Supervised Project ANTA 504:

The South Polar Skua

(*Catharacta maccormicki*)

A study of past research and future opportunity

ANDREW GIVEN

Graduate Certificate in Antarctic Studies

Gateway Antarctica, University of Canterbury

2008/2009

ABSTRACT

The South Polar Skua is a bird well known to those who have spent time in Antarctica. For many it is the only seabird they encounter during their time in the region. It has a reputation as a hostile species, and in many ways is poorly understood. The common perception that all South Polar Skuas rely on penguins for food is unfounded. Research into the phylogenetics of the skua family has shown classification within the group to be problematic. One of the members of the family, the South Polar Skua, has been the subject of research in the Antarctic since the early days of Antarctic exploration. The species is widely distributed around the Antarctic coastline. In the Ross Sea area, work over the last 40 years has provided a good understanding of distribution, with the total population in the region estimated to be about 15,000 individuals. Research into the feeding ecology of the South Polar Skuas shows that their foraging method depends on the particular environment they inhabit as well as the presence of competing species. Siblicide is relatively common in South Polar Skuas, but questions remain as to why the behaviour occurs in some broods and not others. Significant opportunities exist in research relating to South Polar Skuas, with a need for long-term studies to assist in answering some questions.

TABLE OF CONTENTS

1. INTRODUCTION

Skuas are a widespread group of birds, inhabiting temperate and polar habitats in both hemispheres (Ritz *et al.* 2008). They are a group of birds that have been the focus of considerable research and have been the subject of several long-term studies (Catry *et al.* 1997). It is well established that gulls are the closest relatives of skuas (e.g. Furness 1987, Cohen *et al.* 1997, Andersson 1999a), but despite their similarities, there are some key differences between the two groups of birds. Skuas have converged with birds of prey to become efficient hunters, sometimes taking relatively large vertebrate prey (Andersson 1999a). They have toes with hooked claws to aid in this behaviour (Furness 1987). They exhibit strong sexual size dimorphism, with females larger than males (Andersson 1999a), like other birds with raptorial tendencies (Catry *et al.* 1999). In some cases, there is colour dimorphism with pale and dark morphs of both sexes (Andersson 1999a), although skuas are predominantly brown or dark grey (Furness 1987).

There is considerable variety within the group (Fig. 1), but classification has proven to be problematic (Reinhardt *et al.* 1997 and see discussion below). In the Antarctic is one of the most fascinating members of the skua family, the South Polar Skua, traditionally known as *Catharacta maccormicki*.

Adult male and female South Polar Skuas differ slightly in size, with females slightly larger and heavier than males (Ainley *et al.* 1985). Females also tend to be paler in colour. While determining the sex of adult birds is sometimes possible on the basis on morphometrics and physical features, juveniles and chicks are indistinguishable (Miller *et al.* 1997).

The South Polar Skua is a pelagic seabird, breeding around the Antarctic coast and on offshore islands (McGarry 1988). Pairs nest at sites free of snow and ice (Peter *et al.* 1990) and usually lay two eggs (Spellerberg 1971a). Breeding colonies vary markedly in size, with the largest colony numbering approximately 1000 breeding pairs, at Cape Crozier, Ross Island (Ainley *et al.* 1986). South Polar Skuas are thought to be the southernmost breeding bird in the world, with individuals recorded at Amundsen-Scott Station at the South Pole (McGarry 1988).

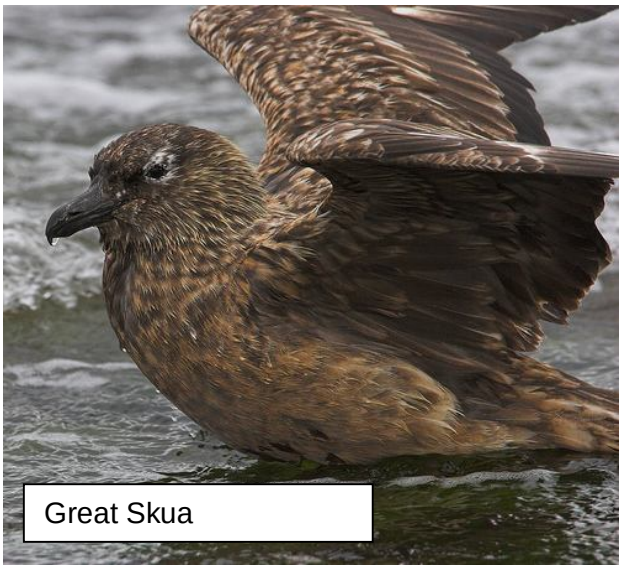

Figure 1. Representatives of the Skua family. For many forms (e.g. the Arctic Skua) there are several colour morphs. Only one morph is shown for such taxa. Photo credits:

Long-tailed skua: http:www.hughharrop.com/gallery/birds/long-tailed-skua4-norway 0707.jpg

Arctic Skua: http://i.pbase.com/o6/62/722262/1/81555729.iCFOnIkA.DSC_0037pbase.jpg

Great Skua: http://farm2.static.flickr.com/1313/615851248_1a6f373927.jpg?v=0

Pomarine Skua: http://farm3.static.flickr.com/2227/2494923669_b1ef3a5dfc.jpg?v=0

Chilean Skua: http://farm1.static.flickr.com/211/460615817_7dfaf59f2c.jpg?v=0

Brown Skua: http://www.greglasley.net/Images/BrownSkua1.jpg

South Polar Skua: A.D. Given

They are long-lived birds, with individuals first breeding at seven to nine years of age (Reinhardt 1997). A study at Cape Crozier showed the breeding span of South Polar Skuas to be almost 16 years (Wood 1971). Mates are retained for multiple seasons and pairs tend to breed in the same location every year (Wood 1971).

South Polar Skuas show a variety of foraging tactics (Pezzo *et al.* 2001), but rely largely on penguins and pelagic fish (Young 1963b). Many skuas breed in association with Adelie Penguins (Young and Millar 1999) and are regarded as the only avian predator that is likely to have a major impact on populations of breeding seabirds in parts of the Antartic (Norman and Ward 1990).

Skuas have an interesting reputation, reflected in the following quotes:

"*During the South Georgia expedition of 1912-13 I have become extremely well acquainted with the Brown Skua, which has left, I believe, a more vivid impression on my memory than any other bird I have met. The skuas look and act like minature eagles. They fear nothing, never seek to avoid being conspicuous, and, by every token of their behaviour, they are Lords of the far south.*"

(Murphy 1936 *in* Furness 1987)

"*Finally, grateful appreciation goes to all my companions at Wilkes Station who helped me while suffering through this study of the Antarctic eagle*"

(Eklund 1961 in reference to his study of the South-Polar Skua)

"*Skuas rank with stinkers at the foulest of plunderers"*

(Mary Gillham 1967 *in* Young 1999)

"The drama of Antarctic birdlife is not without its villain. Theft and pillage, murder, cannibalism, infanticide, these crimes are all in the repertoire of the South Polar Skua"

(in Young 2008)

OVERVIEW OF THE PROJECT

The aim of this project is to provide a summary of what is currently known regarding the South Polar Skua and to identify future areas of research focused on this species.

I begin with an overview of skua phylogenetics and classification, looking at the history of research in this area as well as its current status. I then focus on the most southern of the skua taxa, the South Polar Skua. I look at three key areas of South Polar Skua research: distribution, feeding habits and siblicide.

Finally I discuss the future of South Polar Skua research, highlighting some potential questions for future research.

2. SKUA PHYLOGENETICS AND CLASSIFICATION

Classification within the group has proven to be problematic (e.g. see Cohen *et al.* 1997, Andersson 1999a and 1999b and Braun and Brumfield 1998 and the discussion below). However, it is generally agreed that there are nine taxa within the group, with traditional classification (Furness 1987), largely based on plumage and morphometrics, as follows (Fig. 2):

Genus: *Stercorarius*

1. Long-tailed Skua = *Stercorarius longticaudus*
2. Arctic Skua = *Stercorarius parasiticus*
3. Pomarine Skua = *Stercorarius pomarius*

Genus: *Catharacta*

1. Great Skua = *Catharacta skua skua*
2. Falkland Skua = *Catharacta skua antarctica*
3. Tristan Skua = *Catharacta skua hamiltoni*
4. Brown Skua = *Catharacta skua lonnbergi*
5. Chilean Skua = *Catharacta chilensis*
6. South Polar Skua = *Catharacta maccormicki*

