

Siblicidal brood reduction in South Polar Skuas

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Abstract Siblicide in the South Polar Skua (*Catharacta maccormicki*) was studied at Cape Crozier, Ross Island, Antarctica during the 1993/94 austral summer. Sixty-six two-egg nests were monitored, providing 49 two-chick broods for study. Eighteen pairs of chicks (37% of broods) were raised. Single chicks survived in 27 nests, of which 26 were first chicks. Only three second chicks outlived firsts in the same brood, of which only one survived to at least 20 days.

Attacks began within the first days of the second chick hatching. Second chicks were lost or evicted from the nest area on average 3.05 ± 0.5 days (mean \pm SE) after hatching. Although first and second chicks had almost identical body masses at hatching (68.3 ± 4.7 g versus 69.9 ± 5.6 g), first chicks weighed 102.3 ± 4.2 g when the second hatched. At the peak of attacks at 48 h after the second hatched, first chicks weighed 146.5 ± 4.7 g on average and seconds only 83.3 ± 1.8 g. Between-brood differences in mass and age of chicks in different broods had minimal influence on either the intensity of sibling aggression or its outcome. First chick aggression towards the second persisted for at least 3 weeks in broods kept separately in enclosures at the nest.

All attacks began near the nest, usually at chick feeding. Parents intervened in a high proportion of attacks, invariably in pecking attacks, but did not halt them in the longer term. Twelve of 26 second chicks survived for a time elsewhere on the territory or were

adopted by neighbours after being evicted from the nest area. Brood reduction through siblicide in this species is a two-phase process: eviction from the nest area, followed by death from predation, exposure or starvation.

A review of the literature showed that varying levels of siblicide occur throughout the entire breeding range of the South Polar Skua, and, except for some possible records for the Brown Skua, is uniquely confined to this species within the Stercorariidae. We concluded that brood reduction through siblicide is facultative, its intensity in each population each season determined by local foraging conditions.

Keywords South Polar Skua; *Catharacta maccormicki*; siblicide; Antarctica; Ross Island; Cape Crozier; brood reduction; breeding behaviour; breeding success

INTRODUCTION

Brood reduction through siblicide (fatal sibling aggression) (Mock 1994; Mock & Parker 1997; Drummond 2001b) is common in birds. It is, however, largely confined to just five families, the Acciptridae, Pelecanidae, Sulidae, Gruidae, and Strigidae (reviews in O'Connor 1978; Stinson 1979; Cooper 1980; Mock 1984; Anderson 1990) although there are occasional examples in others. Within the Stercorariidae, siblicide is widespread in the South Polar Skua (*Catharacta maccormicki*) (Young 1963b; Spellerberg 1971b) and possible within Brown Skua (*C. lonnbergi*) (Williams 1980; Bruemmer 1993) but apparently absent from other taxa (Furness 1987).

In almost all siblicidal species the chicks are nidicolous (confined to the nest) so that the younger chicks are unable to escape from sibling attacks, and any chick evicted from the nest bowl is certain to die through starvation or predation. Siblicide in the South Polar Skua is exceptional in that the chicks are nidifigous and semi-precocial, not bound to the nest, so that the younger chick can escape from its older

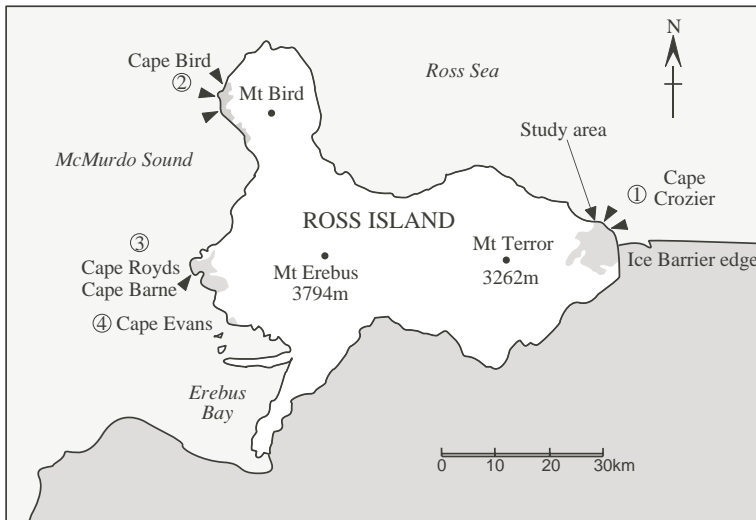


Fig. 1 The skua breeding areas and location of the study site on Ross Island. Shading indicates patches of ice-free ground with skua colonies. The locations of the Adélie Penguin colonies are shown by arrows. Circled numbers identify local breeding concentrations of South Pole Skuas (Table 1 and text).

sibling. The responses of the parents and of adults of neighbouring territories are critical for the survival of the evicted chick. Unusually for siblicidal species, chicks from different pairs can meet and fight for dominance after a chick evicted from its own nest is adopted in another. There are thus two types of chick fighting in this species: between the siblings of a brood, and between unrelated chicks from different broods.

The Ross Island skua colonies (Fig. 1) have attracted most of the research on skua siblicide, and provide data for comparing skua siblicide under different breeding conditions. Skua behaviour and breeding biology have been investigated at Cape Royds by Wilson (1907), Young (1963 a,b), and Spellerberg (1971a,b); at Cape Bird by Williams (1969), Young (1972, 1994), Procter (1975), Ensor (1979), Miller (1992), and Hagelin & Miller (1997); and at Cape Crozier by Wood (1971), Schlatter (1972), Müller-Schwarze & Müller-Schwarze (1973, 1977), Ainley et al. (1990), and Young & Millar (1999). There has not so far been any study (other than aerial surveys) of the skua colonies to the south of the Cape Royds/Cape Barne area (Ainley et al. 1986). All of the skuas breeding in these southernmost colonies are entirely dependent on foraging at sea and their behaviour would provide an interesting comparison with those breeding near penguins.

The skuas on Ross Island comprise a single interbreeding population (Ainley et al. 1990) even though the individual breeding colonies are well separated around the island's perimeter. There are

four local breeding concentrations, three on the western side overlooking McMurdo Sound and one at Cape Crozier fronting directly onto the Ross Sea (Fig. 1). The distance between the colonies at Cape Evans and Cape Royds is 10 km, between Cape Royds and Cape Bird 30 km, and between Cape Bird and Cape Crozier 65 km. The colonies are separated by ice and snow fields. In all colonies nesting is concentrated within basins and along the sandy and stony beaches. There are very few breeding birds on the broad, exposed slopes of the mountain flanks.

