but the difference, although close, was not significant (Mann-Whitney Rank Sum Test:  $t = 1257.0$ ;  $n$  (males) = 37,  $n$  (females) = 40;  $P = 0.059$ ). The distance travelled by birds with

satellite transmitters ranged from 2898 km to 6589 km; a mean distance of 4262 km  $\pm$ 1318 (SD). Mean daily distance was 360 km. Trip duration ranged from 7 days to 16 days (mean duration 12 days). Although female birds travelled slightly further on average (4386km) and for longer (12.29 days) than males (3973km, 11.33 days), these differences were not significant. (Distance:  $t = 0.43$ ; 8 df;  $P = 0.68$ . Duration:  $t = 0.2$ ; 8df;  $P = 0.79$ ) (Fig. 3.2; full table of results in Appendix 1).

2. Mean trip duration was significantly longer for birds equipped with instruments (11.72 days) than for non-equipped birds (9.11 days) (Figure 3.1) Mann-Whitney Rank Sum Test:  $t = 532.0$ ;  $n$  (equipped) = 10,  $n$  (not equipped) = 67;  $P = 0.032$ . However, this result may have been influenced by the stage of incubation as the majority of the equipped birds' departure dates were early in the study period; seven in the period 11 to 13 January and the remaining three on 22 and 23 January.



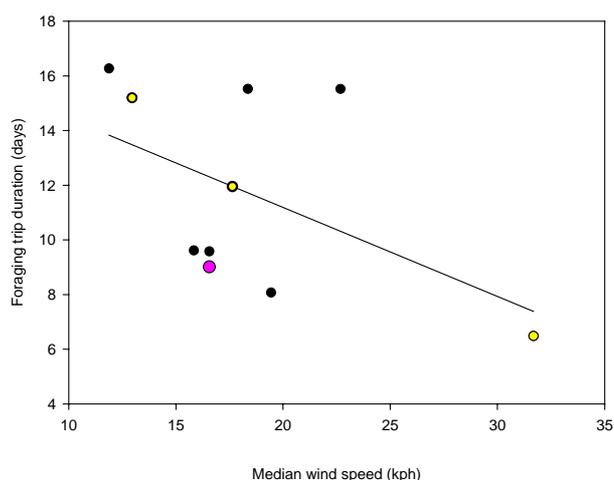
**Fig. 3.1** Foraging trip durations (means + s.e.) between 10 January and 2 February 1999.



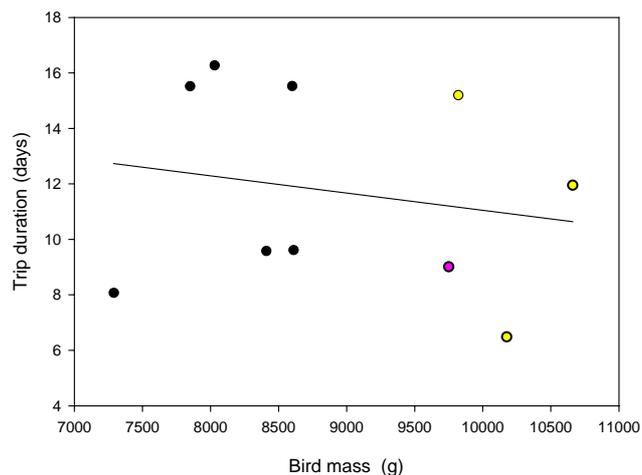
**Fig. 3.2** Foraging trip durations (left axis, full bar height), time spent on the water (dark section of bar) and in flight (lighter section) for each of the ten birds equipped with satellite transmitters and wet-dry data loggers. Maximum distance from the colony (triangle) and cumulative distance flown (circle) are plotted against the right axis. The first seven bars are females and the last three are males.

3. Although there appeared to be a negative relationship between **median wind speed throughout the trip** and foraging trip duration (Fig. 3.3), the relationship was not significant using log transformed data ( $r^2 = 0.32$ ,  $t = 1.95$ ;  $P = 0.087$ ).

4. There was no significant difference in foraging trip duration between **birds by body mass** (Fig. 3.4) using log transformed data ( $r^2 = 0.03$ ;  $t = 0.53$ ,  $P = 0.61$ ).

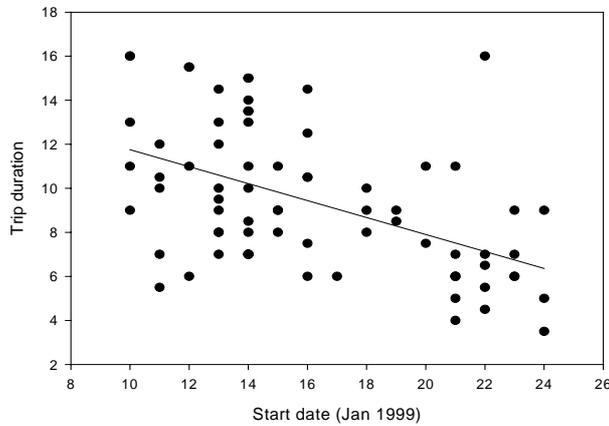


**Fig.3.3** Trip duration in relation to median wind speed throughout full foraging trip ( $n=10$ );  $r^2 = 0.25$ . Male birds are shown as open circles, the heavy female a grey circle, and the remaining females as black circles.



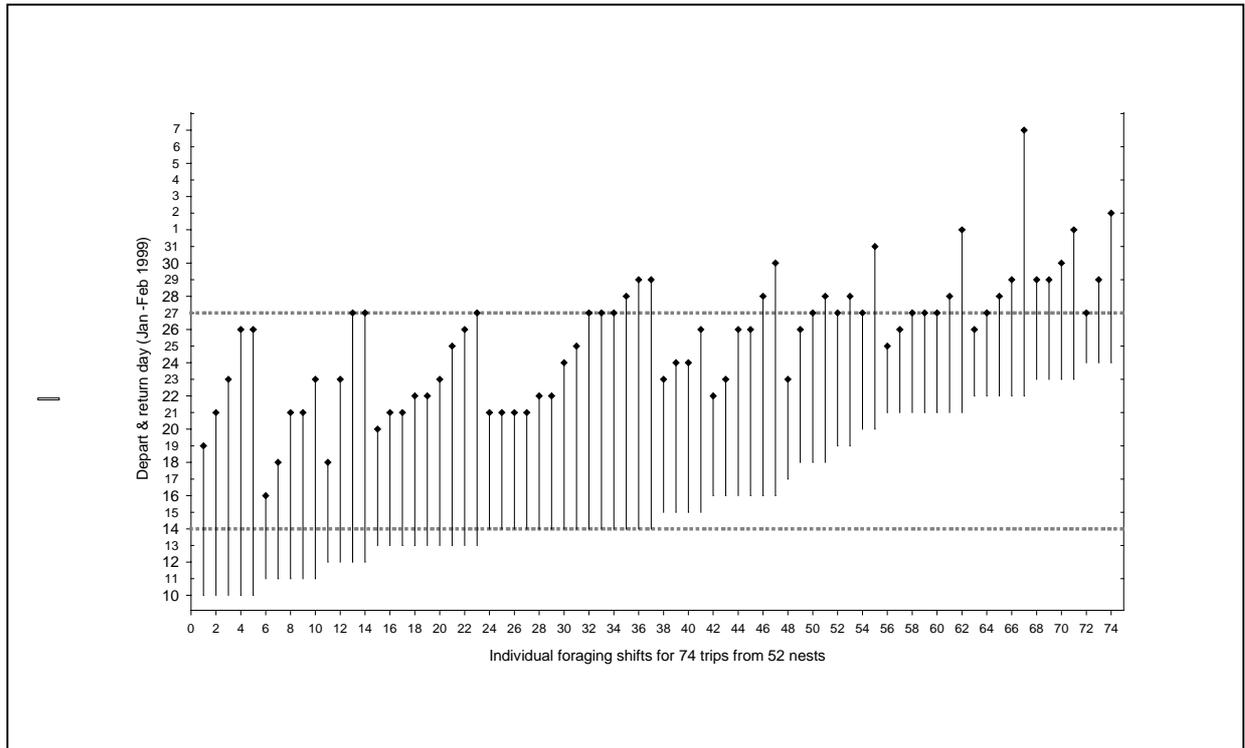
**Fig.3.4** Trip duration in relation to bird mass ( $n=10$ );  $r^2 = 0.04$ . Male birds are shown as open circles, the heavy female a grey circle, and the remaining females as black circles.

5. As **stage of incubation** progressed towards hatching, there was a significant trend for foraging trip duration to shorten ( $r^2 = 0.25$ ;  $t = 4.88$ ;  $P < 0.001$ ;  $n = 77$ ; Fig 3.5).



**Fig.3.5** Trip duration in relation to start date (77 trips).

6. The **pattern of shift changes** on 52 nests throughout the period of observation is shown in Figure 3.6. As seen in Fig. 3.5, the trend towards decreasing duration of shifts as incubation progresses is evident. The number of shift changes tended to peak on certain days. The mean number of shift changes per day was 5.04 (range 1 to 14). The median daily mean wind speed for the 23 days of records was 26 kph (range 9.6 to 46.5). On the two days with the highest number of change-overs (14 change-overs on 14 January and on 27 January) the daily mean wind speed recorded on Campbell Island was 29.9 kph and 43.2 kph respectively. On the only two days with daily mean wind speed  $< 20$  kph, the mean number of shift changes was 2.5. On the five days with wind speeds  $> 30$  kph, the mean number of shift changes was 5.2. There is insufficient data for statistical analysis.



**Fig. 3.6** Vertical lines indicate individual bird's foraging shift duration. The base of each line lies on shift start date; the arrow-head lies on finish date. The two peak shift-change days of 14 changes each are indicated by a dashed line (14<sup>th</sup> January) and a dotted line (27<sup>th</sup> January).

### 3.6 Discussion

#### Factors related to foraging trip duration:

Longer foraging trips for females than males have been noted in other great albatross species at a range of stages during breeding, such as WA (Weimerskirch 1997) but in the present study, although female trips were on average longer than male trips, the difference was not significant. However there may be more marked differences in the period preceding this study, in the early stage of incubation, if females need longer foraging periods to recover from the demands of egg production.

Foraging trip durations were found to be greater for birds with instruments than for birds without instruments. This has been found in smaller petrels such as Sooty Shearwaters (Sohle et al. 2000), but according to Phillips et al. (2003) a difference is expected in cases where the instrument loads exceed 3% of the bird's mass. In this study, instrument loads (<45g) represent < 0.6% of the mass of a 7,500g bird and would be unlikely to influence foraging trip durations. An alternative explanation is that the equipped birds' trip durations were influenced by the distribution of departure dates in relation to hatching compared with those for the non-equipped birds. Another likely source of bias is the exceptionally long foraging trip by one bird that was becalmed off the Otago Peninsula (shown as foraging shift no. 67 in Fig. 3.6). While other, non-equipped birds may have been similarly affected, their return dates were unknown if they returned after the end of the study period, whereas the transmitter allowed the equipped bird's actual return date to be known.

Proximity to hatching: The incidence of shorter foraging trips as incubation approaches conclusion has been observed for other species, including the WA. An explanation that has been proposed is that the bird in attendance at hatching needs to be able to feed the newly hatched chick, which may not be possible in most species after prolonged fasting (Chiaradia and Kerry 1999). As the new chick requires frequent feeding (daily in WA; Weimerskirch et al. 1993) as well as brooding in the days following hatching, the close attendance of both parents would be necessary.

The suggestion of a relationship between median wind strength throughout the trip and foraging trip duration (fig. 3.3) may indicate that within the range of median wind strengths experienced by these birds (11.9 to 31.7 kph), greater wind speed enabled

birds to either forage or commute more efficiently, or both. A larger sample size may be needed to obtain a more conclusive result. Inspection of the detail of individual birds' foraging trips provides an example of a bird (8196b, Caroline) that was apparently 'becalmed' in a large high pressure system for five days off the Otago Peninsula (mean wind speed 3.5 kph), delaying her return commute by an estimated five days. On the other hand, strong winds during the return commute to the colony appear to have added to commuting time in the case of 29455a (Squidgy), who was apparently blown off course during winds of 45 kph around the latitude of Campbell Island, delaying her arrival by an estimated 12 hours. This was a light bird, which may mean she was less able to maintain course in strong winds.