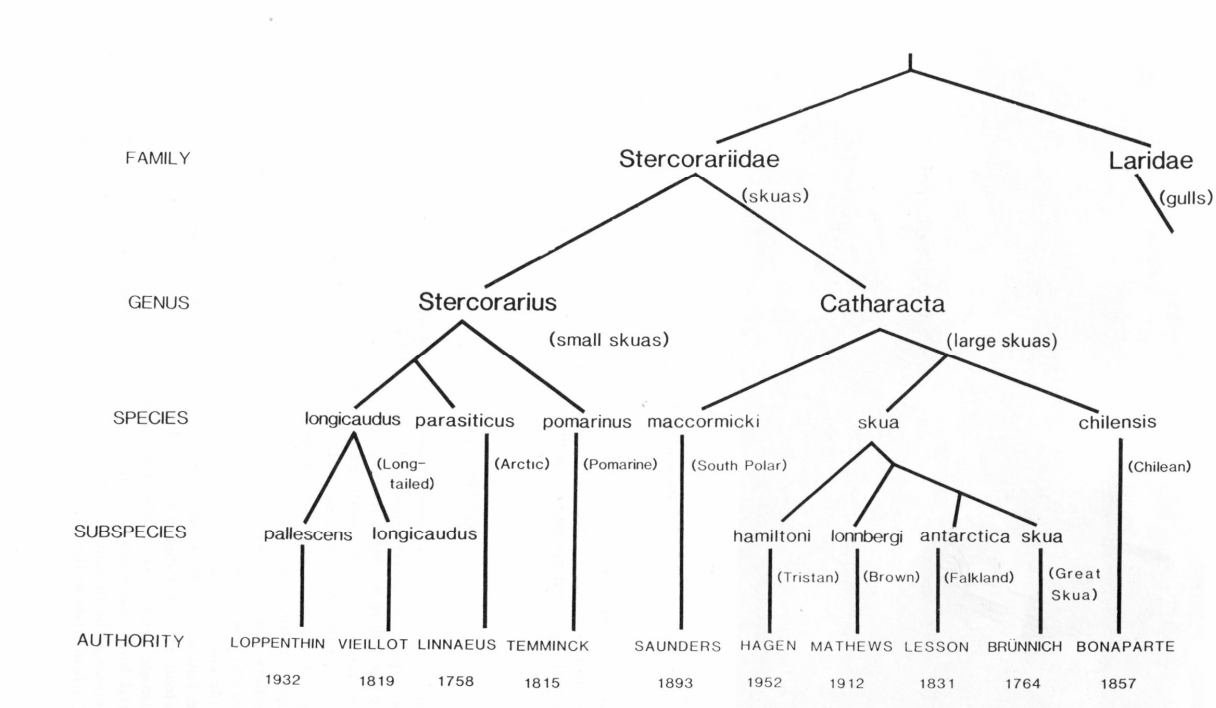

Figure 2: Skua Phylogeny from Furness (1987) based on plumage and morphometrics

Skua classification has always been a difficult task, in part because of the age-related plumages that appear in many species (Furness 1987). There were also numerous mistakes in the 1600s and 1700s as much identification was based on skins (Furness 1987). This improved as ornithologists began making visits to skua breeding grounds. Furness carried out some of the pioneering work in regards to improving the understanding of skua biology. In terms of classification within the group, Furness addressed the question of whether or not there should be two separate genera within skua. Due to the marked differences in plumage, size and distribution, Furness (1987) supported the separation of the group into the two genera *Stercorarius* (including the Long-tailed, Arctic and Pomarine Skua) and *Catharacta* (including the Great, Tristan, Brown, South Polar, Chilean and Antarctic Skua). Furness did not support the placement of the Pomarine skua into the *Catharacta* group on the basis of similarities in behaviour as had been suggested by Andersson (1973). “Few systematists would wish to classify large skuas and the Pomarine Skua in one genus but the Arctic and Long-tailed in another!” (Furness 1987). Instead Furness (1987) saw the splitting of skua into two genera as well supported by the current data. “Since barring of the juvenile plumage in Pomarine Skuas is clearly homologous with barring in juvenile Arctic and Long-tailed Skuas, Brooke’s argument seems to me to win the day. The Pomarine Skua must have branched from a common ancestor with the Arctic and Long-tailed Skuas which had evolved barred juvenile plumage after branching from the common ancestor with the large skuas. The separate genera *Catharacta* and *Stercorarius* are thus justified according to this picture of the evolutionary history of skuas” (Furness 1987).

In 1997, Cohen *et al.* attempted to resolve phylogenetic relationships amongst skua taxa (Fig. 3). They used a range of data types including mitochondrial DNA sequence data (cytochrome B and 12 S), Restriction Fragment Length Polymorphisms (RFLPS), Random Amplified Polymorphic DNA (RAPD), allozymes and information regarding parasites. Cohen *et al*. (1997) highlighted the difficulties in the current classification of skuas. While the Pomarine Skua (*Stercorarius pomarius*) is similar to the other *Stercorarius* species in terms of plumage, size, breeding behaviour and distribution (being a northern hemisphere species), the molecular and ectroparasite data suggested it was most closely related to the Great Skua (*Catharacta skua*). For example, all *Catharacta* skua species and the Pomarine skua share the feather louse *Saemundssonia stresemanni* which is absent in both the arctic and long-tailed skua. Furthermore, the fact that the louse subspecies *Quadraceps normifer stellaepolaris* is only present on Great and Pomarine skua provides further evidence for the close relationship between the species.

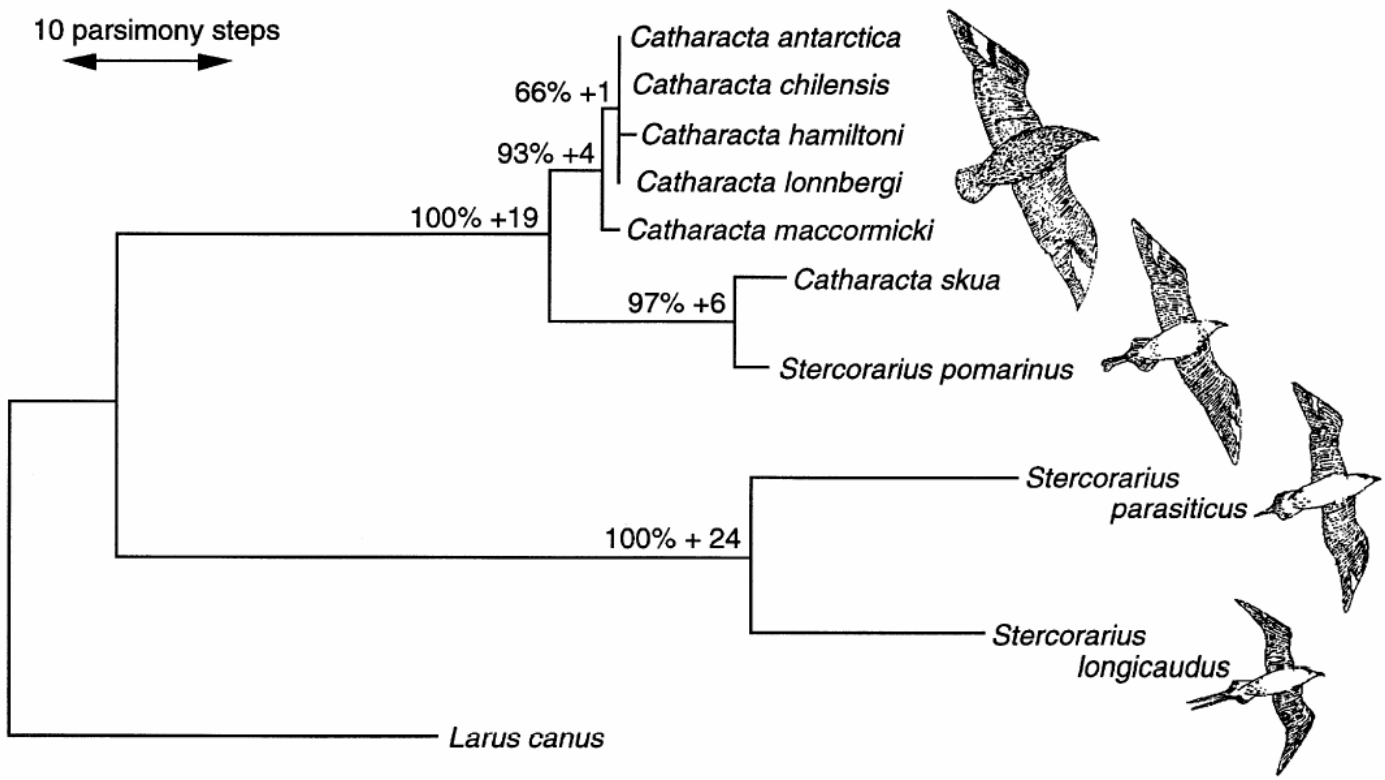

Figure 3: Skua Phylogeny from Cohen *et al.* (1997) based on molecular data

Cohen at al. (1997) explored several possible explanations for the supposed close relationship between the Great Skua and the Pomarine Skua. One possibility is that the similarity is due to ancestral polymorphism. An alternative hypothesis is that the Pomarine skua is the result of hybridization between Great Skua and a *Stercorarius* skua (possibly Arctic skua), followed by several rounds of backcrossing. The resulting individuals would have been reproductively isolated from the parental forms due to behavioural barriers (Cohen *et al*. 1997). Cohen *et al*. (1997) acknowledge the numerous assumptions and difficulties in this hypothesis, but concluded that the current evidence does not exclude this as a possible explanation for the origin of the Pomarine Skua.

They finished with the following, illustrating the inherent difficulties in resolving relationships amongst skua taxa: “The true history of this species *(Pomarine Skua)* is likely to remain enigmatic unless future morphological work sheds light on skua relationships, or new molecular work uncovers diagnostic nuclear markers or a greater variety of mitochondrial genotypes. Further work on the evolution of the Stercorarridae is desirable” (Cohen at al. 1997).

In response to Cohen *et al.* (1997), Bruan and Brumfield (1998) made the point that the conflict between morphology and molecular data is not an uncommon occurrence. They also pointed out that the conclusions drawn by Cohen *et al.* (1997) were largely based on the mitochondrial dataset. When Bruan and Brumfield (1998) reanalyzed the data, they found that there was some support for the monophyly of the *Catharacta* taxa with the Pomarine Skua the sister taxa to this group (Fig. 4).

Bruan and Brumfield (1998) discussed the need to address classification within the Skua group. The treatment of the Pomarine Skua as a member of the *Stercorarius* genus was not supported by molecular data. They suggested there are two options; (1) the single genus *Stercorarius* could be used for all skua or (2) the genera *Stercorarius* and *Catharacta* could be retained and a separate genus (*Coprotheres*) could be applied to the Pomarine Skua to recognize its distinctiveness.