South Polar Skuas are strongly territorial, defending areas ranging between 100 m² (where nesting is concentrated) to over 10 000 m² (on the outskirts of colonies) (Williams 1969). Nests are located anywhere within the territories, preferably where ridges or rocky ground give protection from blowing snow and grit, and (for territories near penguin colonies), from the penguins moving to and from the sea (Hagelin & Miller 1997). The nests are mere scoops in the gravel or sand, with no nest lining. Nest separation is an important factor in breeding success, as egg and chick predation by conspecifics is lower where the nests are widely separated (Williams 1969). Conversely, chicks expelled from a nest have more chance of reaching another and being adopted if nests are closer together. However, adoption is much less significant than predation in determining breeding success at different nesting densities.

The two eggs are laid 1–4 days apart (Spellerberg 1971b; Wang & Norman 1993) and full incubation starts at the laying of the first egg. The chicks hatch

asynchronously so first chicks are substantially heavier and significantly more mature by the time the second hatches. Hatchlings dry within 3 or 4 hours of hatching (Reid 1966) and may take their first forays from the nest soon after. Although they carry a substantial yolk plug reserve at hatching (Reid 1966) they are also fed during the first day. Chicks are brooded for much of the first day or two, but spend increasing amounts of time out of the nest in the later days. However, they are not able to thermoregulate fully until 10 days old (Spellerberg 1969) and even older chicks will be brooded in severe conditions.

Skuas on Ross Island feed both at penguin colonies and at sea. There are breeding colonies of the Adélie Penguin (*Pygoscelis adeliae*) at Capes Royds, Bird, and Crozier, but with the exception of the skuas at Cape Crozier, only a proportion of the breeding skuas in the local area can forage at these (Table 1). Most of the island's skuas forage at sea, predominantly on Antarctic silverfish (*Pleurogramma antarcticum*) (Young 1963b, 1994). Penguin colonies supply little food after about the middle of the skua chick stage, and all skuas then forage at sea. Food supply to the skua chicks during this changeover and towards the end of the season becomes more difficult. Differences among the skua colonies to the extent that breeding birds can forage early in the season from local penguins is important for its bearing on the relationship between food provision and sibling aggression. Abundant food from penguins gives a certainty of supply not

available to skuas foraging at sea, which are constrained far more by weather and sea-ice conditions than those foraging on the penguin colonies (Young 1994).

Research on Ross Island skuas suggests that they are breeding at the limits of the habitable range for this species. The time-span available each season for breeding barely exceeds the minimum necessary (Young 1994), and annual reproductive success is very low. At Cape Bird over five seasons, Young (1994) recorded an overall breeding success (to mid January) ranging between 0 and 0.45 chicks per breeding pair with eggs at the start of the season ($n = 135\text{--}204$ pairs). At Cape Royds, Spellerberg (1971b) reported an average of 0.6 chicks per breeding pair over three seasons, and Young (1963a) reported that 0.28 chicks fledged per pair during the 1959/60 season. A high proportion of pairs in both places laid two eggs. Poor breeding success was due to failure by the parents to protect and nurture the eggs and chicks, and to siblicide.

At Cape Crozier the skua-penguin association is rather different from any observed at penguin colonies at Capes Bird or Royds. Müller-Schwarze & Müller-Schwarze (1973, 1977) recognised that, at least for the western colony, the high density of breeding penguins precluded skuas from nesting within the penguin colony, and because the colony was so huge, the skuas nesting around the margin could not protect more than a fraction of its area by their territorial behaviour. This means that, uniquely for Ross Island, skuas breeding anywhere in the local

Table 1 Foraging association between skuas and Adélie Penguins at colonies on Ross Island and in southern McMurdo Sound.

Skua breeding locality	Numbers of breeding pairs of skuas (1980–85) ¹	Approximate percentage with access to penguin food
Cape Crozier colonies	c. 1000	100% ²
Cape Bird colonies	399	30% ³
Cape Royds colonies (Cape Barne to Rocky Point)	183	5.5% ⁴
South Ross Island colonies (Cape Evans, Dellbridge Islands)	137	0%
Head of McMurdo Sound ⁵ (Dailey Islands to Cape Bernacchi Point)	522	0%

¹Ainley et al. 1986.

²Young & Millar 1999.

³Young 1963b.

⁴Young 1994; pers. obs. The southernmost Adélie Penguin colony in this region is at Cape Royds.

⁵Counts from aerial survey only; colonies not shown on Fig. 1.

area can forage throughout the undefended bulk of this penguin colony. Moreover, a higher proportion of pairs at Cape Crozier than at the other Ross Island colonies raise both chicks of the brood (Wood 1971). The two reports together suggested to us that the foraging conditions at Cape Crozier should ensure better food provision during early chick growth, and that consequently there should be less sibling aggression and a higher survival of hatchling chicks. The causal relationship between food sufficiency and sibling aggression is summarised in the Food Amount Hypothesis (Lack 1966; Mock et al. 1987), and probably applies to all avian species, triggering and sustaining aggression (Drummond 2001a). Procter's (1975) experiments demonstrated that even relatively short periods without feeding would stimulate aggression in skua chicks. Conversely, supplementary feeding of breeding skuas has been variably successful in inhibiting or moderating aggression (Miller 1992; Young & Millar unpubl. obs.) but these experiments are difficult to prosecute and monitor. Inadvertent supplementary feeding of South Polar Skuas at Pointe Géologie, however, gives strong circumstantial support for the role of food amount in regulating siblicide in this species. In 3 years when skuas could feed on kitchen waste almost all pairs of chicks fledged. Before and after this period, skuas had no extra food and fewer than 20% of pairs raised both chicks (Jouventin & Guillotin 1979).

This paper describes the behaviour of siblings and parents during the first days in the life of hatchlings at the skua colony at Cape Crozier on Ross Island. Because all skuas on the island form an interbreeding population, differences among the colonies probably reflect local foraging conditions rather than genotypic variation or quality of breeding birds. The extent of siblicidal behaviour throughout the geographic range of the species has not been quantified previously. We review it here in relation to local ecology and breeding success.

STUDY AREA AND METHODS

Field observations were made between 23 December 1993 (at the start of chick hatching) and 26 January 1994 at Cape Crozier, Ross Island (77°27'S, 169°14'E). We concentrated on the skuas of the shallow valley lying to the west of the western Adélie Penguin colony, between the colony and the lower slopes of the Mt Terror icefield (Fig. 1): i.e., the skua breeding areas C, D, and E in Ainley et al. (1990);

Young & Millar (1999). These skuas all foraged at the neighbouring penguin colony, separated from the study area by over 200 m (Young & Millar 1999). By avoiding the often long periods away from the territory that characterise foraging at sea, both parents were usually together on the territory, and more likely to be present during sibling attacks. Over the period when the chicks were hatching both parents were on average in occupation at nest checks on 74.2% of visits during 1–5 January, and 83.4% of visits during 6–10 January (Young unpubl.).