Other studies have found substantial differences in foraging trip duration between years, apparently linked to changes in prey availability. Xavier et al. (2002) found GHA from South Georgia made foraging trips of 13.3 days on average in a year of sea surface temperature anomalies compared with 1-3 days found in previous studies at the same stage, travelling far greater distances than recorded in previous years. They also switched from their usual squid prey to krill as their main food. Monitoring the duration and destination of foraging trips by the same species over a number of years would be a useful way to assess the quality of resources in a changeable environment.

## References

- Berrow, S. D., and J. P. Croxall. 2001. Provisioning rate and attendance patterns of Wandering Albatrosses at Bird Island, South Georgia. *Condor* **103**:230-239.
- Catard, A., and H. Weimerskirch. 1999. Satellite tracking of White-chinned Petrel and comparison with other Procellariiformes. Pages 3008 - 3023 in N. Adams and R. Slotow, editors. 22nd Ornithological Congress. University of Natal, Durban, Durban, South Africa.
- Chiaradia, A. F., and K. R. Kerry. 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology* **27**:13 - 20.
- Deeming, D. C. 2002. *Avian Incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford.
- Phillips, R. A., J. C. Xavier, and J. P. Croxall. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* **120**:1084-1090.
- Sagar, P. M., and H. Weimerskirch. 1996. Satellite tracking of Southern Buller's Albatrosses from the Snares, New Zealand. *The Condor* **98**:649-652.
- Salamolard, M., and H. Weimerskirch. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Functional Ecology* **7**:643-652.
- Shaffer, S. A., H. Weimerskirch, and D. P. Costa. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* **15**:203-210.

- Sohle, I. S., H. Moller, D. Fletcher, and C. J. R. Robertson. 2000. Telemetry reduces colony attendance by sooty shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology* **27**:357-365.
- Tickell, W. L. N. 2000. Albatrosses. Yale University Press, New Haven and London.
- Tinbergen, J. M., and J. B. Williams. 2002. Energetics of incubation. Pages 421 *in* D. C. Deeming, editor. *Avian Incubation: Behaviour, Environment and Evolution*. Oxford University Press, Oxford.
- Waugh, S. M., P. M. Sagar, and D. Paull. 1997. Laying Dates, Breeding Success and Annual Breeding of Southern Royal Albatrosses *Diomedea epomophora epomophora* at Campbell Island during 1964-69. *Emu* **97**:194-199.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. *Oikos* **64**:464-473.
- Weimerskirch, H. 1995. Regulation of foraging trips and incubation routine in male and female wandering albatrosses. *Oecologia* **102**:37-43.
- Weimerskirch, H., O. Chastel, and L. Ackermann. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav Ecol Sociobiol.* **36**:11-16.
- Weimerskirch, H., T. Guionnet, J. Martin, S. Shaffer, and D. P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* **267**:1869-1874.

- Weimerskirch, H., M. Salamolard, F. Sarrazin, and P. Jouventin. 1993. Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk* **110**:325-342.
- Weimerskirch, H., R. P. Wilson, and P. Lys. 1997. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series* **151**:245-254.
- Xavier, J. C., J. P. Croxall, P. N. Trathan, and A. G. Wood. 2002. Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Marine Biology* **143**:221-232.

## **Chapter 4: Patterns of Southern Royal Albatross foraging trips during incubation and investigation of the role of wind**

### **4.1 Introduction**

Typical patterns of foraging trips made by breeding albatrosses of different species and at different stages of the breeding cycle were identified by Weimerskirch (1997).

They can be summarised as two broad types of foraging strategy:

- 1 Long looped “searching” oceanic flights, feeding along the way. In Wandering Albatrosses from Crozet Island during incubation these flights generally took a looping course, making optimal use of local wind direction to cover maximum distance with minimal energy expenditure. A contrasting strategy used by Sooty Albatrosses during brooding was long searching oceanic flights that were linear.
- 2 Rapid, direct “commuting” flight with few landings (often to a definable bathymetric or oceanographic feature) followed by a period of localised searching or “foraging” flight, characterised by increased turning and increased landing. The flight back to the colony is typically another period of direct “commuting” flight. This is typified by Light-mantled Sooty Albatrosses during incubation.  
(Weimerskirch 1997)

Indications from the pilot study of three SRA tracked for one foraging trip each, conducted in 1997 by Weimerskirch and Waugh, were that foraging flights by SRA during incubation may differ from those of the closely related WA (*D. exulans*) (results included in Chapter 2). The three birds tracked in 1997 each undertook a relatively short, rapid commuting flight to a confined zone where they searched locally for several days before returning rapidly and relatively directly to the colony.

The nature of albatross gliding flight as an adaptation to exploit a challenging environment made it a popular subject of study before much else was known about albatross ecology. Key authors on the subject include: Jack (1953), Pennycuick (1982); and more recently Spear and Ainley (1997a and 1997b), Weimerskirch et al. (2000); Spruzen and Woehler (2002); Nicholls et al. (1994); Murray et al. (2002; 2003a); Murray et al. (2003b); Reinke et al. (1998). A question that underlies much of this interest is how, during breeding, albatrosses and some of the other procelariiformes overcome the separation between nesting sites and foraging grounds, often covering extensive distances in search of patchily distributed prey within the time and energy constraints imposed by breeding. Key findings have been that most albatross species progress by gliding flight, with very little powered flight. This is made possible by the application of dynamic soaring and wave soaring techniques, which are only possible in a windy oceanic environment (Pennycuick, 1982; Alerstam et al., 1993).

The effect of wind speed on the flight of albatrosses has also been investigated. Low wind speed was found to influence flight performance by reducing “cross-country” flight speed in several albatross species (Alerstam et al. 1993) by direct

measurements. Salamolard and Weimerskirch (1993) found that in Wandering Albatrosses, whilst mean flight speeds between satellite fixes varied little with wind speeds above 15 knots (approx. 30 kph), they were lower at 0 – 5 knots than at 5 – 10 or 10 – 15 knots. Mean flight speeds were lower in males than females at most wind speeds. A bird flying slowly covers less water per unit of time, so while searching for prey it is likely to encounter fewer prey items where prey is sparse or randomly distributed than if flying at higher speeds (*ibid*). Lack of wind has been suggested to increase the energy expenditure of petrels and albatrosses (Furness & Bryant 1996). The previous chapter looked for a relationship between foraging trip duration and wind speed, and this chapter looks into the influence of wind speed on the timing of identifiable phases of the foraging trip and on landing activity.

The Weimerskirch (2000) study found that the energetic cost of flying in favourable wind directions was low, in some cases close to basal metabolic rate. The most favourable winds were found here, as in other studies, to be in the stern quarter (between tail and side winds). The birds used strategies that increased the likelihood of encountering favourable wind directions to the extent that unfavourable head winds were encountered on less than 4% of the tracks between fixes. The birds could achieve this, despite being constrained to returning to their starting point at the colony, by predicting prevailing wind directions in different zones of the southern Indian Ocean. Energetic cost based on heart rate data was found to be greatest during take-off and landing, and for up to an hour either side of take-off. (See Appendix II for an example of SRA heart-rates during flight, take-off and landing.) For this reason I have examined the relationship between wind speed and take-off and landing activity in SRAs of different weight categories for any evidence of a strategy that may

reduce these costs. Differences between male and female birds in terms of mass and wing loading were outlined in Chapter 3. As the functional difference between the sexes in relation to flight at a range of wind speeds may be due to mass rather than other sex-based attributes, the birds were separated on the basis of mass rather than sex for this analysis.

## 4.2 Questions

I addressed the following questions:

1. Do SRA employ a ‘commute, forage, commute’ pattern during incubation as suggested in the pilot study (above)?
2. Are wind speed and direction important in the timing of commute phases of the trip (or do SRA undertake long-distance travel regardless of wind speed or direction)?
3. Is there a significant difference in wind speed and in displacement speed between commute and forage phases of trips?
4. Do SRA cover less distance flying at less favourable wind angles, i.e.  $0^\circ$  to  $40^\circ$  (upwind or head winds);  $80^\circ$  to  $100^\circ$  (wind abeam or direct side wind) and  $160^\circ$  to  $180^\circ$  (downwind or direct tail wind) than at other, more favourable bands of relative wind angle (close reach and broad reach) as seen for WA by Jouventin and Weimerskirch (1990) and Weimerskirch et al. (2000)?
5. Do SRA vary their wind angle selection in winds of different strength, as was found for a Gibson’s Albatross (*Diomedea gibsoni*) by Reinke et al. (1998)? It could be that a particular course relative to the wind (eg tail wind) could be flown in moderate winds but not in strong winds.

6. Is SRA mass a factor determining aspects of its foraging strategy relating to use of the wind at different wind speeds?

### **4.3 Methods**

Satellite transmitters and wet-dry recorders were used to determine the type of foraging trip and landing activity undertaken by SRAs during incubation. For details refer to Chapter 2.

Data processing:

The purpose-built software package “Diomedea” (D. Filippi, unpublished programme; further details in Weimerskirch et al. 2000) was used to integrate the satellite locations and activity data. Distances and speeds travelled between locations were calculated and intermediate positions interpolated for every minute, to match the wet-dry recorder data. Birds’ satellite fixes and interpolated intermediate positions throughout their foraging trip were plotted (using Matlab 5) with point size scaled according to time spent per unit area. Time spent in the air and time spent on the water were plotted separately to enable identification of foraging phases.

To further examine the foraging strategies by integrating the birds’ temporal and spatial movements, calculation was made of range extension per 24 hour period as a running minute-by minute calculation. The resulting distances were plotted to give a distribution of range extension distances on a time line throughout the foraging trip for each bird, making it possible to differentiate periods of directional travel (‘commuting’) from periods of localised searching (‘foraging’) and to see the overall pattern of the bird’s movement through time. There was a clear bimodal distribution,

with the upper limit for shorter distances found to be 180 km between 24-hourly positions (Fig 4.1). For subsequent analyses of the two phases of trips, the 180 km threshold was used to divide commuting periods (range extension >180 km per 24 hours) from foraging periods (range extension <180 km per 24 hours).

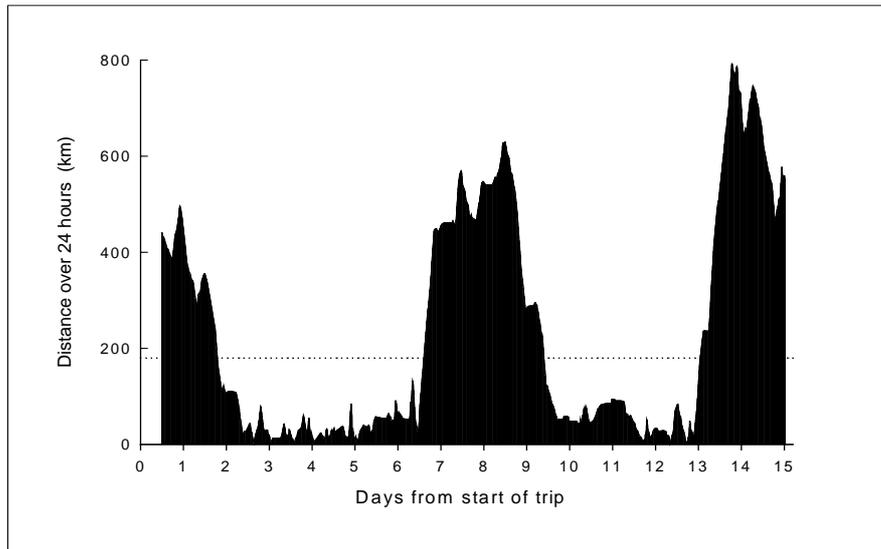


Fig. 4.1 Bird 25069 ('Victoria'): The direct distance between two positions 24 hours apart ('daily range extension') throughout her 16 day trip were calculated, shown here as a running total. Each of the birds showed a similar bimodal pattern of short or long 24 hour range extension with the upper limit for shorter ranges found to be 180 km / 24 hours. This threshold was used to define the different phases of the foraging trip. The dotted line at 180 km shows the threshold used to separate 'commute' data (above the line) from 'forage' data in comparisons.