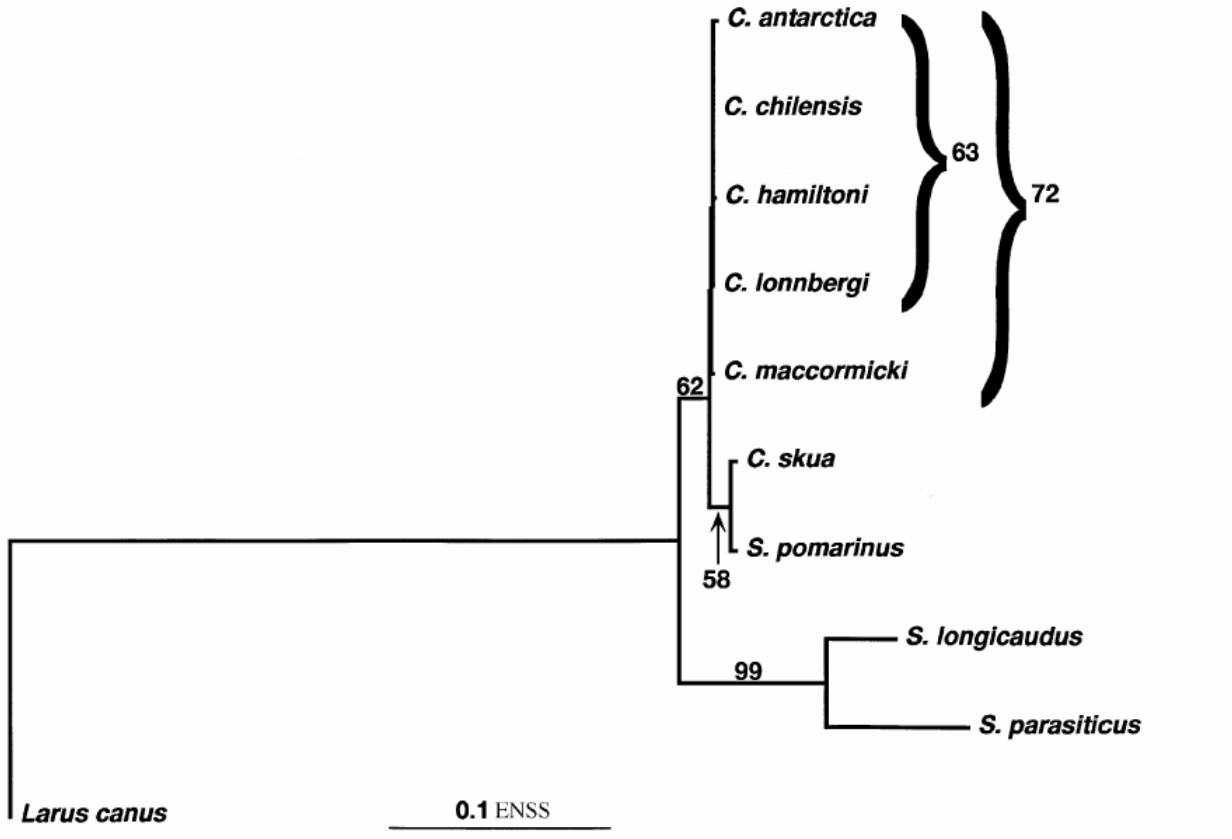

Figure 4: Skua Phylogeny Bruan and Brumfield (1998) based on re-analysis of molecular data from Cohen *et al.* 1997. Numbers at the nodes are bootstrap values indicating the level of support for the various parts of the tree.

Andersson (1999a and 1999b) focused attention once again on the issue of phylogentic relationships amongst skuas and in particular attempted to provide further clarity to the evolution of the Pomarine skua. Andersson concluded that it is highly unlikely that the close evolutionary relationship between Great skua and Pomarine skua is due to ancestral polymorphism, one of the hypotheses put forward by Cohen *et al.* (1997). Instead Andersson (1999a and 1999b) favoured the suggestion that the Pomarine skua was the result of hybridization. Andersson (1999b) concluded by making some suggestions regarding classification. Due to the overwhelming evidence, the traditional classification in which skua are divided into two genera (*Catharacta* and *Stercorarius)*, with the Pomarine skua placed within the latter, should be abandoned (Andersson 1999b). Instead, a single genus *Stercorarius* should be adopted for skua, or the Pomarine skua could be included within the *Catharacta* genus.

EVOLUTION OF THE "SOUTHERN" SKUAS

The evolution and classification of the Catharacta skuas is an equally difficult issue. The Catharacta group are largely southern hemisphere in distribution (Fig. 5). They breed predominantly on the coasts of Antarctica, sub-Antarctic islands and southern South America with only the Great Skua present in the northern hemisphere (Cohen *et al.* 1997). It is generally agreed that the Catharacta skua formed when a Stercorarius-like ancestor from the northern hemisphere founded a southern hemisphere population (Ritz *et al.* 2008, Furness 1987). During a period of geographical separation, the northern hemisphere Stercorarius and southern hemisphere Catharacta diverged (Cohen at al. 1997). The southern population spread around the Antarctic and then the sub-Antarctic region, evolving into the various forms that exist today (Ritz *et al.* 2008). At some point, one of these southern forms is thought to have re-invaded the northern hemisphere, giving rise to the Great Skua (Furness 1987). There is some suggestion that the Tristian Skua, being closest to the Atlantic Ocean, represents the most likely candidate for having made this journey to the north, founding the Great Skua population (Furness 1987).

The southern hemisphere group are very closely related and relatively poorly differentiated due to their recent radiation (Cohen at al. 1997). Of the five southern hemisphere taxa, the South Polar and the Chilean skua appear to be the most distinct (Furness 1987). The Brown Skua shows a relatively high degree of genetic structure perhaps due to its existence on a series of disconnected sub-Antarctic Islands (Ritz *et al.* 2008).

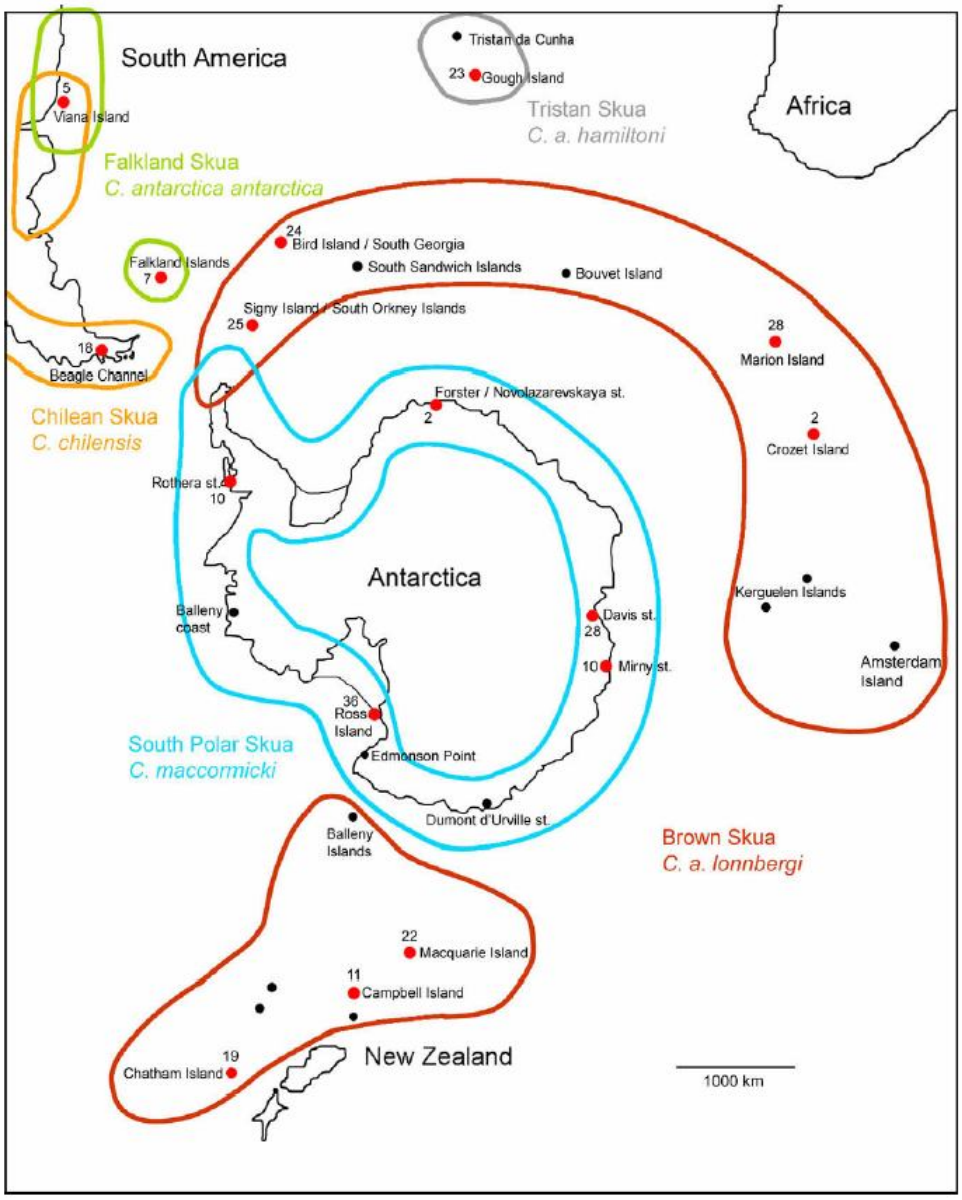

Figure 5: Map showing the distribution of the Southern Hemisphere skua taxa. From Ritz *et al.* 2008. The red dots indicate populations that were sampled for the study conducted by Ritz *et al.* 2008, while the black dots were populations not sampled but included in their analysis.

The recent radiation of the Catharacta skua appears to be only part of the reason for the lack of differentiation between taxa. Analysis of mitochondrial sequence data has revealed that there is still significant gene flow between populations of different southern taxa (Ritz *et al.* 2008). Hybridization amongst individuals of different southern taxa is relatively common and may be preventing further differentiation between taxa. For example, hybridization between Brown Skua and the South Polar Skua has been documented for more than 100 years, particularly on the Antarctic Peninsula (Ritz *et al.* 2006). In South

America, successful mating between Chilean and Falkland Skua has also been recorded (Reinhardt *et al.* 1997). Recently, the presence of hybrids from South Polar and Chilean Skuas on King George Island has been confirmed using analysis of mitochondrial DNA (Reinhardt *et al.* 1997).