All 49 nests with pairs of chicks (the study population) were routinely checked each day between 0800 h and 1100 h. Chick hatching, survival, and any movement from the nest area were recorded, and any significant changes in chick location or condition were followed up with a second visit later in the day. Chicks were weighed each day using "Pesola" spring balances accurate to ± 2 g. New chicks were recorded as first observed on Day 0 if they were seen hatching or had damp down, since Reid (1966) found that the down of the head and back dried in 6 h, the entire body in 9–12 h. Dry chicks were recorded as being 1 day old. Chicks within pairs were easily distinguished by their consistent difference in body mass. From about 10 days old they were also readily distinguished from the lengths of the primary wing feathers, which grow uniformly independently of body mass (Young 1963a). To ensure recognition of chicks away from the nest or on neighbouring territories, they were all individually marked with waterproof coloured inks on the legs and web. In practice there was very little uncertainty about the identity of any of the chicks being monitored. No weighings were possible when either of the chicks was hatching, or during high winds. A significant number of records was lost because of these constraints. Missing chicks were searched for throughout the territory and on neighbouring ones. Searches also looked for traces of blood or down left after predation or cannibalism.

Mass increase in Great Skua (*C. skua*) chicks can be described by a logistic growth equation (Furness 1987) in which the daily gain is approximately linear during the middle half of chick-rearing. Mean gain over this linear-growth period provides a convenient index of chick growth and has been related to food availability (Furness 1987; Hamer et al. 1991). Abundant food, ensuring a high rate of weight gain, should be associated with low or minimal siblicide, and vice versa. Mean growth rates (g day^{-1}) between 10 and 25 days are used in this paper as a basis for predicting the rate of siblicide in different South

Polar Skua populations. They were calculated for the study chicks from the daily growth data. Rates for other populations were taken directly from published figures or estimated from graphs of mass against age. Unless stated otherwise, results are given as mean \pm SE.

Observations were made from hides at the few suitable areas which could be monitored, and opportunistically when working among the birds. Skuas have a characteristic “alarm call” (Stonehouse 1956; Spellerberg 1971a) when they have eggs or chicks, often heard when people approach or enter their territory. This same call may also be heard when the chicks are fighting. This signal attracted our attention, so more sibling attacks were directly observed while we were working around the skua colonies than we would otherwise have noticed.

We attempted to record how long the first chick would persist in its attacks on the second chick by enclosing them separately in 4 m² wire mesh enclosures at the nest area after fighting had started. This manipulation was only partly successful because some parents never learned to feed the chicks evenly when separated, and because continuing bouts of heavy snowfall filled the enclosures so that some chicks could escape.

There is great scope for human disturbance to influence the results. Visits each day to find, capture, and weigh chicks disrupted the breeding groups, sending adults into frenzied flight and causing chicks to run from their hiding places (even from the territory), where they were exposed to heightened conspecific predation while parental attention was focused on attacks at the research intruders. This

problem was particularly acute in areas where the nests were closely packed. Two chicks (not in the study group) were certainly known to have been lost because of our work. The high survival rates we recorded overall is evidence, nevertheless, that our impact was not as severe as it seemed to us at the time. Skuas do not abandon nests or young permanently because of human disturbance.

RESULTS

Hatching interval, survival, and inequality of two chicks of broods

The most accurate records of hatching and survival interval are from 30 nests where at least one chick was observed hatching. Second chicks hatched between 1.5 and 3.5 days after the first (2.32 ± 0.12 days, $n = 30$). Sixteen were lost 3.05 ± 0.5 days after hatching; i.e., 5.25 ± 0.32 days after the first chick hatched. Siblicide in this skua is confined to hatchlings: the oldest chicks for which the onset of fighting was recorded were 8 days old.

The two chicks were very similar in size at hatching: the mean body mass of first chicks was 68.3 ± 4.7 g, $n = 18$, of second chicks 69.9 ± 5.6 g, $n = 12$. This difference was not significant ($t_{28} = 0.856$, $P = 0.399$). Because of asynchronous hatching, however, the first was significantly heavier by the time the second hatched, and this difference was maintained over the first few days of the chicks' lives when sibling attacks took place (Table 2).

Table 2 The asymmetry between the two chicks within broods. Statistics are mass \pm SE.

Time from observed hatching of second chick	Mass of first chicks and statistical test of difference ¹	Mass of second chicks	Ratio of second to first chick mass
At 24 h before hatching	83.6 ± 2.8 g $n = 16$	—	—
At hatching	102.3 ± 4.2 g $t_{26} = 7.64$ $P < 0.001$	69.9 ± 1.6 g	0.69 ± 0.02
At 24 h after hatching	123.8 ± 3.9 g $t_{18} = 13.64$ $P < 0.001$	70.9 ± 1.4 g	0.58 ± 0.019
At 48 h after hatching	146.5 ± 4.7 g $t_{18} = 15.46$ $P < 0.001$	83.3 ± 1.8 g	0.57 ± 0.016
At 72 h after hatching	182.1 ± 4.5 g $t_{14} = 21.12$ $P < 0.001$	102.5 ± 3.7 g	0.56 ± 0.018

¹ t -test at hatching unpaired, remainder were paired t -tests as both chicks could be weighed at these times.

The course of events during sibling attacks

The attacks all necessarily began close to the nest and to parents because second chicks at this young age are still at the nest and are brooded there for a large proportion of their first days. Attacks are possible only when the chicks are off the nest, as they are brooded separately on either side of the parent's body.

Fourteen attacks observed during the study provide details of the typical sequence of events during an attack. In eight attacks the chicks had come together for feeding, in three the chicks had just been released from being brooded at the nest, and the remaining three attacks began as the second chick was attempting to return to the nest area after being chased away earlier. The first chick started the attacks either with an agonistic display ($n = 9$) or without ($n = 5$). In three sequences the first chick did not pursue the attack after its agonistic display; in seven the second chick ran off so promptly that there was no contact between them; in four a full pecking attack ensued, with the first chick crouched over the second pecking at the back, neck, and head. Half of the attacks ended with the second chick escaping, half through the intervention of parents. Because of parental intervention, eight of the 14 sequences ended with the second chick remaining near the nest area, but in six attacks the second chick was effectively evicted.

The behaviour of the chicks and parents during sibling attacks

Hatchlings are capable of well developed agonistic displays, similar to those of adults in the same circumstances. The most easily recognised is the aggressive upright, in which the chick stretches to full height, standing on its feet (the usual stance at this age has both foot and tarsus on the ground), with neck outstretched and the closed bill either directed at the second chick or raised almost vertically. If accompanied by a shrill call it then mimics the long call oblique of adults (Burton 1968; Spellerberg 1971a). The characteristic adult long call oblique incorporates wing raising, holding them fully extended behind the body, but hatchling chicks do not obviously lift their wing stubs in the same way, although they do use their wings both in fighting and for balance when running.