To examine the corresponding wind strength and direction encountered throughout the trips in relation to the bird's location and activity, the satellite tracking and activity data were integrated with meteorological records based on internationally collated sources (interpolated from multiple data collection methods) and supplied by Metéo-France. These records had a spatial resolution of 1.5° latitude by 1.5° longitude, and the temporal resolution was 12 hours.

To investigate the influence of wind speed on the timing of commuting within the overall trip, wind speed was plotted over the 24-hour distance plots and statistical comparisons of wind speed during ‘commute’ and ‘forage’ phases were performed. Wind direction was compared with the birds’ flight course during commuting.

The birds’ angle of flight relative to local wind direction was calculated for each one-minute data point in each bird’s trip time series. The angle was a function of the bird’s overall (as if straight) course between two successive satellite points and the wind data local to its estimated position. The convention relating to vessels was used; i.e. the bird’s direction is given as the heading towards which it was flying; whereas the wind direction is given in terms of whence the wind originated. Hence a relative wind direction of  $180^\circ$  is a tail wind, and  $0^\circ$  degrees a head wind. Left-right symmetry was assumed, so values from  $180^\circ$  to  $360^\circ$  were combined with the corresponding sector between  $0^\circ$  and  $180^\circ$ .

Analysis of the birds’ use of different angles of flight relative to wind direction was done by dividing each bird’s trip record: a) into commuting and foraging phases by the method described above; and b) within those categories, creating 9 bands of 20 degrees each between  $0^\circ$  and  $180^\circ$ . Mean distance flown, flight speed and wind speed were calculated within each  $20^\circ$  band.

Landing activity at different wind strengths was analysed, with the number of landings and take-offs by light birds (6 females <9kg) compared with those of heavy birds (three males and one female > 9kg) across a range of wind speeds.

## 4.4 Results

### 1. Foraging strategies:

Eight of the ten SRA foraging trips showed a pattern of the type ‘commute, forage, commute’ with one or two principal foraging destinations each, rather than the searching looping oceanic flights of WA (Weimerskirch 1997). Two of the three males exhibited more of a hybrid foraging strategy, staying over the Campbell Plateau but moving as if searching and apparently foraging at a variety of sites and features while on the move.

The ten sets of three figures in Fig. 4.2 a–j show for each of the ten birds: (i) the foraging flight track, (ii) locations of time spent on the water, and (iii) the 24 hour range extension graphed as a time series with local wind speed. A simple three-phase commute – forage – commute pattern to a single main foraging destination (the Snares Islands hotspot) was most clearly defined in four birds’ trips ( a, b, c, and d). Queen Mother (a) carried out the most straight forward foraging trip of all the tracked birds, taking just 13 hours to reach the Snares hotspot on a curved course, then foraging within a concentrated area before returning on a direct route to Campbell Island. However Fergy (d) had an additional commuting ‘side trip’ north to the Catlins coast and back from day 1.5 to 3.5, without landing to forage, initiated during a southerly blow. Liz’s (b) return commute was interrupted by a period of very low wind during day 8.

Anne’s (f) commute phase to the Chatham Rise in just over 24 hours is of note, with a peak rate of 845 km in 24 hours. She also flew greater distances during the foraging phase along the southern edge of the Rise than did most of the other birds during

foraging. Her return commute towards Campbell Island was interrupted by short bouts of foraging. Caroline (e), Charlie (j), and Victoria (g) also switched from foraging to commuting for a period in the middle of their trip, travelling on to a new foraging site. Victoria (g) had the most extensive range of the ten birds – west to seamounts of the northern Macquarie Ridge then north to the Chatham Rise. Caroline (e) prospected at two sites before flying north to the Otago coast (SE South Island) where she was apparently stranded by several days of light wind.

Two of the three male birds (Charlie and Albert) prospected to the south of Campbell Island then looped north, while the third (Louis XVI) flew further west than any of the others except Victoria. They exhibit lower peak commuting rates than most of the females (barely exceeding 400 km per 24 hours), and from their landing patterns, Charlie and Louis XVI foraged at numerous sites along their route rather than at clearly defined destinations. While their flights suggested a hybrid strategy between a clear commute-forage-commute and the continuous searching flight seen in WA (Weimerskirch 1997), the sample is too small to suggest a sex difference in foraging strategy.

## 2. Wind speed:

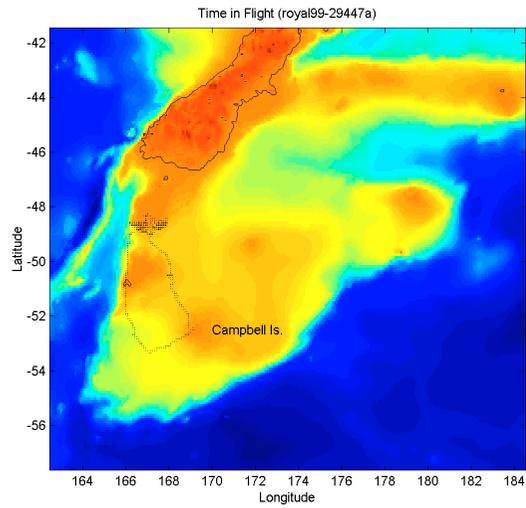
Wind speed appeared to play an important role in the timing of the return commute to Campbell Island. All of the birds appeared to switch to commute mode for the return flight to the colony as wind speed increased to relatively high levels (Fig. 4.2 series iii).

### 3. Wind direction relative to flight track:

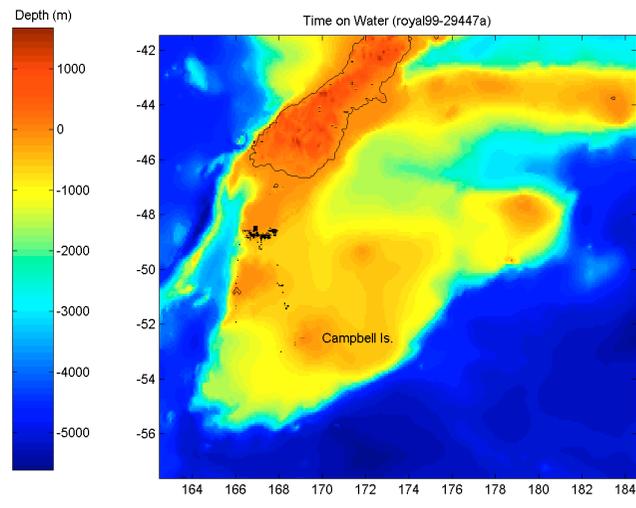
Commute phases were generally conducted with side or stern quarter winds. There were two cases of birds attempting to commute into head winds: Caroline, whose initial commute track was erratic and slow as she attempted to travel upwind in NNW winds; and Squidgy, who encountered strong SW winds while returning to Campbell Island and altered her course, taking her further from the island. The five birds that flew on a southerly sector course from the island did so in northwest conditions, and changed course towards the north once the wind turned.

Fig. 4.2: (following pages)

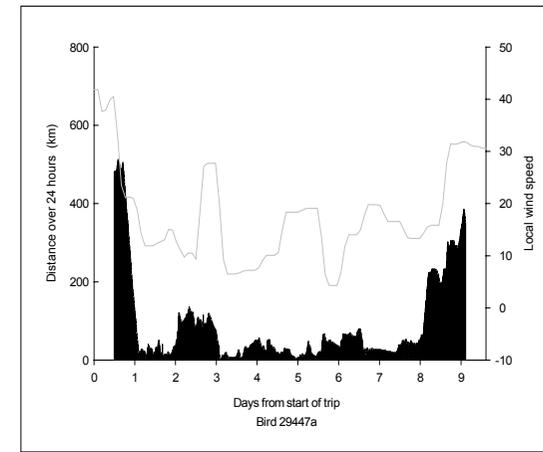
- (i) Track for each bird's foraging trip including satellite fixes and interpolated intermediate positions.
- (ii) Location of landings as an indication of surface activity related to foraging. Scale for time spent:  $0.0833^\circ$  latitude x  $0.0833^\circ$  longitude represents 20 hours of time spent on the water.
- (iii) 24 hour range extension (black): bar width 10 minutes; bar length shows the distance covered in the preceding 12 hours plus the following 12 hours. Wind strength local to the bird's position (grey line). Note that wind speed data are estimates for 12-hour bands, hence there is not an exact temporal overlay.



(i)

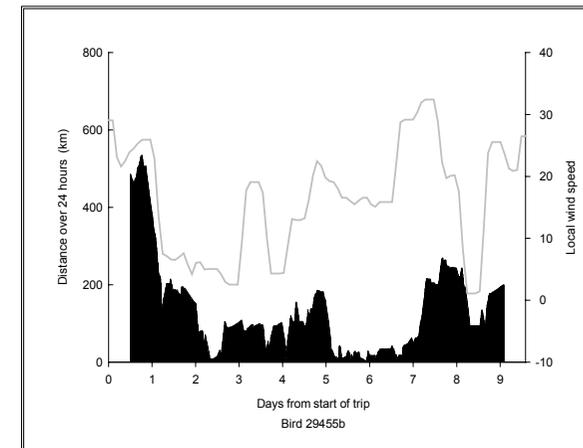
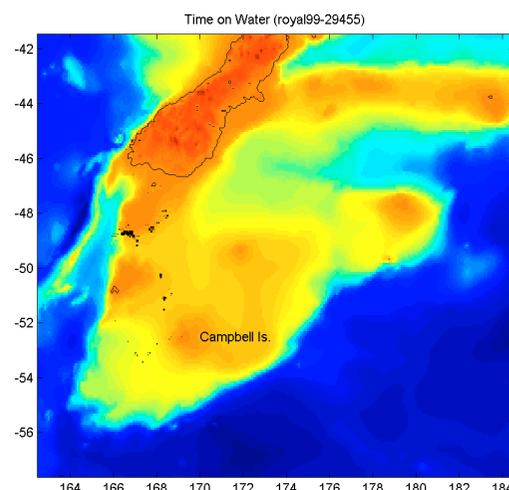
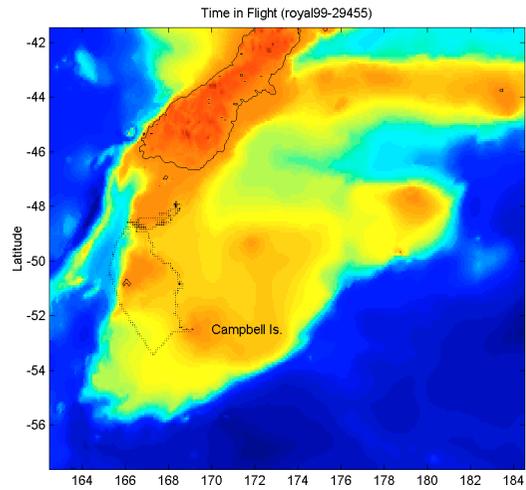


(ii)



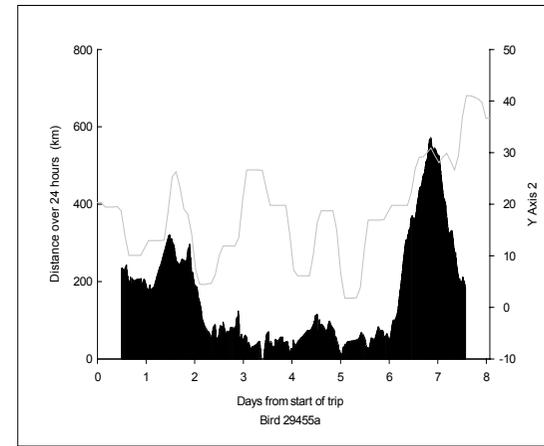
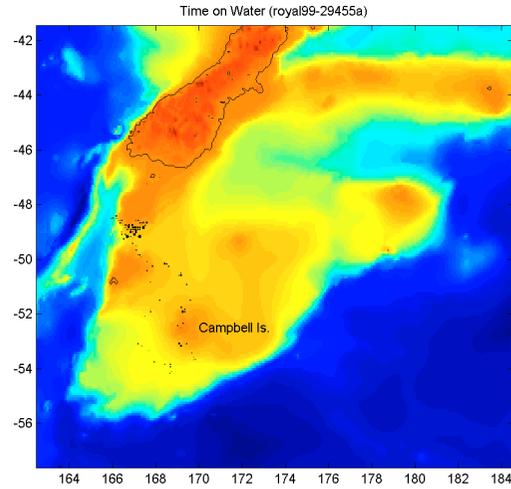
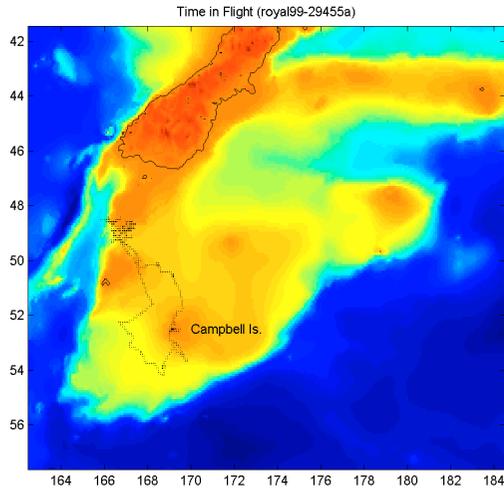
(iii)

a).#29447a - Queen Mother. Wind directions: From Campbell (west track) - NW then W; back to Campbell - W then SW.