The genetic similarity of the southern skuas, combined with the evidence for ongoing hybridization between taxa means making decisions regarding classification within the group difficult. The following was proposed by Sibley and Monroe (1990) on the basis of DNA-DNA hybridization (with no mention of the Tristan Skua):

Great Skua = *Catharacta skua*
Falkland Skua = *Catharacta antarctica*
Brown Skua = *Catharacta lonnbergi*
Chilean Skua = *Catharacta chilensis*
South Polar Skua = *Catharacta maccormicki*

This method of classification recognizes the differences between the species, but appears unwarranted given the recency of divergence in the group and the apparent prevalence of hybridization between taxa. It would seem more appropriate to maintain the use of *Catharacta skua* for the northern hemisphere Great Skua and use *Catharacta antarctica* for the southern species with southern taxa differentiated at the subspecies level as follows:

Great Skua = *Catharacta skua*
Falkland Skua = *Catharacta antarctica antarctica*
Tristan Skua = *Catharacta antarctica hamiltoni*
Brown Skua = *Catharacta antarctica lonnbergi*
Chilean Skua = *Catharacta antarctica chilensis*
South Polar Skua = *Catharacta antarctica maccormicki*

3. SOUTH POLAR SKUA POPULATION STUDIES

Breeding colonies of South Polar Skua in the Ross Sea region are restricted to snow and ice-free land with access to the open ocean (Harper *et al.* 1984). The first work dedicated to determining the status of the South Polar Skua in the region began in the early 1960's. All skua chicks at Cape Crozier that survived to two weeks of age were banded in order to better understand the structure of the population (Ainley *et al.* 1984). The Cape Crozier population is the largest south polar skua colony in the Antarctic (Ainley at al. 1990), with an estimated population of 1000 pairs, 500 more than the next biggest colony (Ainley *et al.* 1986). The south polar skua breeding colony at Cape Crozier is particularly large, particularly when compared to the average colony size in the region of 94 individual birds (Ainley *et al.* 1986).

The study at Cape Crozier continued from the early 1960's until 1970. More data was collected in the breeding seasons, 1974-75, 1975-76, 1980-81, 1981-82 and 1983-84. At this time the total population of South Polar Skua in the Ross Sea region was estimated at 3,900 breeding pairs. It was also determined that skuas at Cape Crozier had low fecundity but were long lived, often reaching 30-40 years of age (Ainley 1981). The age structure of the population also appeared to be rather uneven, with a predominance of older birds. For example, more than 50% of the banded adult population alive in the 1980-81 breeding season were birds born in 1962-63 (Ainley 1981). Ainley (1981) also noted that despite the existence of a fairly large and reliable food supply at the McMurdo station dump, approximately 150 km away, South Polar Skua remained at Cape Crozier and nearby areas (Ainley 1981).

Watson *et al.* (1971) produced a summary of South Polar Skua distribution in the Ross Sea Region using previous studies carried out in the area. Most of the 21 colonies identified at the time were located along the Victoria Land coast and offshore islands (Watson *et al.* 1971).

Between 1980 and 1983, ground and aerial surveys were carried out to improve understanding of skua distribution in the region (Ainley *et al.* 1986) (Fig. 6). These surveys involved ground counts at a number of locations, where the number of nests or defended territories were recorded (Ainley *et al.* 1986). Aerial surveys were also conducted, and at some sites, both methods were employed to determine the accuracy of the aerial method (Ainley *et al.* 1986).

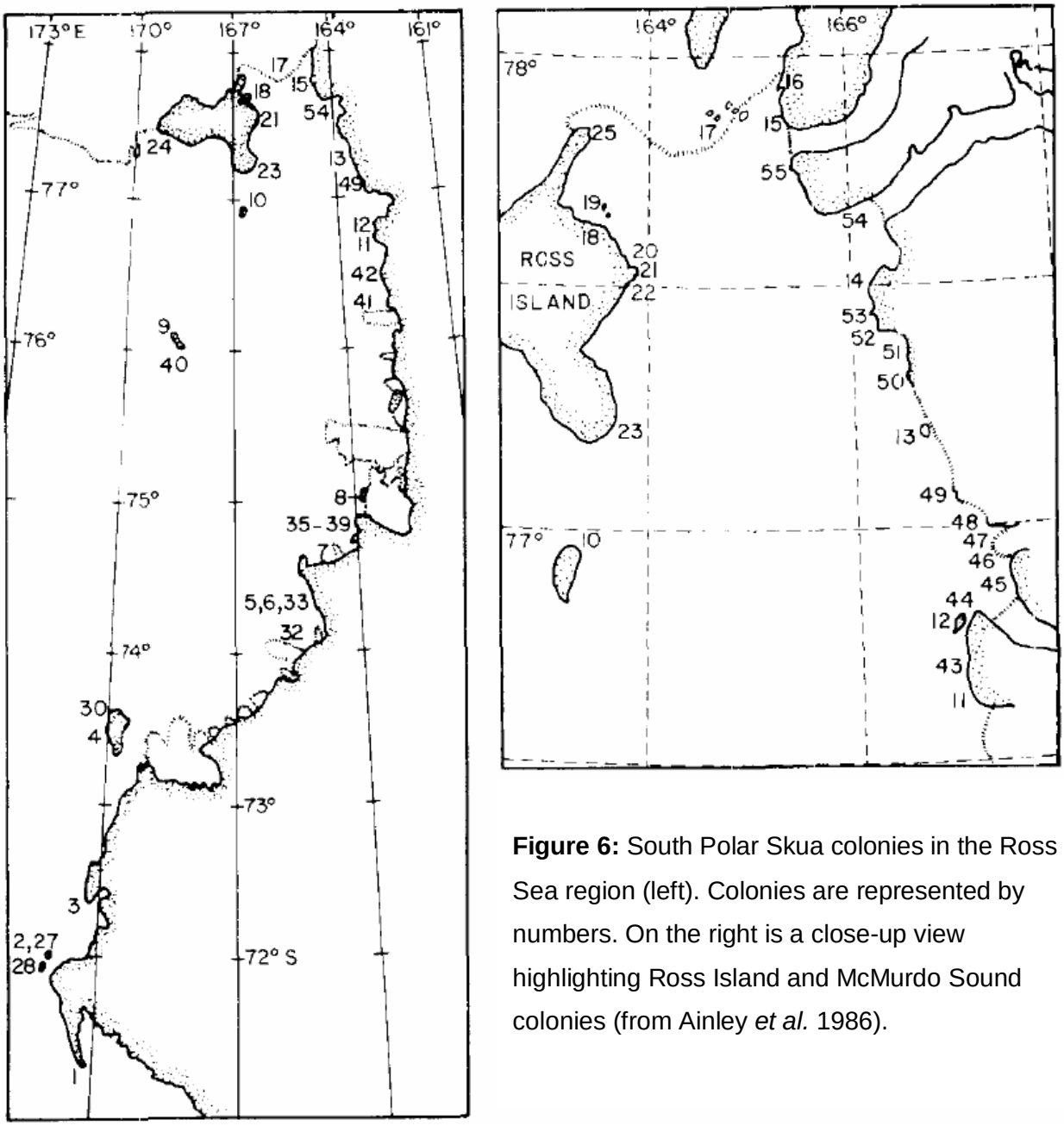

Figure 6: South Polar Skua colonies in the Ross Sea region (left). Colonies are represented by numbers. On the right is a close-up view highlighting Ross Island and McMurdo Sound colonies (from Ainley *et al.* 1986).

When population estimates at locations in the Ross Sea region were compared from year to year, it was revealed that while some populations were increasing, others were decreasing (Ainley *et al.* 1986). For example, at southern McMurdo Sound colonies, skua numbers increased in the 1960's and 1970's (Ainley *et al.* 1986). This was attributed to the presence of human refuse at McMurdo Station, a reliable source of food for skuas in the region. Evidence for this was provided by the presence of items such as bones of chicken, lamb and beef at skua sites (Ainley *et al.* 1986). Jouventin and Guillotin (1979) proposed a similar cause for the doubling of skua numbers at Pointe Geologie, Terre Adelie. In recent years, efforts have been made to improve the storage and processing of human refuse at

many Antarctic bases, and it would be interesting to see whether this has had a negative impact on South Polar Skua numbers nearby.

4. FEEDING ECOLOGY OF SOUTH POLAR SKUAS

A major misconception in relation to the feeding habits of South Polar Skua is that they are reliant on penguin colonies for food. Much of the earlier literature regarding the skuas, were “popular accounts dealing with the villainous part the bird plays with relation to the Adelie penguin, one of its prime food sources during the nesting season” (Ekland 1959). Some even suggested that without Adelie Penguins as a food source, South Polar Skua would not be able to survive in the Antarctic, reflected in the following statement by Maher (cited in Trillmich 1978): “It is probable that the skua could not maintain itself in Antarctica if it were not for the Adelie”. While it is clear that South Polar Skuas do take penguin eggs and chicks e.g. Mund and Miller 1995, the species predominantly feed on the pelagic Antarctic silverfish (*Pleuragramma antarcticum*) (Young 1994, Hemmings 1984) as well as *Electrona antarctica* (Hahn *et al.* 2008). Studying South Polar Skua at Potter Peninsula, King George Island, Hahn *et al.* (2008) found that each skua pair required approximately 140 kg of pelagic fish per breeding season, an indication of the importance of these fish in the diet of South Polar Skua. Research has also shown that skuas are not the “opportunistic feeders” they are often labeled. Instead they appear to be quite choosy in what they consume (Reinhardt *et al.* 2000).