Second chicks usually responded to attacks by crouching, but if the two were standing together when the attack started, second chicks responded by taking up the equivalent of the intimidated upright posture of the adult birds, with the beak and head

pulled back beyond vertical. Chicks in this posture are at risk of having the face and beak caught and used to pull them over onto the ground. Second chicks already crouched before an attack might respond by gaping. Usually, however, they were almost immediately overwhelmed by the ferocity and strength of the first chick's attack, and either crouched close to the ground or ran away. In the 14 attacks observed on hatchling chicks, only one younger chick made an attempt to peck back, but this was ineffectual. Pecking attacks were fiercely pursued with as many as 20–30 blows a minute, alternating with jabbing, pulling, and twisting of any part of the body that could be grabbed. Once the attack started first chicks carried it out silently but second chicks squealed almost continuously.

Second chicks have effectively only three options once attacked: they may simply endure the attack, crouched tightly on the ground; scramble to the nest or parents for protection; or run from the nest area. These are neither trivial nor short-lived episodes. The first chicks are unremitting in the strength and persistence of their attack, and do not give up unless stopped by the parents or the second chick escapes. Attacks stopped by the parents give only temporary relief. Within minutes or hours the attack will be resumed when opportunity arises.

Even when the second chick manages to break away from an attack it is not yet safe, as the first then usually hounds it across the broken ground of the territory, the two chicks scrambling and running for long distances. One chase observed ran a near circular course around the territory for over 40 m. These chases are usually silent. At the end of a chase the first chick returns to near the nest and parents, while the second is marooned by fear some distance from them. Second chicks may approach the nest later, but can be put to flight again with nothing more than a directed stare, a long call, or the first movement towards it by the older sibling.

The end point of severe sibling attack is the permanent expulsion of the second chick from the nest area and from taking part in any feedings with the first chick. From this stage, the parents must feed and brood the two chicks separately if the second is to have any chance of surviving on the territory. The ending is not, therefore, the death of the second chick directly and immediately from the attack. Almost no second chicks in this study were found dead or fatally injured on nest areas, nor did any of the attacks observed end with the death or critical wounding of second chicks. No chicks were discovered with gaping wounds. We cannot, however, be certain that

no second chicks were killed by sibling attacks, as any dying in this way would probably be eaten by the parents. Even those maimed but still alive at the end of an attack are likely to be eaten. Nevertheless, it was surprising that no chicks of this age were found with injuries consistent with these attacks during the routine, often twice daily, nest checks of the total study population of over 200 nests.

Persistence of sibling aggression

Attempts by the first chick to dominate or attack the second persisted for many days after the first attacks even after the chicks were separated in enclosures at the nest area. The determination of the first chick to reach the second, and the equal determination of the second chick to escape from the enclosure in order to get away from its sibling, led to continuing, and only partly resolved, problems with this experiment. Right to the end of the trial, when most chicks were 15–20 days old the first chicks were still extremely aggressive, pacing up and down the common fence and peering over it, while the extreme fear of second chicks was manifest in the number found with cuts and abrasions on the beak and face from struggling to escape through the wire mesh of the far wall of their enclosure. A number of these second chicks had to be released from the cages at this late stage, and then fighting resumed immediately. However, in two broods that were kept separate for 22 and 25 days respectively, second chicks reached the age at which they could defend themselves, and after that the first chick’s sibling aggression ceased and the two lived together without obvious conflict.

The response of parents to sibling fighting

Parents showed a range of behaviours in response to sibling attacks: from apparent indifference through extreme anxiety to increasing levels of intervention (Table 3). The likelihood of parents intervening

increased in direct relation to increasing attack intensity and duration. The two parents might not, however, respond equally, and when both were present at the time of the attack only one might show any interest or act decisively.

Observations of recurring attacks in one territory suggested that the response by parents might wane over time. In the first attack both parents reacted by running to the fighting chicks, and one acted firmly by sitting on them. In the second attack only the female went to them, but made little attempt to stop the fighting and returned to the nest bowl when the second chick escaped and was being chased away. During this second attack the male watched the fighting from near the nest but did not interfere.

The fate of second chicks

Of the 26 missing second chicks, 12 were certainly expelled from the nest area by sibling attacks—they were either observed being chased away or were recorded away from the nest area on the day or days before being lost. There is no information about the remaining 14 chicks, which were all at the nest on the day before being recorded missing. They may or may not have been expelled first. The two pairs of chicks missing together on the same day were, however, certainly killed at the nest or nearby: they were too young to have been very far from it.

Whether second chicks survive after being expelled from the nest area depends on a range of factors, including the size of the parental territory (larger territories allow both greater freedom for escape and greater protection by parents subsequently), the behaviour of parents and neighbouring breeding birds, and more than either of these, a great deal of good fortune. Few expelled chicks survived for longer than a day or two in this study, although there were some notable exceptions. The second chick of one pair, for example, was

Table 3 Responses of parents to different levels of attack on the second chick.

Behaviour of the first chick	Response by parents				
	No obvious response	Alarm calling	Go to chicks	Offer food	Attempt to brood chick(s)
Aggressive postures only	6	0	1	0	0
Aggressive postures and chasing	2	2	4	1	3
Fighting with pecking	0	6	6	3	3

chased from the nest area at 3 days old but survived away from its sibling, always more than 30 m from the nest, for a further 20 days before being killed by a predator. Nevertheless, in spite of the continuing care given by the parents this chick was always considerably lighter for its age than its sibling at the nest. At 5 days it weighed 74.6% of the mass of the first chick, 80% at 10 days, 54% at 15 days and 64% at 23 days when killed. A second chick lived to the end of the study for 17 days 12–16 m from the nest. This chick was cared for rather better, and was 69% of the first chick's mass when they were each 10 days old and 79% at 15 days. However, chicks being raised together at the nest in this colony this season (1993/94) were more equal. In eight pairs that lived closely together, second chicks averaged 88% of the first when each was 5 days old, 95% at 10 days, and 94% at 15 days.

Of 66 two-chick broods, three second chicks (4.4%), were adopted by neighbours. Two were between 2 and 3 days old when found on the new nests, and the third, 4 days old. Adoptions can have dire consequences for original brood members. The chick adopted by a pair with two eggs displaced one egg after 3 days and the remaining chick of its foster parents 2 days later. The one that moved to a single-egg nest caused the egg to be abandoned 6 days later. Both these chicks survived to at least 20 days in their new nests. The third was adopted into a nest already containing a pair of chicks, and became the middle chick of the enlarged brood. During a natural process of brood reduction it would have expelled the third and then probably would have been expelled itself, but before any of that could happen it was returned to an enclosure on its natal territory as part of the experiment on the maintenance of aggression.