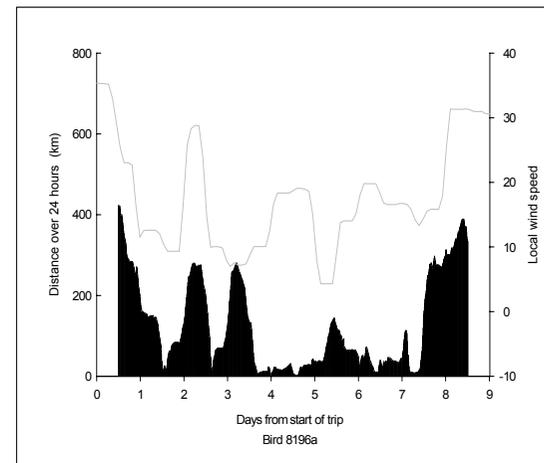
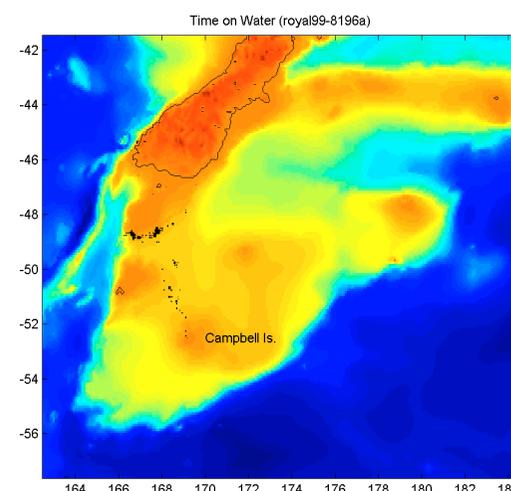
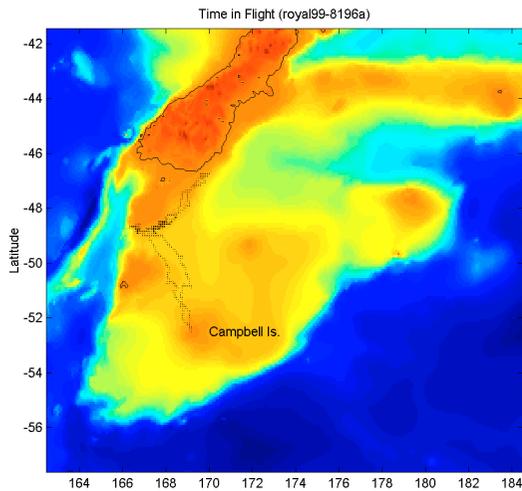


b).#29455b – Liz. Wind directions: From Campbell (west track) - NW then SSW; back to Campbell – NW.

**Fig. 4.2 a & b**

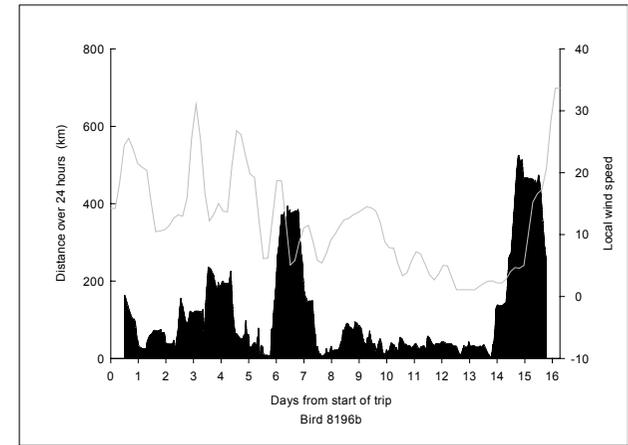
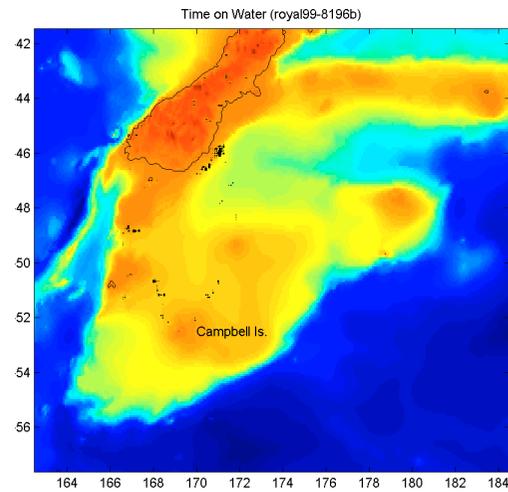
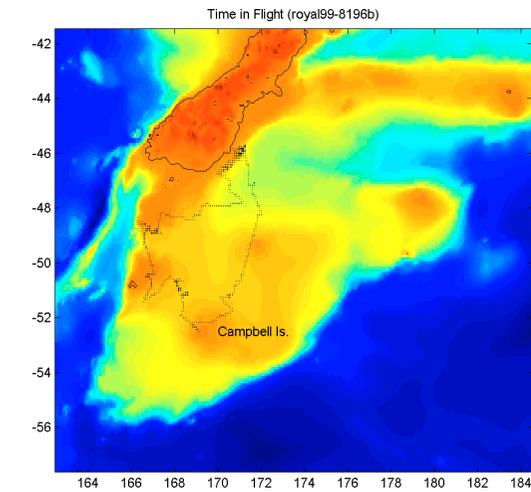


c).#29455a – Squidgy. Wind directions: From Campbell (east track) - NW then WNW; back to Campbell - SSW then SW (erratic flight track in strong winds).

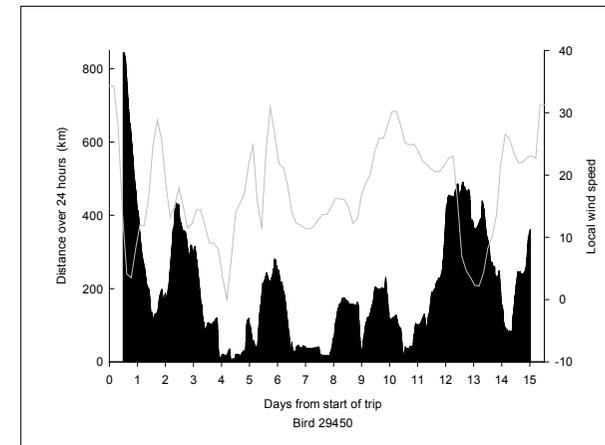
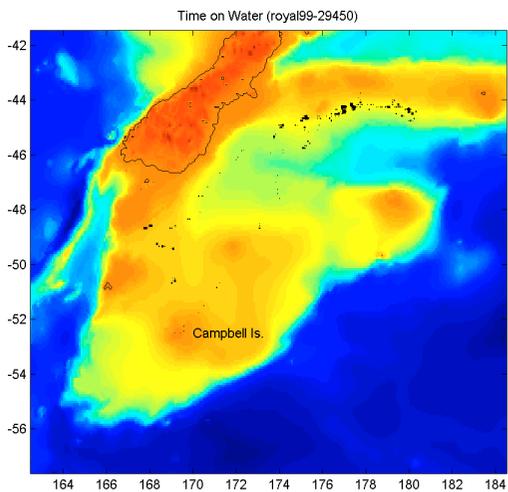
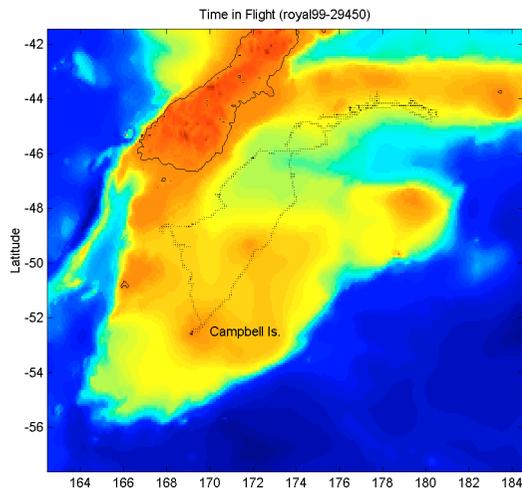


d).#8196a – Fergy. Wind directions: From Campbell (west track crossing to east) - W, NW then N. Side trip towards Southland coast: S (day 2) then N (day 3); back to Campbell – NW, W then WSW.

Fig. 4.2 c & d

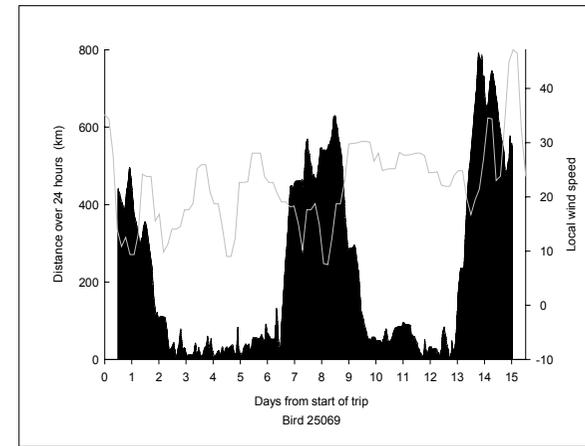
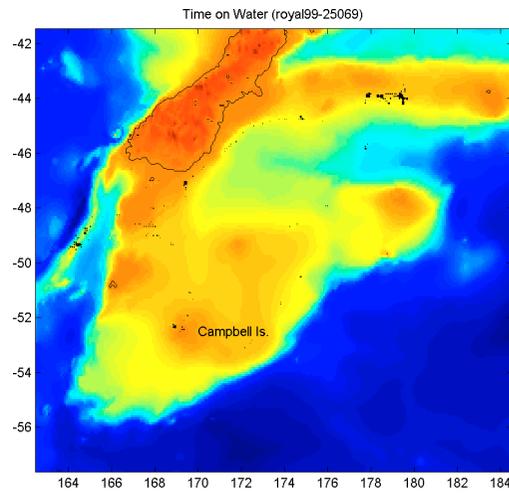
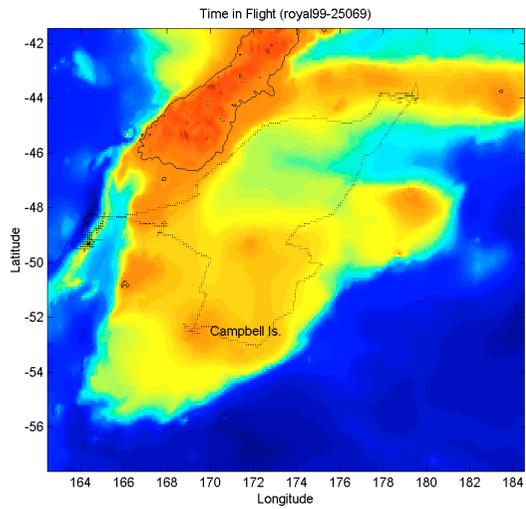


e).#8196b – Caroline. Wind directions: From Campbell (west track) – NNW - slow erratic progress till day 6 - W then NE. Light winds on days 11 – 16 (off Otago coast). Back to Campbell - SW then N.