Reinhardt *et al.* (2000) reviewed the literature relating to diet of Southern Hemisphere skuas, concluding that southern species feed on a variety of food types, as is the case for their northern hemisphere relatives. While data was lacking for some of the southern species (e.g. Chilean and Falkland Skuas), the literature clearly showed that the South Polar Skuas fed on both terrestrial colonies of seabirds (e.g. Adelie Penguins) and on pelagic fish (Reinhardt *et al.* 2000). Of interest is when and why skuas choose these food sources.

As has been mentioned previously, many of the South Polar Skua breeding localities are not in close proximity to Adelie Penguin breeding sites (Ainley *et al.* 1986a), supporting the suggestion that the species is not reliant on penguins for food. However, in cases where skuas and penguins do breed together, the diet of the skuas is often made up predominantly of penguin chicks and eggs.

At Cape Royds and Cape Bird, both locations where Adelie Penguins and South Polar Skuas breed together, only some of the breeding pairs foraged off penguins (Young and Millar 1999). These pairs were those which had territories among the penguin colony.

Other skuas were excluded from feeding on penguins and were “forced” to feed at sea (Young and Millar 1999). However, while some skuas do take penguin chicks and eggs, there is little food available for them from mid January onwards meaning skuas could only rely on penguins for food for a short period in the middle of summer (Young 1994). There is a potential advantage to feeding on penguins. During breeding seasons when sea-ice conditions are extreme or when fog or wind makes access to open ocean difficult, breeding may be limited to those skua pairs with access to penguins (Parmelee *et al.* 1978). Breeding in association with penguins also has its costs. Eggs and chicks are often lost through negligence and eggs are also lost due to attacks by penguins (Young 1994, Hagelin and Miller 1997). Frequent foraging trips into the penguin colony also increased the chances of chick predation from other skuas. “The allure of penguin food, however, appeared to encourage higher levels of territory desertion by foraging skuas, leaving chicks unprotected and exposed to skua predation” (Young and Millar 1999).

Young and Millar (1999) studied the foraging behaviour of skuas at Cape Crozier, the largest of the Ross Sea skua colonies. The relationship between South Polar Skua and the Adelie Penguin was slightly different to that described at Cape Royds and Cape Bird. At Cape Crozier, skua breeding sites were located away from the penguin colony, but most skuas could still forage throughout much of the colony. In contrast, at both Royds and Bird, only skuas with territories within the penguin colony had access to the penguins as a food supply (Young and Millar 1999). The key difference at Cape Crozier was that there were no skuas actively defending the central part of the penguin colony. At Cape Crozier, despite over 25 hours of observations of 1000 pairs of birds, there was no evidence of birds foraging out at sea (Young and Millar 1999). During the middle part of the breeding season, the large penguin colony at Cape Crozier appeared to be adequate in fulfilling the dietary requirements of the resident skua.

Obtaining food easily and relatively quickly, as appears to be the case during the middle part of the breeding season at Cape Crozier, has a direct benefit on reproductive success. It reduces the time adults need to spend away from the nest, and the resulting higher nest attendance means chicks are better protected (Young and Millar 1999, although see discussion above regarding the higher levels of desertion and the resulting skua predation). A reliable food source also means that chicks are less likely to starve, increasing the chances that they will survive to fledge. Overall breeding success is higher at Cape Crozier when compared to the other colonies studied (Royds and Bird) with more parents successfully raising two chicks (Young and Millar 1999).

Another similar study looked at foraging of South Polar Skua at Edmonson Point, Victoria Land (Pezzo *et al.* 2001). The population was similar to Cape Crozier in that the skuas were breeding in association with Adelie Penguins. However, there were some significant differences. Firstly, the number of Adelie penguins at the location was much lower (2000 breeding pairs at Edmonson Point (Pezzo *et al.* 2001) compared with 150,000 pairs at Cape Crozier (Young and Millar 1999)). Furthermore, the number of pairs of skuas also differed (101 at Edmonson Point (Pezzo *et al*. 2001) compared with 1000 pairs at Cape Crozier (Young and Millar 1999)). The ratio of skuas to penguins was therefore much higher at Edmonson Point (1:20) when compared to the ratio at Cape Crozier (1:150). Unlike Cape Crozier, where large parts of the penguin colony were undefended, skua pairs actively defended feeding territories that included penguin nests at Edmonson Point. Nesting close to penguin was clearly advantageous with those pairs defending feeding territories having higher breeding success (Pezzo *et al.* 2001). Pairs with access to penguins could also feed at sea, but the extensive ice cover in the region made this a less favourable option (Pezzo *et al.* 2001).

It is interesting to note that South Polar Skuas are also found breeding in association with seabirds other than Adelie Penguins. For example, in the eastern Larsemann Hills, the most abundant seabird species in the vicinity is the Snow Petrel *Pagodroma nivea* (Zipan and Norman 1993). Analysis of regurgitated pellets and food remains indicated that the petrels made up the vast majority of the skuas diet at the site. This provides further evidence for the fact that South Polar Skua are not reliant on Adelie Penguins as a food source and will forage on other species where they are available.

Perhaps most fascinating is the foraging behaviour of South Polar Skua when they are sympatric with Brown Skuas as is the case in a number of locations on the Antarctic Peninsula. In a study of skua near Palmer Station over two seasons (1979/80 and 1980/81), Pietz (1987) found that the diet of the two taxa differed markedly. While more than 70% of the diet of Brown Skua was made of penguin chicks and eggs, pelagic fish formed about 70% of the diet of South Polar Skua at the same site (Pietz 1987). Breeding success of Brown Skua was higher when compared to South Polar Skua, and was attributed to their ability to forage on penguin, a more predictable food supply that fish (Pietz 1987). In addition to this, feeding at sea, as was the case for South Polar Skua at the site, required more time, reducing attention at the nest. Some South Polar Skua were able to feed on penguins and these pairs fledged more chicks than those that fed primarily

at sea, providing more support for the suggestion that both species preferred to feed at the penguin colony (Pietz 1987).

Malzof and Quintana (2008) looked at the diet of Brown and South Polar Skua at Cierva Point, Antarctica Peninsula over two seasons (1992/93 and 1995/96). While they found that South Polar Skua consumed more fish than Brown Skua, for both species, fish was still the most common prey item (Malzof and Quintana 2008). It may have been that the small size of the penguin colony at the site (only about 1000 breeding pairs) was unable to meet the dietary needs of the skuas.

It appears that on the Antarctic Peninsula, where the two taxa breed in close proximity, South Polar Skua are prevented from feeding on penguins (Young 1994). In some situations (e.g. Pietz 1987), data regarding breeding success suggests that penguins represent the most desirable food type. South Polar Skua appear to be outcompeted by the larger and more aggressive Brown Skua, who can therefore monopolize the penguin colony as a food source (Pietz 1987).

Foraging of South Polar Skuas appears to be affected by a number of factors. The presence of South Polar Skuas with Adelie Penguin colonies appears to be largely due to the common need for ice and snow free ground for breeding (Young 1963b). When these penguin colonies are large enough, they represent a reliable food source for part of the breeding season. This seems to be particularly true in locations where the sea ice makes access to open water difficult, and weather conditions make foraging trips difficult. However, in many locations (e.g. those without penguin colonies or other seabirds), pelagic fish make up the majority of the diet of South Polar Skua. This is also the case where South Polar Skua breed sympatrically with Brown Skua, and in association with penguin colonies. In these locations, South Polar Skua are largely excluded from feeding within the penguin colonies and instead forage at sea. At these sites, breeding success of South Polar Skua pairs is often lower, a result of their inability to utilize the reliable penguin food supply.

5. SIBLING AGGRESSION AND SIBLICIDE IN SOUTH POLAR SKUAS

Like all other skua species, South Polar Skuas usually lay two eggs (Furness 1987) with eggs laid one to four days apart (Spellerberg 1971a). First eggs are normally marginally larger than second laid eggs (Wang and Norman 1993) with eggs incubated by both parents (Spellerberg 1971b) for an average of 29.5 days before hatching (Reid 1966). The two eggs normally hatch a few days apart and due to the hatching asynchrony, there is normally a significant difference in weight and the stage of development of the two chicks once the second hatches (Furness 1987). While it is possible for two chicks to be raised to fledging (Young and Millar 2003), in many cases the second chick does not survive (Furness 1987). Aggression shown by the chick hatching first has been shown to be a primary reason for the death of younger chicks, a phenomenon termed ‘siblicide’.

Siblicide has been observed in a number of other birds including pelicans, boobies, gannets, eagles, egrets and kittiwakes (Gerhardt *et al.* 1997). However, while siblicide appears to be relatively widespread in the South Polar Skua (Young and Millar 2003), it is largely undocumented in other skua taxa (although it has been recently documented in the Brown Skua (Capuska *et al*. 2008)). Despite siblicide being observed in South Polar Skuas across the range of the species, the rate at which it occurs appears to vary.

In other bird species in which siblicide has been described, the chicks are confined to the nest. In South Polar Skuas, this is not the case, with chicks evicted from the nest able to survive (Young and Millar 2003). Young and Millar studied South Polar Skua siblicide at Cape Crozier during the 1993/94 breeding season. In this study, 69 nests were monitored, all of which contained two eggs. Nests were regularly checked, with chicks weighed, growth rates determined and observations of behaviour made from hides (Young and Millar 2003).

In 49 of the 69 nests, two chicks were hatched, with 18 of these pairs of chicks surviving to fledge (Young and Millar 2003). In 27 nests, only a single chick survived with 26 of these chicks being the first hatched of the two. In many cases, aggression shown by the chick hatching first was seen as the major cause of death in the younger chicks.