Factors possibly implicated in the prevalence and intensity of sibling attacks in this population

In 35 broods we were able to compare age, mass of the first chick, and difference between the two chicks at 48 h after the second chick hatched in (1) broods with both chicks surviving and (2) broods in which the second was lost or expelled from the nest through sibling attack. There were 16 broods in the first group, 19 in the second. Variation in the degree of hatching asynchrony was not significant. The mean difference in ages between first and second chicks was 2.5 ± 0.7 days (mean \pm SD) in broods in which the second chick was lost or expelled; 2.6 ± 0.5 days in broods where the second was able to stay at the nest ($t_{33} = 0.172$, $P = 0.864$, two-tailed). We used

these data to test two hypotheses. First, if hunger promotes aggression, first chicks of broods in which siblicide was observed were predicted to be lighter on average and less well grown at the same age than first chicks of broods where fighting was absent or inconsequential to survival. Such a difference was not apparent in this sample. First chick body mass at 48 h in surviving broods was 151 ± 4.9 g, and 153.6 ± 4.2 g in broods from which the second chick was lost or expelled ($t_{33} = 0.258$, $P = 0.398$, one-tailed). Second, the success of any attack on second chicks, and the ultimate outcome, might depend on the difference in mass between the chicks at the time of any attack, because the wider the difference the less should second chicks be able to resist attacks. At 48 h the second chick weighed 0.59 ± 0.02 of the mass of first chicks in pairs where the two chicks remained together at the nest compared with 0.58 ± 0.02 when the second chick was lost or expelled. This difference was not significant ($t_{33} = 0.245$, $P = 0.40$, one-tailed).

Chick growth rates as an index of nutrition levels

We have growth data on two sets of chicks in this population: single chicks, either the only one of brood surviving or the survivor of siblicide; and pairs of chicks. Growth rates in singletons, and of first and second chicks of pair broods, measured as g day^{-1} for growth between 10 and 25 days, could not be differentiated: single chicks averaged 42.6 ± 1.3 g day^{-1} , $n = 16$, first chicks 41.6 ± 1.51 g day^{-1} , $n = 13$, second chicks 40.2 ± 1.4 g day^{-1} , $n = 13$, ($F_{2,39} = 0.752$, $P = 0.48$).

Contribution of siblicide to brood reduction and overall breeding success

Statistics on the survival of 49 pairs of chicks over the 10 days following the hatching of the second chick, the period when siblicidal attacks take place, are shown in Table 4. Eighteen pairs of chicks

Table 4 The statistics of chick survival in 49 two-chick broods to 10 days after the second chick hatched.

Both chicks survive	18 broods (36.8%)
One chick survives	
First chick survives	26 broods (53.1%)
Second chick survives	1 brood (2.0%)
Neither chick survives	
Chicks lost at same time	2 broods (8.2%)
Second briefly outlives first	2 broods (8.2%)
First briefly outlives second	0 broods

survived and four pairs were lost. Single chicks survived in 27 broods. In 26 broods the first chick survived, and the second chick survived in one after the loss of the first. The impact of siblicide on the survival statistics of these hatchlings is, thus, very evident. In its absence a further 26 second chicks might well have survived, giving a total of 88 (89.7%) chicks alive at this stage, out of the 98 hatching. In this sample, three second chicks outlived first chicks; one by 1 day, one by 6 days and one surviving until the end of the study.

DISCUSSION

The impact of siblicide on the Cape Crozier population

This study reports a high level of sibling aggression in the Cape Crozier population in the 1993/94 season, but its incidence was lower and impact not as severe as in either the Cape Bird or Cape Royds populations. Whereas 36.8% of pairs at Cape Crozier hatching both chicks were able to raise them together successfully well beyond the siblicidal period, few pairs at Cape Royds and almost none at Cape Bird were able to do so (Table 5). The obvious difference among these colonies is in the skua feeding ecology during the period the chicks are hatching. At Cape Crozier all skuas were able to feed at the very large, local penguin colony (Young & Millar 1999). At Cape Bird only 30% of birds had territories with penguins, mostly quite low numbers (Young 1994), at Cape Royds only 5.5% had penguins (Young 1963b). Not only was much more food available at Cape Crozier, it was also so much easier to obtain so that the skua foraging times were much shorter than at either of the other sites (Young & Millar 1999). Better food availability is the most likely factor explaining both the higher proportion of pairs raising both chicks, as seen also by Wood (1971), and their high growth rate (Table 5).

The study has confirmed again that the burden of brood reduction at the hatchling stage falls on second chicks. In 27 broods in which only one chick survived, 26 survivors were first chicks. Only three second chicks outlived firsts, and only one of these three lasted longer than a day or so. The two key factors combining to determine the overall impact of sibling attacks in any population are the incidence and intensity of the attacks, and the resulting outcome. All the evidence from these and earlier observations (Young 1963a unpubl. obs.) is that

some aggression between the chicks is routine in all broods. The critical difference among different broods and populations is that in some, but not others, this aggression escalates into sustained intolerance and attack, leading to the eviction of the second chick, but the reason for this remains unexplained. We found no evidence that the expression of siblicide, its initiation and its outcome, is influenced by differences between the two chicks of broods, either from different levels of hatching asynchrony affecting maturity differences between the hatchlings, or from differences in mass at hatching or from differential growth. Contrary to earlier research (Young 1963a; Spellerberg 1971b), mass of first chicks and age or mass difference between the chicks were not significant factors in provoking siblicide or determining its outcome. Broods that remained together at the nest (sibling aggression weak) were very similar to those in which the second chick was evicted (sibling aggression strong). In retrospect, failure to demonstrate any such effects is only to be expected considering the very large inequality consequent on the hatching asynchrony between the hatchlings at the time sibling attacks occur. First chicks are more mature, more mobile, stronger and heavier than their siblings. If fighting begins, first chicks invariably win, irrespective of any small variation in the differential in mass or age. It is in fact a misnomer to talk of sibling fighting. 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.

In addition to the obvious age and size difference there are other chick features that should be examined. For instance, there could well be subtle differences related to genetic identity (whether the chicks are full siblings or not) and from the gender composition of the brood. Millar et al. (1997) have shown that there is little or no egg dumping or extra-pair copulations in these populations, and that all chick pairs tested by minisatellite DNA fingerprinting comprised full sibs. The only place, therefore, where fighting is not between full sibs is where parents adopt unrelated chicks expelled from other nests. Nothing is known, however, of the influence of gender on sibling aggression and of the second chick's response. It is conceivable that male-male pairs might react differently to female-male pairs, but sex determination in relation to siblicide has not been attempted so far in these populations. We have, however, established that in *C. lonnbergi* on the Chatham Islands there were equal numbers of each sex at hatching, and in 65 two-chick broods

Table 5 Records of siblicide, breeding success, and chick growth rates in different populations of the South Polar Skua. Breeding success recorded as chicks/pair and chicks from eggs hatching. Growth rates recorded as grams/day between 10 and 25 days. *, first chicks in broods; **, single chicks; ***, mean growth for the population, includes single chicks, and first and second chicks of pair broods.