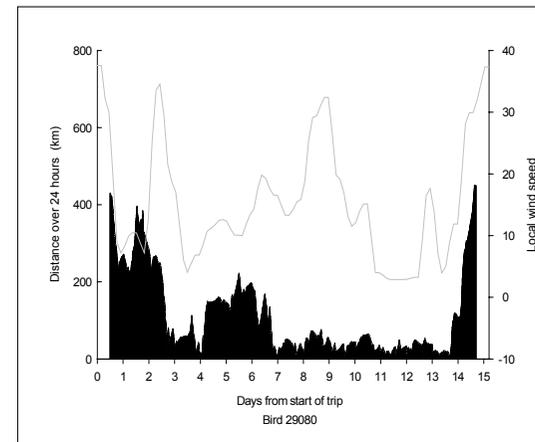
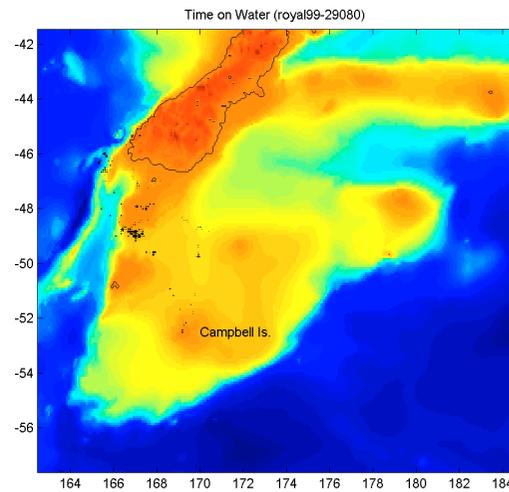
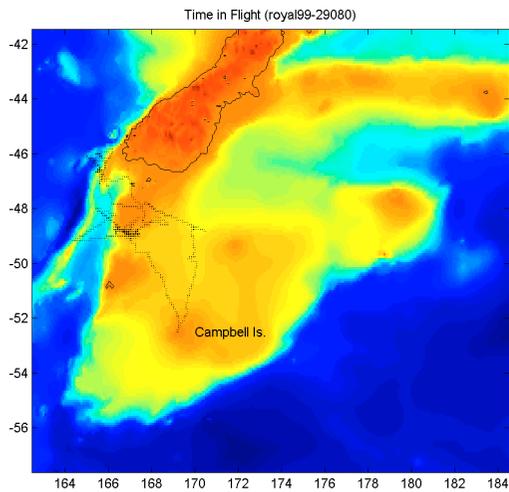


f).#29450 – Anne. Wind directions: From colony (east track) - W. Days 11-12: NE. Days 14-15 (Snares shelf to Campbell) - W then NW.

**Fig. 4.2 e & f**

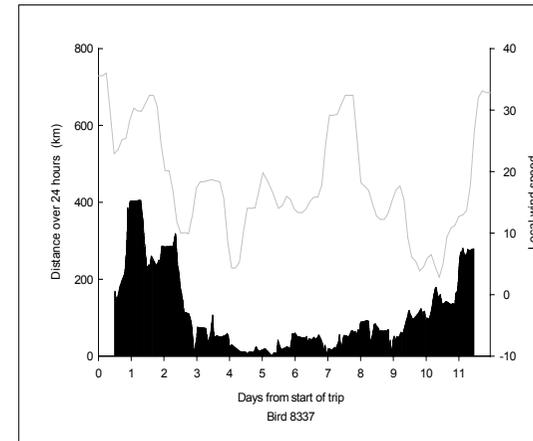
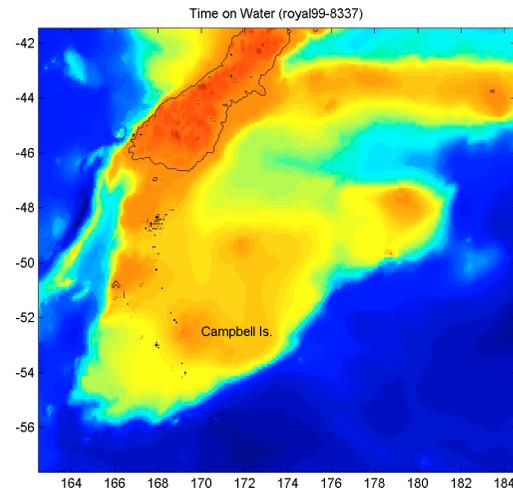
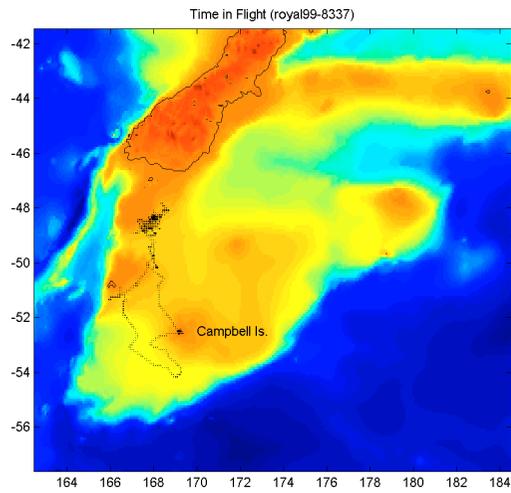


g).#25069 – Victoria. Wind directions: From Campbell (west track) - S then SW. Days 7 – 9 (to Chatham Rise): W, SW, S, SE. Back to Campbell - NE then W then N.

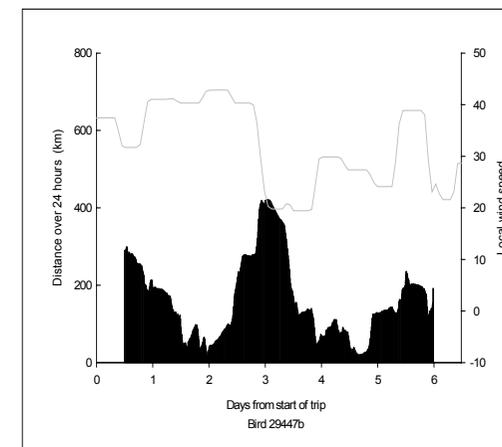
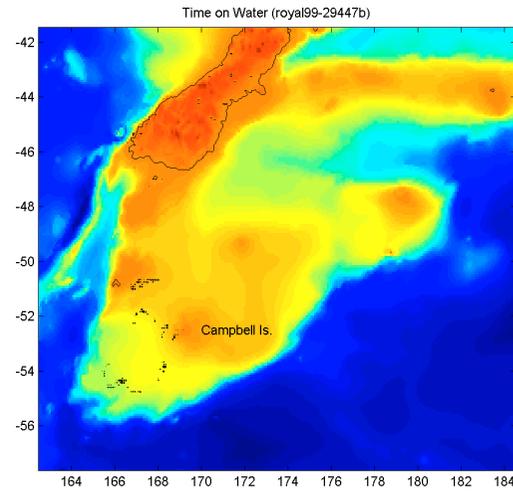
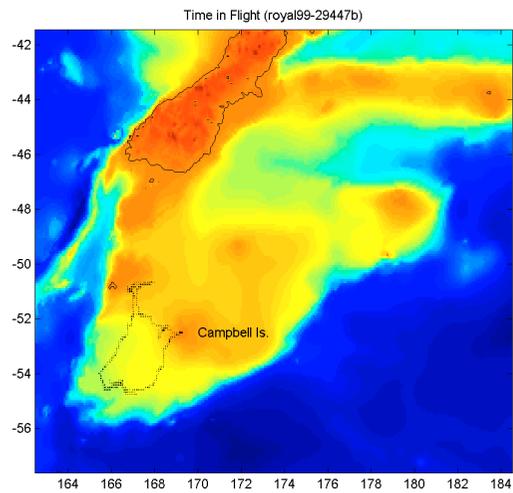


h).#29080 – Louis XVI. Wind directions: From Campbell (east track) - WNW then S; back to Campbell - NW then SW.

Fig. 4.2 g & h



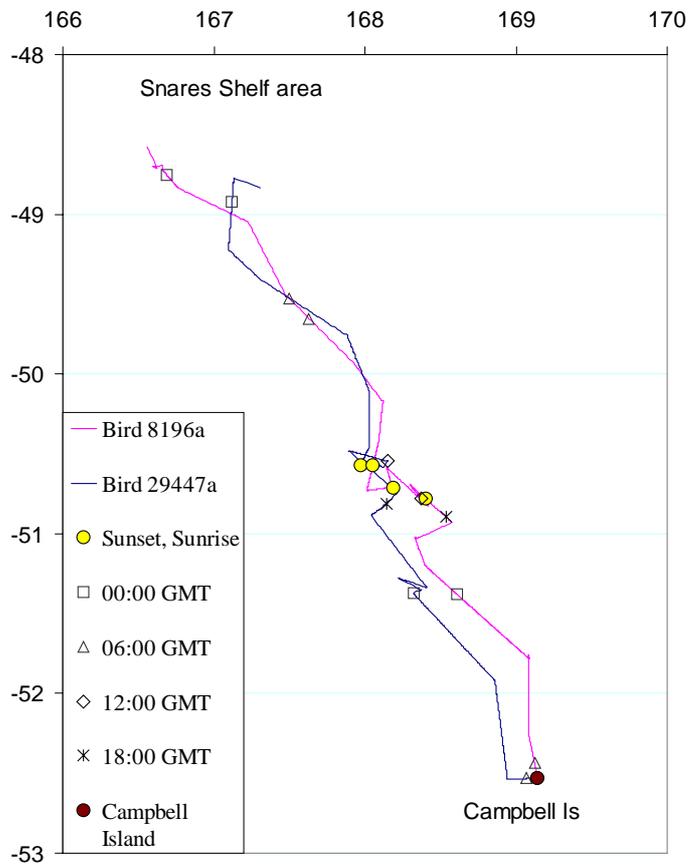
i).#8337 – Albert. Wind directions: From Campbell (to south first) - NW, W then SW; back to Campbell - NNW.



j).#27447b – Charlie. Wind directions: From Campbell (to south first) - NW. Days 2-3 - NW, N, W. Back to Campbell - WNW.

Fig. 4.2 i & j

Close inspection of the timing of two return trips provides an additional indication that an increase in wind speed from an appropriate quarter triggers the return commute to the colony. Queen Mother and Fergy, who had been foraging over different parts of the Snares shelf, converged within a short time of each other at the shelf edge and tracked each other's course within a few kilometres for the return trip to the colony, as if in response to the same meteorological trigger.



**Fig. 4.3.** Two birds (Queen Mother – 29447a and Fergy – 8196a) converged from different directions at foraging grounds (S. Snares shelf area), 470 km from Campbell Island. Shown here from before 0:00 GMT on 20 January, their flight paths and timing are closely matched, although separated by several kilometres. Both birds arrived at Campbell Island soon after 06:00 GMT on 21 January.

### **Analysis of wind speed, wind angle and displacement speed:**

The mean wind speed for all birds during commuting (23.3kph  $\pm$ 1.7 SE) was significantly higher than during foraging (16.6kph  $\pm$ 1.9 SE):  $t = -4.27$ , 9 df;  $P = 0.002$  (2-tailed paired sample test).

The mean displacement rate between successive uplinks for all birds during commuting (28.6 kph  $\pm$  1.93 SE) was significantly higher than during foraging (15.1 kph  $\pm$  1.4 SE) ( $t = -8.17$ ; 9df;  $P = 0.001$ ).