Despite the fact that second eggs laid by South Polar Skua are often smaller than first laid (Furness 1987), there was no significant difference in chick weight at the time of hatching. However, due to the fact that second chicks hatched between 1.5 and 3.5 days later than

first chicks, there was a significant difference in weight by the time the second chick hatched (Young and Millar 2003). For example, the average weight of first chicks was 102.3 grams, 30 grams more than second chicks by the time the younger chick hatched (Young and Millar 2003).

During the study, 14 cases of older chicks attacking their younger siblings were observed. The older chicks attacked their siblings soon after they hatched and attacks always occurred relatively close to the parents (Young and Millar 2003). Attacks were generally very aggressive, with the attacker continuing until the younger chick escaped, or one of the parent birds intervened. Younger chicks appeared unable to fight back, opting instead to crouch and endure the attack or attempt to escape (Young and Millar 2003). “The participants are so unequal that there is little if any fighting: there is only an attack by the first chick on the more or less unresisting second” (Young and Millar 2003). In one case, an attack was observed in which the two chicks ran a circular course around the territory covering over 40 metres (Young and Millar 2003). In some cases, parents intervened in attacks, attempting to end the aggression by feeding chicks, charging their offspring or brooding them. However, in the long term, parental intervention appeared to be unable to prevent continued attacks on their younger offspring.

Younger chicks were not killed during the aggressive encounters. However, 12 of the 26 second hatched chicks that did not survive to fledging, were observed being chased from their nests or were subsequently seen at locations away from their original nest site (Young and Millar 2003). Most of these chicks appear unable to survive, being either attacked and eaten by other skuas or dying of starvation (Millar, Lambert and Young 1997). However, in one case, a chick was observed surviving for 20 days after expulsion, before being killed by a predator (Young and Millar 2003). Three second hatched chicks were also successfully adopted by other breeding pairs, with one of these subsequently displacing an egg in the nest and then the younger chick (Young and Millar 2003). Using DNA minisatellites, Millar, Lambert and Young (1997), detected a possible case of adoption in South Polar Skua.

Despite a good understanding of how and where siblicide occurs there is still a lack of understanding as to why the behaviour occurs. While siblicide was observed in the Cape Crozier colony, in 37% of two chick broods, no siblicide occurred with both chicks surviving to fledge. The question of why siblicide occurs in some broods but not in others remains unanswered. Young and Millar (2003) concluded that the degree of hatch asynchrony was

not an important factor in terms of whether or not siblicide occurred. Because of the time between hatching of first and second chicks, older chicks were always at an advantage even if the gap between hatching was minimal. The difference in weight of the two chicks also failed to explain the occurrence of siblicide (Proctor 1975), with broods in which siblicide occurred no different in terms of mass difference to broods in which both chicks survived (Young and Millar 2003).

Rates of siblicide have been shown to vary across the range of South Polar Skuas. On Ross Island, the incidence of siblicide and its subsequent impact were lower at Cape Crozier than at colonies at Cape Royds and Cape Bird (Young and Millar 2003). This is illustrated by the number of pairs raising two chicks, with 38.6% of pairs doing so at Cape Crozier compared to very low numbers at Cape Royds and almost none at Cape Bird (Young and Millar 2003). The key difference in these colonies is the way food is obtained during the time that skua chicks are raised. At Cape Crozier (as discussed previously), the skua colony is supported by a large Adelie Penguin colony (Young and Millar 1999). Due to the size of the colony, all skuas appear to have access to the central part of the penguin colony, providing adult skuas with a reliable source of food for offspring. A similar situation occurs at Magnetic Island, where the skuas have access to a relatively large penguin colony, and low levels of sibling aggression are observed (Hull *et al.* 1994). In contrast, only some skua pairs at Cape Bird and Cape Royds have access to penguins, holding territories including pairs of breeding penguins (Young and Millar 1999). Skuas without easy access to penguins have to resort to feeding at sea, an approach that takes more time, is less reliable and reduces time at the nest.

While the availability of food appears to help explain why rates of siblicide are lower at Cape Crozier when compared to Cape Bird and Cape Royds, the question remains as to why siblicide is observed in some broods and not in others. Young and Millar (2003) suggest several possibilities that warrant further work in an attempt to better understand this behaviour in South Polar Skuas.

Firstly, it would be interesting to investigate whether or not the make-up of two chicks broods in terms of sex has an impact on the incidence of siblicide. Frank *et al.* (1991) found that siblicide in spotted hyenas was most common in same-sex litters, with both siblings in mixed-sex litters surviving. Molecular work carried out on samples from Brown Skuas from the Chatham Islands revealed that there was an unbiased hatching sex ratio and equal numbers of sex combinations in a sample of two-chick broods (cited in Young

and Millar 2003). Despite this, it would still be worthwhile to investigate whether or not there is any link between the sex makeup of broods and the incidence of siblicide. Another area of potential research focuses on the “quality” of parents. While most of the focus of siblicide studies has been on the chicks, the quality of the parents may have an impact. It may be that younger, less experienced parents are unable to forage efficiently and this leads to siblicide in offspring. It has been suggested that the factor that most affects breeding success is breeding age with a significant increase in breeding success up to a certain age (Reinhardt 1997). At Cape Crozier, where a relatively high proportion of pairs raise two chicks, it would be interesting to determine the factors that lead to higher breeding success as these may shed further light on why siblicide occurs in broods of less successful pairs.

While many questions remain, siblicide does seem to be facultative, varying in the rate at which it occurs. As with spotted hyenas (Smale *et al.* 1999), siblicide in South Polar Skua appears to largely occur when resources are insufficient to successfully raise two offspring.

6. FUTURE DIRECTIONS IN SOUTH POLAR SKUA RESEARCH

POPULATION GENETICS OF ROSS SEA SOUTH POLAR SKUA

Previous work has shown that South Polar Skuas tend to breed at the same colony, in the same territory and often in the same nest scoop each season (Wood 1971). This would suggest that there would be a high degree of genetic structuring within the Ross Sea region. While Ritz *et al.* (2008) looked at phylogeography of the southern skua complex, a more detailed investigation of population genetics within the South Polar Skua would be interesting. Use of hypervariable control region sequences (as used in Ritz *et al.* 2008) and polymorphic microsatellites (e.g. Tirard *et al.* 2002) could be used on South Polar Skua samples from throughout the Ross Sea to determine the degree of genetic structuring in the region. This would shed further light on the amount of gene flow that exists between the various colonies within the Ross Sea.

SYSTEMATICS

More work will no doubt be carried out in an attempt to clarify relationships amongst the various skua taxa. Of particular interest is the classification of the Pomarine Skua (as detailed above). However, it appears that like other groups of closely related taxa, such as the Herring Gull complex (Liebers *et al.* 2004), classification will continue to be difficult due to regency of divergence and relatively frequent hybridization between taxa. It would be helpful if agreement could be made as to the most appropriate names to use for the various skua taxa. For example, the use of both *Catharacta maccormicki* (e.g. Ritz *et al.* 2006) and *Stercorarius maccormicki* (Ritz 2007) as names for the South Polar skua is confusing.

HYBRIDIZATION

The issue of hybridization in the South Polar Skua is one that merits further work. There have been a number of studies describing the phenomenon, particularly on the Antarctic Peninsula where the species interbreeds on occasion with Brown Skua (e.g Ritz *et al.* 2006, Reinhardt *et al.* 1997). Large scale sequencing of mitochondrial DNA (e.g. control region) from Brown Skua and South Polar Skua in these hybrid zones as well as genotyping using fast-evolving markers (e.g. microsatellites) would shed light on how prominent hybridization is in these regions. Sequencing and genotyping of Red-billed Gulls

(*Larus novaeholladiae scopulinus)* and Black-Billed Gulls (*Larus bulleri*) in New Zealand revealed relatively high levels of hybridization, despite limited evidence from field studies (AD Given and AJ Baker, unpublished data).

SIBLICIDE

While there has been dedicated research into the issue of siblicide in South Polar Skua (e.g. Young and Millar 2003), understanding of the phenomenon is still not complete. Young (2007) stated that it is an issue that "has to be looked at again" and that it was something on which he had been "so wrong, so often". Improving our understanding of South Polar Skua siblicide will require intensive observations of chicks in the nest, but can be assisted by the use of cameras to record multiple nests in a single season. As discussed earlier, the question of why siblicide occurs in some nests and not in others remains unanswered. Utilizing molecular tools (see above) the effect of the sex of chicks on siblicide could also be investigated. Another potential area of interest would be investigating the impact of parental quality on siblicide. Do "high quality" parents who are able to adequately provide for two offspring reduce the probability of siblicide within their brood?