Location	Siblicide frequency and impact on breeding success	Breeding success chicks/pair (c/pr) and chicks from eggs hatching (c/eggs hatch)	Chick growth rate g/day
South Atlantic islands			
Signy Island ¹ 60°43'S, 45°38'W	Low incidence, negligible impact	1.27 c/pr, 0.9 c/eggs hatch	38.7*
King George Island ² 62°12'S, 58°58'W	Siblicide not recorded	1.03 c/pr, 0.62 c/eggs hatch	37.8*
Antarctic Peninsula			
Anvers Island ^{3,4} 64°46'S, 64°03'W	“Siblicide amongst week old chicks ... appeared not to be important” ³ High mortality among maturing chicks from late January construed as siblicide ⁴	1.5, 1.52 c/pr in two seasons, 0.55 in one season. 0.87, 0.88 c/eggs hatch in two seasons, 0.34 in one ³	
Antarctic Continental Margin			
Windmill Islands, Wilkes Land ⁵ 66°15'S, 110°31'E	Siblicide inferred, but “it does not appear so serious as that claimed by Wilson (1907)”	0.85 c/pr, 0.77 c/eggs hatch	
Pointe Géologie, Terre Adélie ⁶ 66°40'S, 140°01'E	Chick survival directly related to food abundance, siblicide minimal in abundant food seasons	10–90% of pairs raising both chicks in different seasons	
Magnetic Island, Prydz Bay ⁷ 68°30'S, 77°50'E	“observed lack of sibling aggression”	1.29–1.46 c/pr (three seasons), 0.84 (1990/91) c/eggs hatch	
Larsemann Hills, Princess Elisabeth Land ⁸ 69°21'S, 76°00'E	Common, with moderate impact	0.5 c/pr 22.5 ± 4.1 *** Days 5–10 43.9 ± 8.2 *** Days 20–30	30.8*
Victoria Land Coast, Ross Sea			
Cape Hallett ^{9,10} 72°19'S, 170°13'E	Common with moderate to high impact ¹⁰	0.77 c/pr ⁹	46.3 *** ¹⁰

Ross Island, McMurdo Sound

Cape Bird^{11,12,13}
77°13'S, 166°28'E

Very high incidence, obligate;
very high impact on breeding

0.21 c/pr
0.48 c/eggs hatch¹¹
0.33 c/pr (range 0.12–0.53)
Seven seasons, 0.49 c/eggs hatch¹³

38.6 ± 1.64** (1965/66)
44.9 ± 1.36** (1968/69)¹²

Cape Crozier^{14,15}
77°27'S, 169°14'E

Moderate influence, occurring
in 40% of 2-chick broods¹⁵

0.33 c/pr (range 0.12–0.60)
in eight seasons¹⁴

41.6 ± 1.51*

Cape Royds^{16,17}
77°33'S, 166°09'E

Very high incidence with very
high impact on breeding

0.46 c/pr, 0.24 c/eggs
0.29 c/eggs hatch¹⁶
0.60 c/pr (range 0–0.79)
over three seasons¹⁷

42.6 ± 1.27**¹⁵
32.3 ± 0.93**¹⁶

Authorities: ¹Hemmings 1984; ²Peter et al. 1990; ³Neilson 1983; ⁴Pietz 1987; ⁵Eklund 1961; ⁶Jouventin & Guillinot 1979; ⁷Hull et al. 1994; ⁸Wang & Norman 1993; ⁹Trillmich 1978; ¹⁰Reid 1966; ¹¹Young 1994; ¹²Wood 1971; ¹³Miller 1992; ¹⁴Wood 1971; ¹⁵Young & Millar, this paper; ¹⁶Young 1963a; ¹⁷Spellerberg 1971b.

equal numbers of the four possible combinations of chicks based on hatch order (Millar & Young unpubl. data). However, at Capes Royds and Bird almost no second chicks survived, so that except for research on the detail of the interactions between the chicks, or of their possibly differential growth (Edwards & Collopy 1983), gender influence on survival must be almost negligible.

Sibling aggression in skuas does not, however, usually result directly in siblicide—the attacks are rarely directly lethal. Second chicks are simply chased away from the nest area, and die from starvation, exposure or predation. There is little information on how second chicks die from these early sibling attacks. Only one corpse was found on a natal territory, and enough remains were found of another to indicate it had been eaten by the parents. All other chicks simply disappeared between nest checks. This situation contrasts with our experience later in the season, when wounded, dead, and partly eaten chick bodies were commonly found. Over 21–23 January, for example, all six chicks lost from the study population were found as remains on their natal territories. This difference reflects the fact that hatchling chicks can be carried away in flight or swallowed whole in a minute, whereas older chicks are so big that they cannot easily be removed from the territory and cannot quickly be dismembered and eaten.

All the sibling attacks observed in this study, and inferred from the loss of second chicks, involved very young chicks, within a day or so of the second chick hatching. Attacks begin, therefore, during the period when the relative mass difference between the chicks is highest and the dominance advantage of the first chick greatest, as in other siblicidal species (Drummond 2001b). This finding has both theoretical and practical implications. At a theoretical level it suggests that the threshold of hunger rises as the chicks age, being lowest soon after hatching and rising over the following days. Primary siblicide attacks provoked by hunger become rare after 10 days and cease altogether after about 3 weeks, even in first chicks that were initially very aggressive. At Cape Crozier, unless fighting began soon after hatching it was absent for the rest of the season. At a practical level the finding that natural siblicide begins with very young chicks indicates that any studies of siblicide in this species must focus on hatchlings. This is especially significant in experimental manipulations attempting to intensify aggression by causing hunger or reduce its intensity by supplementary feeding. Any experimental manipulations after this early period, the sensitive

period, are dealing with rather different and more tolerant chicks, less sensitive to the amount of food offered. At the very least one would expect that higher levels of hunger and more obvious malnutrition would be needed to stimulate aggression in older chicks that have never fought earlier.

The pattern of interaction seen between hatchling siblings was different from that between unrelated chicks striving for dominance at a nest after one or the other had been adopted. The adopted chick may not fall into the comfortable hierarchy of size and strength which permits the lethal dominance of the first chick in natural broods. Fights between chicks of equal strength and ability, as with fights between adults, are much more likely to be protracted, and more likely to lead to injury and exhaustion on both sides. Williams (1969) recorded one such fight between two chicks, each 3 days old and each weighing 132 g, continuing through several hours. The fight comprised seven bouts, one of which lasted for 24 min, in which alternately one chick then the other was victorious.

Emphasis so far in research on siblicide in skuas has been on the chicks, but in most colonies, where only a proportion of pairs are affected by siblicide, the questions of incidence and outcome depend very significantly on the parents. High quality and experienced parents are better able to provision the chicks, spend less time foraging, and are more effective in diverting aggression if it begins. Adult age and condition have been found to be important determinants of foraging efficiency and breeding success in Great Skuas (Hamer & Furness 1991; Ratcliffe et al. 1998; Ratcliffe & Furness 1999; Bearhop et al. 1999; Catry & Furness 1999), but there is no information on these factors in the South Polar Skua, although they may be expected to be similar.