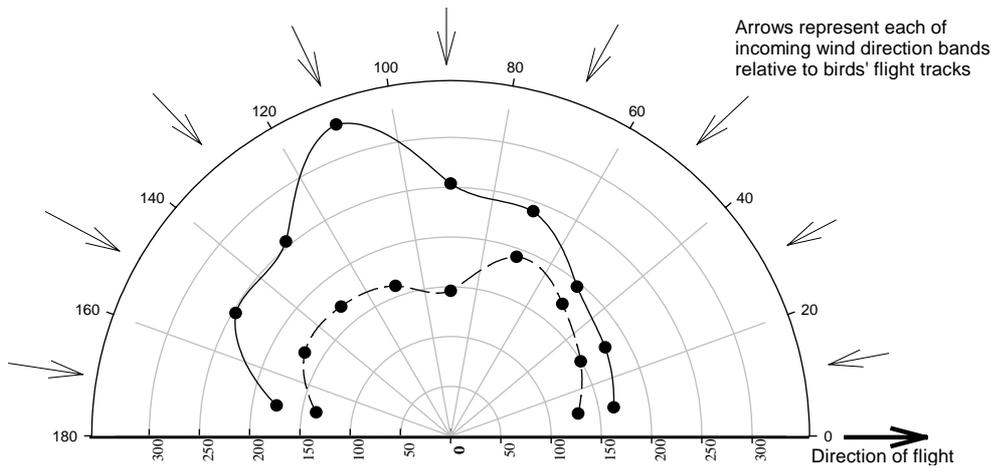
The following results are for commuting and foraging phases combined. Commuting and foraging data are plotted separately in Figures 4.4a, b and c.

The prediction that SRA will cover less distance flying at less favourable wind angles, i.e.  $0^\circ$  to  $40^\circ$  (upwind or head winds);  $80^\circ$  to  $100^\circ$  (wind abeam or direct side wind) and  $160^\circ$  to  $180^\circ$  (downwind or direct tail wind) than at other the bands of relative wind angle (close reach and broad reach) was confirmed. There was a significant difference between the mean distance covered at more favourable angles (426km) and at less favourable angles (333km) to the wind:  $t = 3.08$ ; 7 df;  $P = 0.018$ .

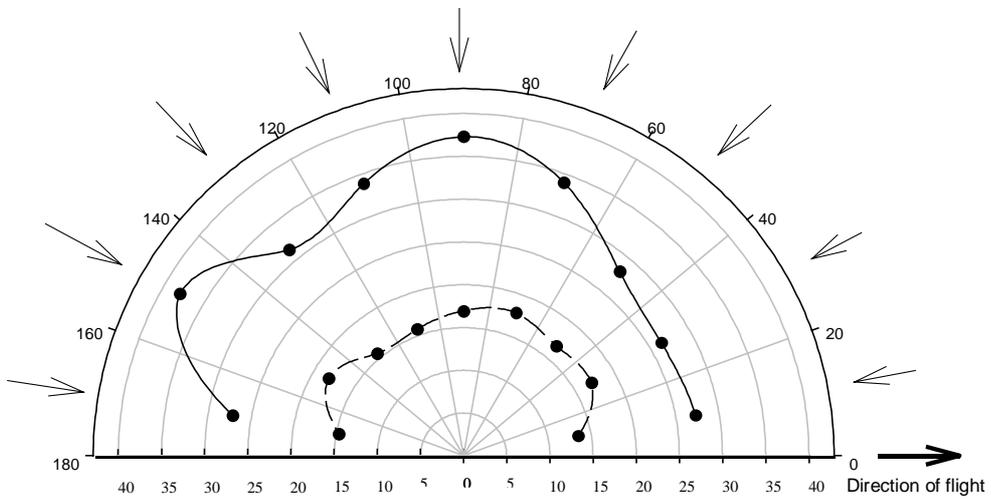
(See Fig. 4.4a.)

However, mean displacement speed was not found to vary significantly between the wind directions expected to be more favourable (27.6 kph) and those expected to be less favourable (24.9 kph);  $t = 1.30$ ; 7 df;  $P = 0.235$ . (See Fig. 4.4b.)

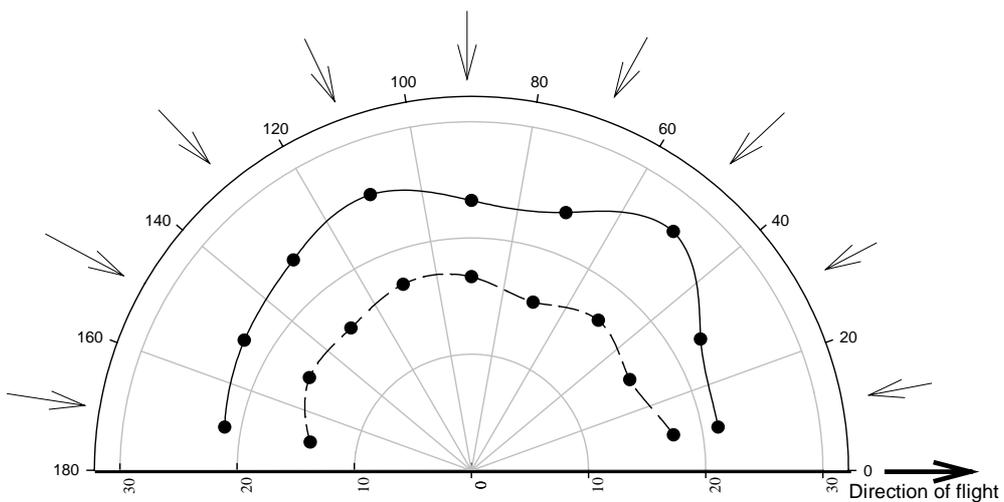
The difference in mean wind speed at different flight angles (for more favourable angles: 21.63kph; and for less favourable flight angles, 20.07kph) was not significant:  $t = 2.01$ ; 7 df;  $P = 0.084$ . Differences in wind speed did not appear to cause SRA to adjust their flight angles (See Fig. 4.4c.).



**Fig. 4.4a** Cumulative distance flown (km, bottom axis) at each wind sector during commute (solid line) and forage (dashed line) phases; means for all 10 birds.

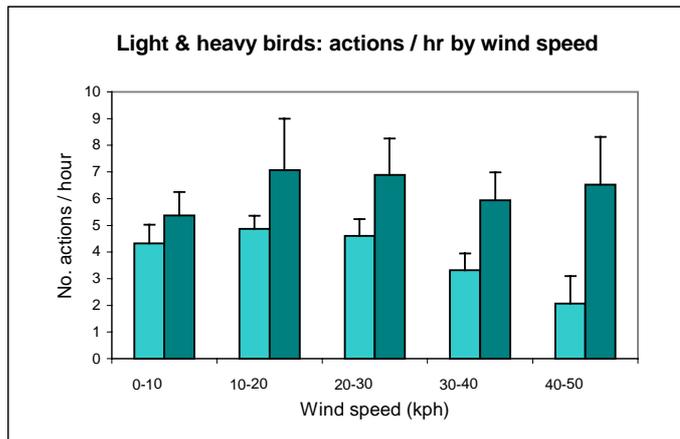


**Fig. 4.4b.** Mean displacement speed (kph, bottom axis) at each wind sector during commute (solid line) and forage (dashed line); means for all 10 birds.



**Fig. 4.4c.** Mean wind speed (kph, bottom axis) at each wind sector during commute (solid line) and forage (dashed line); means for all 10 birds.

Differences in landing activity by heavy and light birds were observed across a range of wind speeds, with heavy birds landing at a similar rate regardless of wind speed, whereas light birds made fewer landings and take-offs at higher wind levels (Fig. 4.5).



**Fig. 4.5.** Number of landing/take-off actions per hour for 4 birds >9kg (3 males & 1 female; dark bars) and 6 birds <9kg (all female; light bars) over water less than 1500m depth (potential foraging areas) (means + s.e.)

#### 4.5 Discussion

This study has shown that SRA utilise a ‘commute, foraging, commute’ pattern as their principal foraging strategy during incubation, demonstrated by the distance over time plots showing the shape of foraging trips of the ten SRA. The switch between scales from long-range directional travel to localised searching exemplifies the scale-dependant hierarchical adjustments in the foraging patterns of long-ranging seabirds described by Fritz et al. (2003). The authors describe how broad scale long distance searching on a scale of tens to hundreds or thousands of kilometres is undertaken to locate prey in a patchy environment, then searching at a local scale (in this case 1 to 10’s of kilometres) for prey items within a patch. Some other albatross species such as WA foraging from Crozet Island during incubation typically switch from one scale

or fractal dimension to the other intermittently throughout their foraging trip as prey is encountered, in contrast to SRA which apparently conduct most of their searching at features such as shelf breaks after a period of directed flight. This more closely resembles the foraging behaviour of light-mantled sooty albatross *Phoebastria palpebrata* (LMSA) during incubation. In contrast to LMSA, however, SRA spent all of their time over continental shelf and slope waters.

The commute – forage – commute type of foraging trip seen here is considered to be more energetically costly than the searching looping flights of Crozet Island WA and Amsterdam Albatross, *Diomedea amsterdamensis* (AmA) (Waugh and Weimerskirch 2003). In long looping flights, the birds achieve a high degree of flight efficiency by optimal use of wind direction (Weimerskirch et al. 2000). When flight is targeted on specific foraging destinations (such as identifiable bathymetric features associated with high productivity) as is the case with SRA, the birds may expend more energy by flying at less favourable wind angles and take longer to cover distance. SRA were found to spend a greater proportion of their time in flight, and to engage in more flight involving frequent turning (relating to the foraging phase of their trip) than either WA or AmA (Waugh and Weimerskirch 2003). There appears to be a trade-off played out in these contrasting strategies; on one hand flying to sites with relatively predictable prey availability but working harder in flight (SRA), or on the other hand flying at minimal cost but taking a chance with sparse and dispersed prey (WA). They can increase their chance of encountering prey items by travelling fast, as more distance will be searched per unit of time.

SRA may be able to minimise some of the drawbacks of their commute – forage – commute strategy by being selective about when they undertake the commute leg of their trip. These results suggest this is the case. The commencements of return trips appear to be synchronous with an increase in wind speed, and mean wind speed during commuting is significantly higher than during foraging. However, differences in wind speed should be interpreted with some caution. As the wind speed data has a resolution of 12 hours, and wind strength is likely to be stronger in the region of Campbell Island than further north, it is difficult to be certain from these results that change in wind strength is a trigger to departure towards the island, rather than just a feature associated with reaching more southerly latitudes.

Fig 4.2 shows that wind direction during return trips was favourable (i.e. not head winds) for the course required to fly to Campbell Island. The fact that two birds (Queen Mum and Fergy) foraging apart on the Snares Shelf selected the same timing and course to return to the colony further suggests that certain weather conditions are selected for the flight back.

On the other hand, most departures from Campbell Island at the start of foraging trips took place within two to four hours of being relieved at the nest by the returning partner, the longest delay being around six hours. SRA were apparently not constrained by wind strength, as none encountered low wind speeds at that time. However, the wind direction at the time of departure appeared to influence the direction taken by the birds, and they made subsequent changes of course as the wind veered.

Although these findings indicate that SRA modify their flight plan in accordance with wind direction and speed, they may fly more of a compromise course than WA so as to reach a site associated with high productivity; SRA may fly the best possible course to reach a destination, rather than the most energy conserving course on a relatively more 'open itinerary' by WA (Waugh and Weimerskirch 2003).

Mean displacement speed between successive uplinks (after subtracting time spent on the water) was found to be significantly lower during foraging than commuting.

During foraging a bird turns more frequently than during commuting (as seen from the tracks), but additional turns made between uplinks were not individually recorded.

Birds will have flown a longer route than is measured, hence appear in our data to be flying more slowly than they are. But as wind speed was found to be lower during foraging, it is possible that even flight speed measured directly would be slower than during commuting.