THE START AND THE END OF THE BREEDING SEASON

We now have a good understanding of many aspects of the breeding biology of South Polar Skua. However, the majority of this knowledge pertains to what occurs after birds have established themselves early on in the season. Little is known about what goes on at the start and the end of the breeding seasons (Young 2007). South Polar Skuas breeding at Ross Island arrive in the McMurdo Sound area during October and disperse towards the middle of March (Spellerberg 1969). When the timing of South Polar Skua studies in the Ross Sea Region is considered (Fig. 7), it is clear that little research in the region corresponds to the very early and the very late stages of the skua breeding season. The window of opportunity for research in the Antarctic field is limited, with access to field sites determined by sea ice and general climatic conditions. However, South Polar Skua field research at some of the Ross Island colonies early in the season could improve understanding of how the breeding season commences. For example, it is not clear how skuas establish their feeding territories, associated with breeding Adelie Penguins. Similarly, research late in the breeding season (e.g. February/March) would shed light on

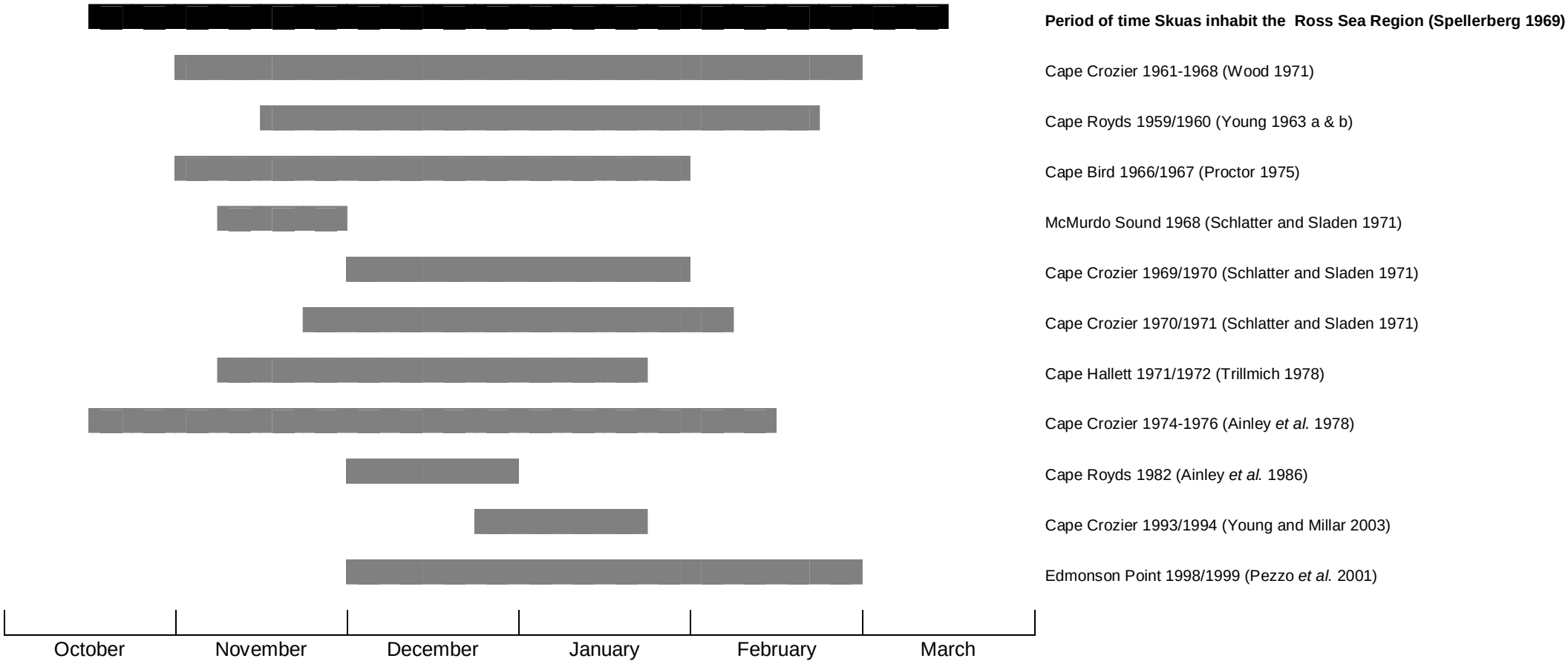

Figure 7: Graph showing the time in the breeding season research has been carried out on South Polar Skua in the Ross Sea region. The figure was limited to publications which stated the time research was conducted within the season. Many research activity was excluded because the publication simply stated “during the austral summer” or “during the breeding season”. Shown in black at the top of the figure is the approximate time during which South Polar Skuas inhabit the Ross Sea region (from Spellerberg 1969).

what happens at the end of the season. It is well established that once Adelie Penguin chicks are large enough, they are able to defend themselves and cease to be a reliable source of food for South Polar Skuas. Research at the end of the season would allow a better understanding of how foraging changes at colonies that are reliant on penguins during the middle of the season. How skuas leave the breeding areas (i.e. do chicks leave first?) would also only be answered by dedicated study during the latter months.

OTHER AREAS OF RESEARCH OPPORTUNITY

Young (2007) highlighted several other areas of potential research focused on South Polar Skuas. He pointed out that very little work has been carried out on the physiology of the species. There is also a lack of knowledge regarding the migration of South Polar Skuas, who every year migrate to the Northern Hemisphere during the austral winter. The way South Polar Skuas forage at sea is also poorly understood. It is well established that the species feeds predominantly on the pelagic Antarctic silverfish (*Pleuragramma antarcticum*) when foraging at sea (Young 1994, Hemmings 1984). However, how the birds are able to obtain the large quantities of this fish species, which is not found near the surface of the sea, is a mystery (Young 2007).

THE FUTURE

Despite the efforts of names such as Young, Spellerberg and Ainley, the South Polar Skua represents a species which has received little attention in terms of research when compared to some other species in the region. The lack of knowledge regarding the species can not simply be attributed to the harsh climate that skuas inhabit. The volume of research carried out on South Polar Skua pales into insignificance when compared to the research carried out on Adelie Penguins. Searches were made of three publication databases (Scopus, Web of Science and the Antarctic New Zealand database) for literature on South Polar Skuas and Adelie Penguins. In all three databases, approximately 80% of the literature obtained related to Adelie Penguins, meaning there were approximately four papers on Adelie Penguins for every paper published on South Polar Skuas (Fig. 8). One of the major weaknesses of current scientific endeavors in the Antarctic is the lack of opportunity for long-term population studies. The large body of knowledge regarding the Great Skua (*Catharacta skua*) is largely due to the more than 25 year of research carried out by Bob Furness at Foula, Shetland (e.g. Furness 1987). Perhaps the best way to improve our understanding of South Polar Skuas is to initiate and

commit to long term studies of the species, something which appears unlikely given the challenges in securing funding for multi-season science.

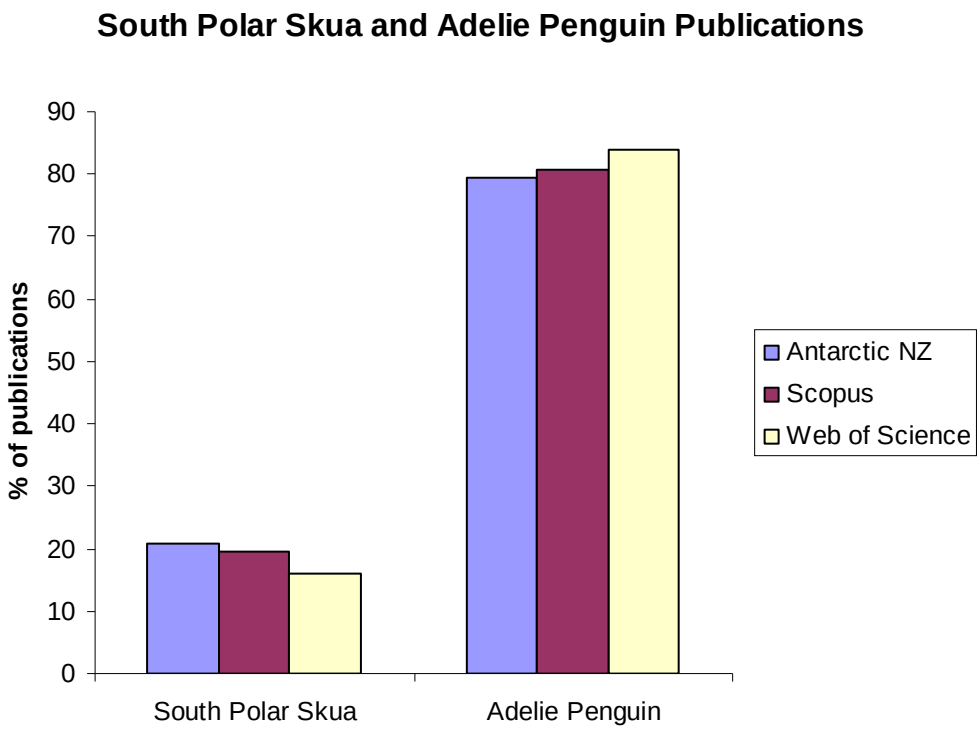

Figure 8: Graph showing the relative number of publications relating to research on South Polar Skuas (left) and Adelie Penguins (right). Three independent publication databases were searched (Antarctic New Zealand, Scopus and Web of Science).

7. CONCLUSION

The South Polar Skua is a fascinating seabird with an interesting reputation. While research has improved our understanding of this species in terms of its distribution, foraging and breeding biology, many questions remain. More research is required, particularly long-term studies, to better understand one of Antarctica's most enigmatic species.

8. ACKNOWLEDGEMENTS

Thank you to Euan Young for his supervision with this project and to Michelle Rogan-Finnemore for advice and guidance.

9. REFERENCES

Ainley, DG, Ribic, CA and Wood, RC (1990) A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. *Journal of Animal Ecology,* vol. 59, pp. 1-20.

Ainley, DG, Morrell, SH and Wood, RC (1986) South polar skua breeding colonies in the Ross Sea region, Antarctica. *Notornis,* vol. 33, pp. 155-163.

Ainley, DG, Spear, LB and Wood, RC (1985) Sexual color and size variation in the south polar skua. *Condor,* vol. 87, no. 427-428.

Ainley, DG, Ribic, CA and Wood, RC (1984) Population studies of the South Polar Skua. *Antarctic Journal of the United States*. Vol. 19. no. 5, pp. 167-168.

Ainley, DG (1981) Population studies of the South Polar Skua. *Antarctic Journal of the United States*. Vol. 16. no. 5, pp. 148.

Ainley, DG, Wood, RC and Sladen WJL (1978) Bird life at Cape Crozier, Ross Island. *Wilson Bulletin,* vol. 90, pp. 492-510.

Andersson, M (1999a) Hybridization and skua phylogeny. *Proceedings of the Royal Society of London, Series B.,* vol 266, pp. 1579-1585.

Andersson, M (1999b) Phylogeny, behaviour, plumage evolution and neotony in skuas Stercorariidae. *Journal of Avian Biology,* vol. 30, pp. 205-215.