There is another reason that the influence of parents modifies the association between food supply and sibling aggression. During the first 2 or 3 days of life, skua chicks are fed by both parents holding small bits of food for them. For skuas foraging at sea most of this food is brought by the male parent, continuing his incubation period feeding role (Young 1963b; Williams 1969), and the female competes with the chicks for any food offered. The amount of food reaching the chicks during this period of high risk of siblicide therefore depends not only on the foraging efficiency of the male but also on the behaviour of the competing female. In pairs feeding at penguin colonies, females also forage during incubation and begin to feed chicks directly after hatching.

Although parental intervention during sibling attacks has been described in a number of avian species (Anderson 1995; Lougheed & Anderson 1999) in none is it so consistently obvious as in this skua. In almost every attack we witnessed that involved pecking of one chick by the other, parents indicated high anxiety. Parental "alarm calling" and displacement activity were commonly recorded, and in a high proportion of attacks either one or both parents effectively intervened by offering food, charging at first chicks, or attempting to brood both chicks to stop the fighting. However, although these interventions were effective in the short term, parents were usually unable in the longer term to prevent the second chick being chased away.

The reproductive value to parental fitness of the second chick at Cape Crozier can be calculated by the method developed by Mock & Parker (1986). They recognised that the total reproductive value (RV) to parental fitness of the youngest chicks in siblicidal broods comprised two components, depending on whether these chicks were or were not predeceased by senior chicks. Extra reproductive value (R_{Ve}) is added when they survive together with the senior chicks; insurance reproductive value (R_{Vi}) when they replace senior chicks. At Cape Crozier in 1993/94, of 49 two-chick broods in which at least one chick survived, there were only three in which the second chick outlived the first, and of these only one survived to the end of the study. Second chicks survived, however, in a high proportion of pairs. From these data the total RV was 0.399, of which R_{Ve} was 0.377, and R_{Vi} an insignificant 0.022. These figures contrast with the values of 0.11 and 0.45 for extra reproductive value and insurance value respectively for second chicks determined by Lamey (1995) for Falkland Skuas (*C. antarctica*), which lack siblicide. In the South Polar Skua populations at Capes Royds and Bird, where very few second chicks survive in two-chick broods because of intense siblicide, any contribution of second chicks to parental RV can only result from their insurance value.

Distribution of siblicide throughout the breeding range of South Polar Skuas in relation to local environment

It is evident from our review of the incidence of siblicide (Table 5) that, with the possible exceptions of the South Atlantic islands and Antarctic Peninsula, siblicide is common throughout the breeding range of this skua.

Breeding success is a good indicator of the degree of siblicide in individual populations. Those with consistently high success, better than one chick fledged per pair on average, are unlikely to show much siblicidal behaviour. At the other extreme, populations like those at Cape Bird with success rates between 0.2–0.4 chicks per pair are likely to have high siblicide rates. An even better predictor of siblicide levels in the absence of observational data would be the fledging success of broods hatching two chicks, but this statistic is only rarely recorded in the accounts of skua biology. Fledging success, however, includes any late season weather impact so therefore chick survival in broods up to 10 days of age—to beyond the stage when siblicide is a serious cause of chick mortality—would provide superior prediction.

The likely significance of food availability, especially of its certainty and reliability, as a proximate factor in provoking siblicide suggests that records of chick growth rate might be an even better predictor of siblicide levels in populations than overall breeding success. Growth rates summarised in Table 5 varied between 30.8 and 46.3 g day⁻¹ calculated from age 10–25 days, and were not correlated with either breeding success or siblicide incidence. There are both very high and very low growth rates in the Ross Island populations, while the Signy Island skuas had modest chick growth rates, but very high breeding success and negligible siblicide. The figures for growth rates shown here are admittedly preliminary estimates and come from a variety of records. Dedicated research may well produce a more persuasive relationship between growth, food provision, and siblicide.

Although skill in food provision by skuas is related to breeding age (Ratcliffe et al. 1998; Ratcliffe & Furness 1999), this factor can be discounted in comparisons among these colonies, which can be expected to have, on average, similar age structures. Within a single colony, however, as at Cape Crozier, the overall level of siblicide per season no doubt reflects in part the age structure of the breeding birds, as experienced birds are more likely to be able to feed their chicks well, and because they are absent for shorter periods foraging are able to care for them more successfully than less experienced parents. In contrast, at Cape Bird and other localities where the skuas forage at sea under extremely difficult conditions, not even the most experienced and skilled adults can maintain sufficient food to satisfy the chicks at all times.

The variable incidence of sibling aggression over the breeding range of *C. maccormicki* indicates that for the species as a whole siblicide is facultative (Mock & Parker 1997), expressed only under certain environmental circumstances, even though it appears obligatory within some populations. Study of only the Cape Bird population, for example, where sibling aggression seems to arise in almost every brood, would certainly suggest without this broader knowledge that it was obligatory for the species. In fact, the level of siblicide within each breeding colony reflects the specific environmental features acting there.

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REFERENCES

- Ainley, D. G.; Morrell, S. H.; Wood, R. C. 1986: South Polar Skua breeding colonies in the Ross Sea region, Antarctica. *Notornis* 33: 155–163.
- Ainley, D. G.; Ribic, C. A.; Wood, R. C. 1990: A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. *Journal of Animal Ecology* 59: 1–20.
- Anderson, D. J. 1990: Evolution of obligate siblicide in boobies. 1. A test of the insurance egg hypothesis. *American Naturalist* 135: 334–350.
- Anderson, D. J. 1995: The role of parents in siblicidal brood reduction of two booby species. *Auk* 112: 860–869.
- Bearhop, S.; Griffiths, R.; Orr, K.; Furness, R. W. 1999: Mean corpuscular volume (MCV) as a measure of condition in birds. *Ecology Letters* 2: 352–356.
- Bruemmer, F. 1993: Low, lean killing machine. *Natural History* 11: 55–60.
- Burton, R. W. 1968: Agonistic behaviour of the Brown Skua, *Catharacta skua lonnbergi* (Mathews). *British Antarctic Survey Bulletin* 16: 15–39.
- Catry, P.; Furness, R. W. 1999: The influence of adult age on territorial attendance by breeding Great Skuas *Catharacta skua*: an experimental study. *Journal of Avian Biology* 30: 399–406.