Differences in distance covered across the range of wind angles (Fig. 4.4a) may indicate wind angles that are optimal for SRA to fly. During commuting more distance was covered at a relative wind angle of  $100^{\circ}$  –  $120^{\circ}$  than at other angles. Low distances were covered at bands from  $0^{\circ}$  –  $60^{\circ}$  (head winds to close reach) and  $160^{\circ}$  –  $180^{\circ}$  (direct tail winds). Winds from  $100^{\circ}$  –  $120^{\circ}$  may provide maximum energy compared to head winds, while direct tail winds may produce instability.

Mean wind speed was found to be similar at any flight angle. This suggests that SRA do not avoid certain angles in stronger or weaker winds, in contrast to the findings of Reinke et al. (1998) in a study of one Gibson's albatross.

Foraging differences between males and females have been found in other species. Male WA from Crozet forage further south than females, in a region with stronger wind conditions (Weimerskirch 1997). Shaffer et al. (2001) show that differences in wing loading between heavier males and lighter females can explain sex differences in habitat preference with regards to wind strength. The lightest SRA in this study, Squidgy, flew an erratic course taking her further away from the destination of Campbell Island when the wind increased to 30 to 40 kph (Fig. 4.2 c). She may have been less able to hold a course in strong winds because of a relatively low wing loading. As low mass is an indication of young age, she may also have been inexperienced at navigating the optimal course.

The finding in this study that heavier birds carry out a greater proportion of their landing activity in strong winds than lighter birds further supports the hypothesis that birds are adapted to different wind environments according to their wing loading. A larger sample size might reveal an overall tendency for male and female SRA to use different foraging zones. In this study, two of the three males (Albert and Charlie) travelled further south than any of the females to the southern edge of the Campbell Plateau, where higher wind speeds would be anticipated. The journey direction of these males, however, could have been a function of wind direction at the time of departure from Campbell Island.

SRA were found to have greatly elevated heart rates when taking off from the water, and heart rate remained elevated for one to two hours following take-off (Appendix II). In steady flight, SRA heart rates were at a similar level to those of SRA motionless on the nest during incubation, within the range of 50 – 70 beats per minute

(bpm). During take-off, heart rate reached 200 bpm or higher, and remained between 150 and 100 bpm for up to two hours following take-off. This is consistent with findings for WA (Weimerskirch et al. 2002). Heart rate serves as an index of instantaneous energy expenditure (Bevan et al. 1995), and periods of prolonged elevated heart rate indicate significant additional energy expenditure. The cost of taking off from water may be lower when taking off in wind speeds that are optimal for the wing loading of the individual bird, and in general for the species. If so, wind speed at foraging zones should be a factor influencing where a bird should forage, in addition to the consideration of optimal conditions for long distance flight. This question requires further investigation. Differences in wing loading between the four taxons of great albatross breeding in the New Zealand region could help explain why they appear to have relatively little overlap in their foraging distribution from tracking studies to date.

## References

- Alerstam, T., G. A. Gudmundsson, and B. Larsson. 1993. Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. *Philosophical Transactions of the Royal Society of London* **B340**:55-67.
- Bevan, R. M., P. J. Butler, A. J. Woakes, and P. A. Prince. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society of London* **B350**:119-131.
- Fritz, H., S. Said, and H. Weimerskirch. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London B*. **270**:1143 - 1148.
- Jack, A. 1953. *Feathered Wings: A Study of the Flight of Birds*. Methuen & Co Ltd., London.
- Jouventin, P., and H. Weimerskirch. 1990. Satellite tracking of Wandering albatrosses. *Nature* **343**:746-748.
- Murray, M. D., D. G. Nicholls, E. Butcher, and P. J. Moors. 2002. How Wandering Albatrosses use weather systems to fly long distances. 1. An analytical method and its application to flights in the Tasman Sea. *Emu* **102**:377-385.
- Murray, M. D., D. G. Nicholls, E. Butcher, and P. J. Moors. 2003a. How Wandering Albatrosses use weather systems to fly long distances. 2. The use of eastward-moving cold fronts from Antarctic LOWs to travel westwards across the Indian Ocean. *Emu* **103**:59-65.

- Murray, M. D., D. G. Nicholls, E. Butcher, P. J. Moors, K. Walker, and G. Elliott. 2003b. How Wandering Albatrosses use weather systems to fly long distances. 3. The contributions of Antarctic LOWS to eastward, southward and northward flight. *Emu* **103**:111-120.
- Nicholls, D. G., M. D. Murray, and C. J. R. Robertson. 1994. Oceanic Flights of the Northern Royal Albatross *Diomedea epomophora sanfordi* using satellite telemetry. *Corella* **18**:50-52.
- Pennycuik, C. J. 1982. The flight of petrels and albatrosses (procellariiformes), observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society of London* **B300**:75-106.
- Reinke, K., E. C. Butcher, C. J. Russell, D. G. Nicholls, and M. D. Murray. 1998. Understanding the flight movements of a non-breeding wandering albatross, *Diomedea exulans gibsoni*, using a geographic information system. *Australian Journal of Zoology* **46**:171-181.
- Salamolard, M., and H. Weimerskirch. 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Functional Ecology* **7**:643-652.
- Shaffer, S. A., H. Weimerskirch, and D. P. Costa. 2001. Functional significance of sexual dimorphism in Wandering Albatrosses, *Diomedea exulans*. *Functional Ecology* **15**:203-210.
- Spear, L. B., and D. G. Ainley. 1997a. Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis* **139**:221-233.

- Spear, L. B., and D. G. Ainley. 1997b. Flight speed of seabirds in relation to wind speed and direction. *Ibis* **139**:234-251.
- Spruzen, F., and E. Woehler. 2002. The influence of synoptic weather patterns on the at-sea behaviour of three species of albatross. *Polar Biology* **25**:296 - 302.
- Waugh, S. M., and H. Weimerskirch. 2003. Environmental heterogeneity and the evolution of foraging behaviour in long ranging greater albatrosses. *Oikos* **103**:374-384.
- Weimerskirch, H. 1997. Foraging strategies of Indian Ocean albatrosses and their relationships with fisheries. Pages 168-179 *in* G. Robertson and R. Gales, editors. *Albatross Biology and Conservation*. Surrey Beatty & Sons, Chipping Norton.
- Weimerskirch, H., T. Guionnet, J. Martin, S. Shaffer, and D. P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* **267**:1869-1874.
- Weimerskirch, H., S. Shaffer, G. Mabile, J. Martin, O. Boutard, and J. L. Rouanet. 2002. Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation and the effects of human disturbance. *The Journal of Experimental Biology* **205**:475 - 483.

## Chapter 5 : General Discussion

### 5.1 Introduction

This study of SRA foraging strategies and behaviour during incubation has added to our knowledge of this species by investigating little studied aspects of their lives. This study has also provided insights into aspects of the environment on which SRA depend. Investigating foraging strategies at this key stage of the breeding cycle has demonstrated SRA's functioning within a range of conditions, and the constraints that apply as they exploit their environment. Our understanding of the foraging ecology of this species has been extended.

Key foraging sites used by SRA during the latter half of incubation were identified in Chapter Two. We confirmed that SRA are outer shelf and shelf-break foragers. The majority of the birds made intensive use of the southern and south-eastern edge of the Snares shelf, while some of the birds used a secondary site at the more distant Chatham Rise. This knowledge is important in relation to the conservation of the species for determining key areas for special consideration such as management of seasonal fishing activity and establishing priorities for marine reserves.

The predominant foraging strategy of SRA was identified in Chapter Two as commuting directly to locations that are defined by their physical attributes, which include underwater topography, in particular outer shelf and shelf breaks, and the frontal interface between subantarctic and subtropical waters. These bathymetric and oceanographic features are associated with high productivity and with distribution of specific prey species (Imber 1999). SRA's strategy of targeting physical features is expected to have relatively high energy costs, as it necessitates travelling to these relatively fixed features in variable wind conditions, but with a high probability of encountering relatively concentrated prey. This strategy differs from that employed by some other *Diomedea* such as WA, which undertakes rapid looping oceanic flights, expending minimal energy by making optimal use of local wind conditions while searching for sparsely distributed prey (Weimerskirch et al. 2000). The foraging strategy seen in SRA also differs from GA from the Auckland Islands but is similar to

NRA. However, in contrast to NRA studied to date (on the Otago Peninsula), SRA foraging trips are of greater duration and distance. It may be that SRA from Campbell Island lack highly productive grounds in close proximity compared with NRA from the Otago Peninsula, which are close to the East Coast shelf break and the Chatham Rise. Foraging trips by SRA are similar in duration to those of WA, despite the fact that the maximum distance travelled to from the colony is less than for WA.

As discussed above, the foraging pattern seen in SRA differs from foraging strategies seen in another Campbell Plateau breeding albatross of the genus *Diomedea*. GA from the Auckland Islands have not been found to use the apparently productive Snares shelf zone close to their nesting island that was used by SRA (Walker et al. 1995). Instead, GA were found to travel to considerably more distant sites. The lack of use by GA of the nearby Snares hotspot was confirmed by direct observation from fishing vessels. Petyt (1995) reports that members of the WA group, including GA, are only occasionally seen there, in contrast to groups of up to 60 SRA at a time within sight of a fishing vessel. Whether this lack of use of an apparently productive zone near their colony by GA is a direct result of competitive exclusion by the slightly larger SRA, or is driven by other factors leading to evolution of different foraging strategies or different habitat requirements (including differences in prey preference), it is an interesting case of resource partitioning between the two *Diomedea* species. Differences between these species in mass and wing loading may have a bearing on the foraging zones and strategies used by the two species, as observed in Chapter 4 in relation to differences in mass within SRA. It would be useful to investigate this question to gain a deeper understanding of the processes of radiation within the *Diomedea* genus.

Chapter Three investigated factors influencing the duration of foraging trips. Foraging trips became significantly shorter as hatching approached, which is consistent with other seabirds. Foraging trips also tended to be shorter when the median wind speed was higher (though not significantly so). The influence of these factors on trip length warrants further investigation with a larger sample size, and over a longer period with a greater range of weather conditions. Another indication that wind speed has an influence on the timing of return flights to the colony was that days

on which the most birds from 52 nests returned to the colony had higher wind speeds than the average for the period.

Chapter Four further investigated the role of the wind in relation to the pattern of foraging trips. Aspects of the birds' foraging trips were plotted to demonstrate the birds' movement in space, in time, and in relation to wind conditions. The importance of wind speed as a factor in the timing of commute phases of foraging trips seen in Chapter Three was supported by the finding that mean wind speed was significantly higher during commuting phases than during foraging phases. The timing of return trips to the colony associated with increased wind speed is reinforced by visual inspection of the trips of individual birds in relation to wind strength (plotted in Figs 4.2, a - j). Another indication that birds' return flight to the colony may be linked to a meteorological trigger is the near simultaneous departure from foraging grounds, parallel flight track, similar timing of pauses, and concurrent arrival at the colony of two tracked birds.

That wind direction is also a component of the overall pattern of foraging trips is supported by the finding that birds covered significantly greater distance at more favourable wind angles. Inspection of each trip shows that birds leave the island in a range of wind directions, and alter their flight path accordingly. They may vary their choice of destination according to wind direction (while still meeting the requirement to target features associated with productivity discussed above). However, for the return flight to the colony, the destination is fixed. Given the finding that SRA cover a greater distance at some wind angles than at others, they could be expected to wait for wind from a favourable sector before commencing the return trip. This is supported by visual inspection of the return commute flights of individual birds in relation to wind direction (shown in Figs 4.2, a - j).

Our results also suggest that wind strength during the foraging phase may affect the birds' ability to feed effectively. Light birds undertook proportionally fewer landings and take-offs at sea during strong winds. However, our results did not show heavy birds reduced their landing activity significantly in light winds; they may, however, have energetic higher energetic costs taking off in light winds than in stronger winds.

Overall, there appears to be an ideal band of wind conditions within which the SRA can operate optimally. There are time costs when winds are either below or above the optimal range for particular individuals, which impacts on the mate left on the nest to incubate. This was highlighted by two individuals: Caroline, who was ‘trapped’ by light winds for several days, delaying her return to the colony, and Squidgy, a light bird who encountered very strong winds and went substantially off course, which delayed her return also.