Braun, MJ and Brumfield, RT (1998) Enigmatic phylogeny of skuas: an alternative hypothesis. *Proceedings of the Royal Society of London, Series B.,* vol 265, pp. 995-999.

Capuska, GM, Russo, P, Copello, S and Casaux, R. (2008). First observation of siblicide in brown skua (*Catharacta lonnbergi*) at Harmony Point, Nelson Island, Antarctica. *Notornis,* vol. 55, no. 1, pp. 43-44.

Catry, P, Phillips, RA and Furness, RW (1999) Evolution of reversed sexual size dimorphism in Skuas and Jaegers, *The Auk,* vol. 116, no. 1, pp. 158-168.

Catry, P, Ratcliffe, N and Furness, RW (1997) Partnerships and mechanisms of divorce in Great Skua, *Animal Behaviour,* vol. 54, pp. 1475-1482.

Cohen, BL, Baker, AJ, Blechschmidt, K, Dittmann, DL, Furness, RW, Gerwin, JA, Helbig, AJ, De Korte, J, Marshall, HD, Palma, RL, Peter, H-U, Ramli, R, Siebold, I, Willcox, MS, Wilson, RH and Zink RM (1997) Enigmatic phylogeny of skuas (Aves: Stercorariidae). *Proceedings of the Royal Society of London, Series B.,* vol 264, pp. 181-190.

Eklund, CR (1961) Distribution and life history studies of the South-Polar Skua. *Bird Banding*. Vol. 32, pp. 187-233.

Frank, LG, Glickman, SE and Licht, P (1991) Fatal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. *Science.* vol. 252, issue 5006, pp. 702-704.

Gerhardt, RP, Gerhardt, DM and Vasquez, MA (1997) Siblicide in swallow-tailed kites. *Willson Bulletin,* vol. 109, no. 1, pp. 112-120.

Hagelin, JC and Miller, GD (1997) Nest-site selection in South Polar Skuas: Balancing nest safety and access to resources. *The Auk.* Vol. 114, no. 4, pp. 638-645.

Hahn, S, Ritz, MS and Reinhardt, K (2008) Marine foraging and annual fish consumption of a South Polar skua population in the maritime Antarctic. *Polar Biology,* vol. 31, no. 8, pp. 959-969.

Harper, PC, Knox, GA, Spurr, EB, Taylor, RH, Wilson, GJ and Young, EC (1984) The status and conservation of birds in the Ross Sea sector of Antarctica. In *Status and Conservation of the World's Seabirds.* Ed. Croxall, JP, Evans, PGH and Screiber, RW, pp. 593-608. Cambridge, UK.

Hemmings, AD (1984) Aspects of the breeding biology of McCormick's Skua *Catharacta maccormicki* at Signey Island, South Orkney Islands. *British Antarctic Survey Bulletin,* no. 65, pp. 65-79.

Hull, C, Carter, R and Whitehead, MD (1994) Aspects of breeding chronology and success of the Antarctic skua *Catharacta maccormicki* at Magnetic Island, Prydz Bay, Antarctica. *Corella,* vol. 18, no. 2, pp. 37-40.

Liebers, D, de Knijff, P and Helbig, J (2004). The herring gull complex is not a ring species. *Proceedings of the Royal Society of London, Series B.,* vol 271, pp. 893-901.

McGarry, R (1988) Survey of McCormick Skua colonies in Southern McMurdo Sound. *Antarctic Record,* vol. 8, pp. 5-10.

Miller, CD, Lambert, DM and Young EC (1997) Minisatellite DNA detects sex, parentage and adoption in the South Polar Skua. *Journal of Heredity*, vol. 88, pp. 235-238.

Mund, MJ and Miller, GD (1995) Diet of the south polar skua *Catharacta maccormicki* at Cape Bird. Ross Island, Antarctica. *Polar Biology,* vol. 15, no. 453-455.

Norman, FI and Ward, SJ (1990) Foods of the South Polar Skua at Hop Island, Rauer Group, East Antarctica. *Polar Biology,* vol. 10, pp. 489-493.

Parmelee, DF, Bernstein N and Neilson, DR (1978) Impact of unfavourable ice conditions on bird productivity at Palmer Station during the 1977-1978 field season. *Antarctic Journal of the United States,* vol. 13, pp. 146-147.

Peter, H-U, Kaiser, M and Gebauer, A (1990) Ecological and morphological investigations on South Polar SKuas (*Catharacta maccormicki*) and Brown Skuas (*Catharacta skua lonnbergi*) on Fildes Peninsula, King George Island, South Shetland Islands. Zoologische Jahrbuecher Abteilung Für Systematik Oekologie und Geographie der Tiere, vol. 117, pp. 201-218.

Pezzo, F, Olmastroni, S, Corsolini, S and Focardi, S (2001) Factors affecting the breeding success of the south polar skua *Catharacta maccormicki* at Edmonson Point, Victoria Land, Antarctica. *Polar Biology,* vol. 24, pp. 389-393.

Pietz, PJ (1987) Feeding and nesting ecology of sympatric South Polar and Brown Skuas. *The Auk,* vol. 104, pp. 617-627.

Proctor, DLC (1975) The problem of chick loss in the South Polar Skua *Catharacta maccormicki. Ibis,* vol. 117, no. 452-459.

Reid, BE (1966) The growth and development of the South Polar Skua (*Catharacta maccormicki*). *Notornis,* vol. 13, pp. 71-89.

Reinhardt, K (1997) Breeding success of Southern Hemisphere skuas *Catharacta* spp.: The influence of latitude. *Ardea,* vol. 85, no. 1, pp. 73-82.

Reinhardt, K, Hahn, S, Peter, H-U and Wemhoff, H (2000) A review of the diets of Southern Hemisphere skuas. *Marine Ornithology,* vol. 28, pp. 7-19.

Reinhardt, K, Blechschmidt, K, Peter, H-U and Montalti, D (1997) A hirthero unknown hybridization between Chilean and South Polar skua. *Polar Biology*, vol. 17, pp. 114-118.

Ritz, MS, Millar, C, Miller, GD, Phillips, RA, Ryan, P, Sternkopf, V, Liebers-Helbig, D and Peter, H-U. (2008) Phylogeography of the southern skua complex – rapid colonization of the southern hemisphere during a glacial period and reticulate evolution. *Molecular Phylogenetics and Evolution,* vol. 49, pp. 292-303.

Ritz, MS, Hahn, S, Janicke, T and Peter, H-U (2006) Hybridisation between South polar skua (*Catharacta maccormicki*) and Brown skua (*C. Antarctica lonnbergi*) in the Antarctic Peninsula region. *Polar Biology*, vol. 29, pp. 153-159.

Schlatter, RP and Sladen, WJL (1971) Nonbreeding South Polar Skuas: studies at Cape Crozier, 1969-1971. *Antarctic Journal,* vol. 6, pp. 103-104.

Sibley, CG and Monroe, BL (1990) *Distribution and Taxonomy of the Birds of the World.* New Haven, Connecticut: Yale University Press.

Smale, L, Holekamp, KE and White, PA (1999) Siblicide revisited in the spotted hyaena: does it conform to obligate or facultative models? *Animal Behaviour,* vol. 58, no. 3, pp. 545-551.

Spellerberg, IF (1969) Incubation temperatures and thermoregulation in the McCormick Skua. *The Condor,* vol. 71, no. 1, pp. 59-67.

Spellerberg, IF (1971a) Aspects of McCormick Skua breeding biology. *Ibis.* Vol. 113, pp. 357-363.

Spellerberg IF (1971b) Breeding behaviour of the McCormick Skua *Catharacta maccormicki* in Antarctica. *Ardea,* vol. 59, no. 189-227.

Tirard, C, Helfenstein, F and Danchin, E (2002) Polymorphic microsatellites in the black-legged kittiwake *Rissa tridactyla. Molecular Ecology Notes,* vol. 2, pp. 431-433.

Trillmich, F (1978) Feeding territories and breeding success of South Polar Skuas. *The Auk,* vol. 95, pp. 23-33.

Wang, Z and Norman FI (1993) Timing of breeding, breeding success and chick growth in South Polar Skuas (*Catharacta maccormicki*) in the Eastern Larsemann Hills, Princess Elizabeth Land, East Antarctica. *Notornis*, vol. 40, pp. 189-203.

Wood, RC (1971) Population dynamics of breeding South Polar Skuas of unknown age, *Auk,* vol. 88, no. 4, pp. 805-814.

Young EC (2008) Great Skuas. *New Zealand Geographic.* vol 89, pp. 82-95.

Young, EC (2007) Skua Research. In *Antarctica: 50 years on the ice – just the tip of the iceberg.* 2nd – 6th July 2007, Wellington, New Zealand, Antarctic New Zealand.

Young, EC and Millar, CD (2003) Siblicidal brood reduction in South Polar Skuas. *New Zealand Journal Of Zoology,* vol. 30, pp. 79-93.

Young, EC and Millar, CD (1999) Skua (*Catharacta* sp.) foraging behaviour at the Cape Crozier Adelie Penguin (*Pygoscelis adelia*) colony, Ross Island, Antarctica, and implications for breeding. *Notornis,* vol. 46, pp. 287-297.

Young, EC (1999) *The Millennium Bird: Cooperative breeding in Chatham Island skuas*. Witherlea Press, Blenheim.

Young, EC (1963a) The breeding behaviour of the South Polar Skua. *Ibis,* vol 105, pp. 203-233.

Young, EC (1963b) Feeding habits of the South Polar Skua *Catharacta maccormicki. Ibis,* vol 105, pp. 301-318.

Zipan, W and Norman FI (1993) Foods of the South Polar Skua *Catharacta maccormicki* in the eastern Larsemann Hills, Princess Elizabeth Land, East Antarctica. *Polar Biology*, vol. 13, pp. 255-262.