- Cooper, J. 1980: Fatal sibling aggression in pelicans—a review. *Ostrich* 51: 183–186.
- Drummond, H. 2001a: A revaluation of the role of food in broodmate aggression. *Animal Behaviour* 61: 517–526.
- Drummond, H. 2001b: The control and function of agonism in avian broodmates. *Advances in the Study of Behaviour* 30: 261–301.
- Edwards, T. C.; Collopy, M. W. 1983: Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100: 630–635.
- Eklund, C. R. 1961: Distribution and life history studies of the South-Polar Skua. *Bird-Banding* 32: 187–223.
- Ensor, P. H. 1979: The effects of storms on the breeding success of South Polar Skuas at Cape Bird, Antarctica. *Notornis* 26: 349–352.
- Furness, R. W. 1987: The Skuas. Calton, Poyser.
- Hagelin, J. C.; Miller, G. D. 1997: Nest-site selection in South Polar Skuas: balancing nest safety and access to resources. *Auk* 114: 638–645.
- Hamer, K. C.; Furness, R. W. 1991: Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *Journal of Animal Ecology* 60: 693–704.
- Hamer, K. C.; Furness, R. W.; Caldow, R. W. G. 1991: The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. *Journal of Zoology, London* 223: 175–188.
- Hemmings, A. D. 1984: Aspects of the breeding biology of McCormick's Skua *Catharacta maccormicki* at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* 65: 65–79.
- Hull, C.; Carter, R.; Whitehead, M. D. 1994: Aspects of breeding chronology and success of the Antarctic Skua *Catharacta maccormicki* at Magnetic Island, Prydz Bay, Antarctica. *Corella* 18: 37–40.
- Jouventin, P.; Guillotin, M. 1979: Socio-ecologie du Skua Antarctique a Pointe Géologie. *Terre et la Vie, Revue Ecologique* 33: 109–127.
- Lack, D. 1966: Population studies of birds. Oxford, Clarendon Press.
- Lamey, C. S. 1995: Chick loss in the Falkland skua *Catharacta skua antarctica*. *Ibis* 137: 231–236.
- Lougheed, L. W.; Anderson, D. J. 1999: Parent blue-footed boobies suppress siblicidal behavior of offspring. *Behavioural Ecology Sociobiology* 45: 11–18.
- Millar, C. D.; Lambert, D. M.; Young, E. C. 1997: Minisatellite DNA detects sex, parentage and adoption in the South Polar Skua. *Journal of Heredity* 88: 235–238.
- Miller, G. D. 1992: Reproductive success of South Polar Skuas at Cape Bird, Ross Island. *Antarctic Journal of the United States* 27: 150–151.
- Mock, D. 1984: Infanticide, siblicide, and avian nesting mortality. In: G. Hausfater, G.; Hrdy, S. B. ed. *Infanticide: comparative and evolutionary perspectives*. New York, Aldine. Pp. 3–30.
- Mock, D. W. 1994: Brood reduction: narrow sense, broad sense. *Journal of Avian Biology* 25: 3–7.
- Mock, D. W.; Lamey, T. C.; Ploger, B. J. 1987: Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology* 68: 1760–1772.
- Mock, D. W.; Parker, G. A. 1986: Advantages and disadvantages of egret and heron brood reduction. *Evolution* 40: 459–470.
- Mock, D. W.; Parker, G. A. 1997: The evolution of sibling rivalry. Oxford, Oxford University Press.
- Müller-Schwarze, D.; Müller-Schwarze, C. 1973: Differential predation by South Polar Skuas in an Adélie Penguin colony. *Condor* 75: 127–131.
- Müller-Schwarze, D.; Müller-Schwarze, C. 1977: Interactions between South Polar Skuas and Adélie Penguins at Cape Crozier, Antarctica. In: Llano G. A. ed. *Adaptations within Antarctic ecosystems*. Washington, Smithsonian Institution. Pp. 619–646.
- Neilson, D. R. 1983: Ecological and behavioral aspects of the sympatric breeding of the South Polar Skua (*Catharacta maccormicki*) and the Brown Skua (*Catharacta lonnbergi*) near the Antarctic Peninsula. Unpublished thesis, University of Minnesota.
- O'Connor, R. J. 1978: Brood reduction in birds: selection for fratricide, infanticide, and suicide? *Animal Behaviour* 26: 79–96.
- Peter, H-U.; Kaiser, M.; 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 Fuer Systematik Oekologie und Geographie der Tiere* 117: 201–218.
- Pietz, P. J. 1987: Feeding and nesting ecology of sympatric South Polar and Brown skuas. *Auk* 104: 617–627.
- Procter, D. L. C. 1975: The problem of chick loss in the South Polar Skua (*Catharacta maccormicki*). *Ibis* 117: 452–459.

- Ratcliffe, N.; Furness, R. W. 1999: The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of Great Skuas (*Catharacta skua*). *Journal of Zoology, London* 249: 195–201.
- Ratcliffe, N.; Furness, R. W.; Hamer, K. C. 1998: The interactive effects of age and food supply on the breeding ecology of Great Skuas. *Journal of Animal Ecology* 67: 853–862.
- Reid, B. E. 1966: The growth and development of the South Polar Skua (*Catharacta maccormicki*). *Notornis* 13: 71–89.
- Schlatter, R. P. 1972: Social organisation of non-breeding South Polar Skuas at Cape Crozier, Antarctica. Unpublished PhD dissertation, Johns Hopkins University, Baltimore.
- Spellerberg, I. F. 1969: Incubation temperatures and thermoregulation in the McCormick Skua. *Condor* 71: 59–67.
- Spellerberg, I. F. 1971a: Breeding behaviour of the McCormick Skua *Catharacta maccormicki* in Antarctica. *Ardea* 59: 189–229.
- Spellerberg, I. F. 1971b: Aspects of McCormick Skua breeding biology. *Ibis* 113: 357–363.
- Stinson, C. H. 1979: On the selective advantage of fratricide in raptors. *Evolution* 33: 1219–1225.
- Stonehouse, B. 1956: The Brown Skua *Catharacta skua lonnbergi* (Mathews) of South Georgia. Falkland Islands Dependencies Survey Scientific Reports, No. 14. 25 p.
- Trillmich, F. 1978: Feeding territories and breeding success of South Polar Skuas. *Auk* 95: 23–33.
- Wang, Z.; Norman, F. J. 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* 40: 189–203.
- Williams, A. J. 1980: Variation in weight of eggs and its effect on the breeding biology of the Great Skua. *Emu* 80: 198–202.
- Williams, J. M. 1969: Territorial ecology and ethology of McCormick's Skua *Catharacta maccormicki* (Saunders) at Cape Bird, Ross Island, Antarctica. Unpublished MSc thesis, University of Canterbury.
- Wilson, E. A. 1907: National Antarctic Expedition 1901–1904. Natural history—zoology. Vol. 2. Aves. London, British Museum Natural History.
- Wood, R. C. 1971: Population dynamics of breeding South Polar Skuas of unknown age. *Auk* 88: 805–814.
- Young, E. C. 1963a: The breeding biology of the South Polar Skua *Catharacta maccormicki*. *Ibis* 105: 203–233.
- Young, E. C. 1963b: Feeding habits of the South Polar Skua *Catharacta maccormicki*. *Ibis* 105: 301–318.
- Young, E. C. 1972: Territory establishment and stability in McCormick's Skua. *Ibis* 114: 234–244.
- Young, E. C. 1994: Skua and penguin. Predator and prey. Cambridge, Cambridge University Press.
- Young, E. C.; Millar, C. D. 1999: Skua (*Catharacta* sp.) foraging behaviour at the Cape Crozier Adélie Penguin (*Pygoscelis adeliae*) colony, Ross Island, Antarctica, and implications for breeding. *Notornis* 46: 287–297.