This study has provided important information on the foraging destinations of SRA from Campbell Island during incubation. It has also increased our understanding of SRA foraging strategies, and of variables that increase their costs in terms of time spent on foraging trips. We have a better understanding of the range of conditions within which SRA are able to operate and to carry out foraging activities relating to successful breeding. This has been possible despite the limitations of a small sample of birds and a small window of time in which to sample a range of wind conditions. The sample consisted of ten birds, only three of which were males. Comparisons made within the group for differences in foraging trip duration involved very small groups of three or four (birds above and below 9kg, males versus females, earlier and later incubation). Despite this limitation, some statistically significant results were found, and other trends detected may well be significant with larger samples.

Other species and populations of great albatross have been studied in much greater detail than SRA (for example the Crozet Island and South Georgia populations of WA), but as we have found here, SRA are significantly different from other great albatrosses in their foraging strategies, and generalisations cannot be made across even closely related species.

## **5.2 Directions for further research**

To gain a more complete picture of foraging strategies of SRA during breeding, other stages of the breeding cycle should be investigated. The next priority should be the guard stage, when adults must work hard to meet the demands of the chick as well as meeting their own needs; making frequent feeding visits while one parent is still

constrained to being at the nest in a brooding role. Foraging sites closer to the colony may be used at this stage. Many procellariiform seabirds exhibit a dual foraging strategy of short and long foraging trips during the guard stage as a way of balancing the needs of the adults and the chick (Weimerskirch et al. 1994, Baduini and Hyrenbach 2003), but whether this is the case in SRA is not known.

Tracking studies combined with analysis of wind conditions undertaken over successive years would enable us to understand the degree of variation to which SRA must adjust their foraging destination. It would also contribute to our understanding of the marine ecosystem in this region, and enable monitoring of changes over time. Differences from year to year are a valuable indication of variation of key aspects of the marine environment such as prey availability. Substantial differences between years in foraging zones visited, foraging trip duration, and distance from the colony have been found elsewhere (Berrow and Croxall 2001), and these have been linked to changes in food availability, for example as a result of sea surface temperature anomalies (Inchausti et al. 2003).

In the medium term, several factors could affect the future viability of SRA breeding on Campbell Island. Climate change predictions by the Intergovernmental Panel on Climate Change and others suggest that as well as changes in the marine environment resulting from changes in currents and their nutrient, chemical and thermal characteristics, changes above the water's surface are to be expected in the form of changes in wind direction and strength. Periodic monitoring of foraging strategies would detect adaptations the birds make in adjusting to such changes.

Differences in wind regime could affect SRA's ability to reach foraging grounds within the time constraints imposed by breeding. Other potential factors include reduced prey availability because of depletion of key prey stocks by fishing activity, or because of rapid climate change (Croxall et al. 2002). Changes leading to a small annual decrease in breeding success have a large long-term impact on a long lived, slow breeding species such as SRA. The concentration of almost the entire population at one breeding site makes SRA more vulnerable to changes within its range. This study provides important baseline information, and ongoing monitoring of the

parameters studied would enable the impact of any environmental and ecological changes to be understood, and appropriate management decisions to be made.

SRA and the other great albatrosses may be relatively adaptable in their use of the environment. In the course of their evolutionary history there have been many changes in climate, but there can be constraints in terms of available breeding sites within range of new foraging sites that are habitable for albatrosses. However, the challenges they could face in some predicted climate change scenarios would be on a more rapid time frame than before, and on a different scale from some other albatross species for the reasons outlined above. If we have adequate knowledge of their current foraging patterns and constraints on foraging during breeding, it will be possible to model the impact of a range of future scenarios.

An expanded study of this kind will be useful not only for understanding potential impacts on this species, but through studying its use of the environment, would allow a greater understanding of complex interactions of variables that are difficult to study individually. The apparently stable nature of the SRA breeding population currently makes this an ideal species to study, through interseasonal and interannual variations in foraging strategies, to read signals from the marine ecosystem as well as about the wind conditions from SRA's response to these. Studying foraging strategies over the entire breeding cycle would allow us to investigate SRAs' tolerance of a wider range of wind conditions and foraging opportunities. If this were integrated with studies of variation in diet, energetics and breeding success, this would become a valuable system for remote monitoring of a complex ecosystem.

## References

- Baduini, C., and K. D. Hyrenbach. 2003. Biogeography of Procellariiform foraging strategies: does ocean productivity influence provisioning? *Marine Ornithology* **31**:101-112.
- Berrow, S. D., and J. P. Croxall. 2001. Provisioning rate and attendance patterns of Wandering Albatrosses at Bird Island, South Georgia. *Condor* **103**:230-239.
- Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* **297**:1510-1514.
- Imber, M. J. 1999. Diet and Feeding Ecology of the Royal Albatross *Diomedea epomophora* - King of the Shelf Break and Inner Slope. *Emu* **99**:200-211.
- Inchausti, P., C. Guinet, M. Koudil, J. P. Durbec, C. Barbraud, H. Weimerskirch, Y. Cherel, and P. Jouventin. 2003. Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. *Journal of Avian Biology* **34**:170-176.
- Petyt, C. 1995. Behaviour of seabirds around fishing trawlers in New Zealand SubAntarctic waters. *Notornis* **42**:99-115.
- Walker, K., G. Elliott, D. Nicholls, D. Murray, and P. Dilks. 1995. Satellite tracking of Wandering Albatross (*Diomedea exulans*) from the Auckland Islands: preliminary results. *Notornis* **42**:127-137.
- Weimerskirch, H., O. Chastel, L. Ackermann, T. Chaurand, F. Cuenot-Chaillet, X. Hindermeyer, and J. Judas. 1994. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* **47**:472-476.
- Weimerskirch, H., T. Guionnet, J. Martin, S. Shaffer, and D. P. Costa. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* **267**:1869-1874.

## Acknowledgments

I would like to acknowledge the contribution and support of the following people and organisations:

- Sue Waugh and Henri Weimerskirch for the opportunity to take on the project
- The Department of Conservation (Southland Conservancy) for supporting the project, for their assistance and access to facilities
- Peter Moore (DoC Science and Research) for assistance and support in the field
- Antoine Catard who assisted before, during and after the fieldwork and whose toil, experience and company were greatly appreciated
- Le Centre Nationale de Recherche Scientifique (CEBC, Chizé) for a substantial part of the project costs, and for the opportunity to work on site at Chizé
- The staff and students at Chizé and Dominique Filippi for help and support in the early stages of the project
- Lincoln University for financial and institutional support; and in particular the Ecology and Entomology group for such a stimulating environment and good bunch of people, staff and students; the wonderful Library staff and facilities; and the Recreation Centre, in particular the Yoga programme without which the hours at the computer would have meant certain death
- Rob Harcourt and all the staff of the Graduate School of the Environment at Macquarie University for giving me a welcoming base and collegial environment while I was in exile in Sydney
- Friends and family for unstinting support; and in particular Andrew Troup and Bruce McCallum who have been my personal software Wizards and Help Desk and have stuck around when the going got tough; and my mate Penny for supporting me in every way imaginable
- My exceptional supervisor, Adrian Paterson, who seems to know instinctively when to step in with a pertinent question as well as when to leave me to make my own way, and whose support in the final hours has been legendary
- My associate supervisor, Kerry-Jayne Wilson, generous with her extensive knowledge and insights, and alternately very stern and very funny.

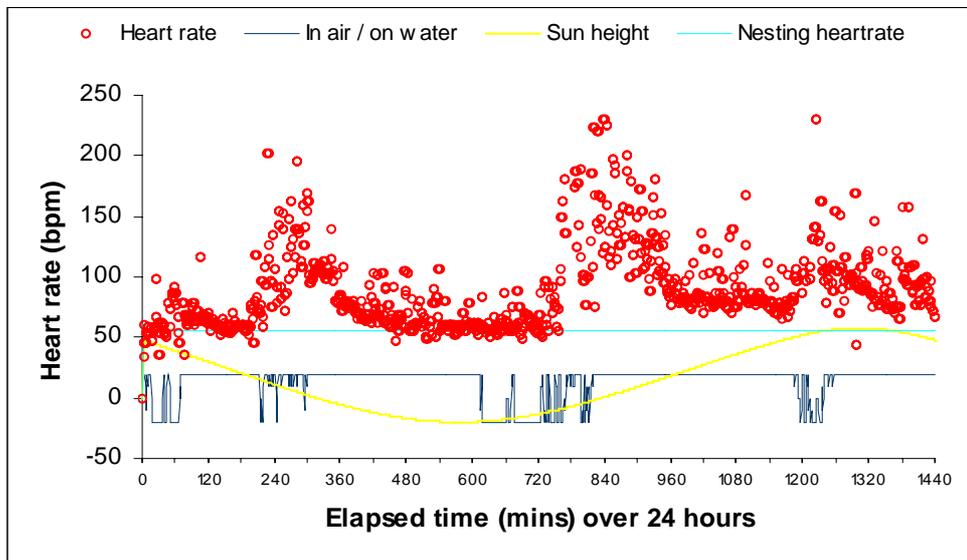
My hearty thanks to you all.

## APPENDIX I

**Table 3.** Summary of foraging trip details for each of 10 Southern Royal Albatrosses

BIRD # & Sex	Name	% time on water	Dist. flown cumulative (km)	Displ. speed mean (time in air only) (kph)	Overall trip speed mn (incl. time on water)	Total time (days)	Max range (km)
25069 F	Victoria	32.44	6589	25.40	17.16	16.00	1259
29450 F	Anne	43.63	6051	28.02	15.80	15.96	1214
8196b F	Caroline	21.34	4456	14.51	11.41	16.27	517
29455a F	Squidgy	32.40	3581	25.38	17.16	8.70	768
29447a F	Queen Mum	58.46	3487	36.38	15.11	9.61	493
8196a F	Fergy	43.17	3338	27.16	15.43	9.01	506
29455b F	Liz	36.49	3202	22.71	14.42	9.25	512
29080 M	Louis XVI	20.83	5497	19.04	15.07	15.20	773
8337 M	Albert	9.71	3523	12.67	11.44	12.84	638
29447b M	Charlie	43.32	2898	31.28	17.73	6.81	343

## APPENDIX II



**Fig.** Heart rate trace for a SRA over a 24 hour period (open circles) plotted with the corresponding wet-dry activity record (dark blue line) shows the increase in heart rate during take-off into flight and subsequent recovery time, discussed in Chapter 4. The dark blue line indicates whether the bird is on the water (negative values) or in the air, and vertical lines indicate take-off and landing. Incomplete take-offs or landings are seen as short vertical lines (alternating wet-dry readings at 15 second intervals). Day and night time are shown as positive and negative values for sun height.

Heart rate recorders were fitted to three SRA to investigate the energetic cost of aspects of foraging. The increase in heart rate when taking off from the water indicates the high cost of this activity (Weimerskirch, 2000). An important difference between SRA and WA is the high number of repeated landings and full or partial take-offs in rapid succession shown in activity records of SRA. Interpretation of these data is problematic, but can be assisted by overlaying the heart-rate data to indicate whether full take-offs have occurred. Some full landings in quick succession may be explained if SRA tend to encounter more prey within a small area, and land repeatedly to take prey. It may also be that they have more interactions with other foraging birds at these sites with relatively more concentrated prey than the more dispersed WA, or for other reasons are more active at the surface of the water. The wet-dry alternations at < 1 minute intervals may be generated by activity such as fighting, paddling, prey-handling or preening. (The activity recorders were placed on the tarsus, and as electrodes at both ends of the cylinder must be submerged for a 'wet' reading, activity such as paddling or running across the water during take-off attempts may expose one end intermittently.)

### APPENDIX III



**Fig. 6.2.** Attachment of PTT transmitter using TESA surgical grade fabric tape to feathers on back of SRA.



**Fig. 6.3.** Attachment of wet-dry activity recorder to Davik band on tarsus of SRA