FEEDING AND NESTING ECOLOGY OF SYMPATRIC SOUTH POLAR AND BROWN SKUAS

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ABSTRACT.—In the 1979–1980 and 1980–1981 austral summers, I examined nesting and feeding ecology of South Polar (*Catharacta maccormicki*) and Brown (*C. lonnbergi*) skuas near Palmer Station, Antarctica. As earlier studies had suggested, South Polar Skuas fed mostly at sea on fish, and Brown Skuas fed mostly on penguin eggs and chicks. These dietary differences correlated with differences in the skuas' time budgets, activity patterns, territory types, breeding chronologies, nest densities, clutch sizes, and fledging success. With combined data from this and other studies at Palmer, I calculated average productivity for both species over 7 breeding seasons. Brown Skuas fledged higher and more consistent numbers of young per pair, probably because of their more accessible and reliable food source. *Received 13 March 1985, accepted 18 January 1987.*

SKUAS of the Southern Hemisphere are well known for their opportunistic feeding habits. South Polar Skuas (*Catharacta maccormicki*) and Brown Skuas (*C. lonnbergi*)[1] have been recorded as predators, scavengers, and kleptoparasites on a wide variety of organisms (e.g. Stonehouse 1956; Young 1963a, 1978; Burton 1968; Johnston 1973; Moors 1980; Sinclair 1980; Maxson and Bernstein 1982; Osborne 1985; Green 1986). Despite their opportunism, most skuas depend primarily on a few prey types. Where they nest allopatrically on the coasts of the Antarctic Continent, South Polar Skuas generally fish at sea, prey on penguin eggs and chicks, or both (Eklund 1961, Young 1963a, Le Morvan et al. 1967). On subantarctic islands, allopatric Brown Skuas feed primarily on penguin eggs and chicks or on adults of small Procellariiformes (Stonehouse 1956, Young 1978, Jones 1980, Moors 1980, Sinclair 1980, Fraser 1984, Osborne 1985). Brown and South Polar skuas nest sympatrically in a few areas, mostly along the Antarctic Peninsula between 61° and 65°S. At these sites there appears to be a sharp partitioning of food resources; Brown Skuas monopolize the terrestrial food source of penguin eggs and chicks, and South Polar Skuas forage almost exclusively at sea (Parmelee et al. 1978, Trivelpiece et al. 1980, Hemmings 1984).

One might expect to find other differences in Brown and South Polar skua ecology that correlate with these differences in diet. A few such correlates already have been documented. Neilson (1983), near Palmer Station on Anvers Island (64°46'S, 64°03'W), and Trivelpiece and Volkman (1982), at Point Thomas on King George Island (62°10'S, 58°30'W), noted parallels between breeding chronology and food habits. Neilson also noted differences in average duration of foraging trips, and both Trivelpiece et al. (1980) and Neilson observed differences in fledgling success.

My purpose was to examine skua ecology and behavior for correlates of the observed dietary differences. Possible correlates such as time budgets, diurnal activity patterns, and variation in egg and clutch size received little or no attention in earlier studies. Aspects of skua ecology studied previously merit further attention because skuas are long-lived birds (probably a 30–40-yr life span; Ainley 1981) and experience tremendous variability in feeding conditions within (Parmelee et al. 1978) and between (e.g. Trillmich 1978, Trivelpiece et al. 1980) nesting grounds.

STUDY AREA AND METHODS

This study was conducted during the 1979–1980 and 1980–1981 austral summers on several small islands and peninsulas within 5 km of Palmer Station. The ice-free areas around Palmer provide nesting sites for nearly a dozen bird species (Parmelee et al. 1977), including over 200 pairs of South Polar Skuas and up to 12 pairs of Brown Skuas. Each year there is also at least one mixed-species pair, usually consisting of a

[1] Pending resolution of their taxonomic status, I refer to these as full species. For discussions of skua systematics and nomenclature, see Pietz (1984, 1985).

South Polar Skua male and Brown Skua female. These mixed pairs produce viable hybrid offspring, capable of producing viable F_2 offspring (Parmelee and Rimmer pers. comm.).

Most skuas involved in this study were color-banded to allow individual recognition at a distance. Birds were captured with long-handled hand nets at the nest sites, or with rocket nets at bait sites. Most had been banded in previous years and thus had known breeding histories. Sexes were determined from observations of their copulatory positions, their roles in courtship feedings, or both.

Diet.—Neilson studied skua feeding habits at Palmer in the mid-1970's; he noted (Neilson 1983) that many Brown Skua pairs defended Adélie Penguin (*Pygoscelis adeliae*) colonies near their nest sites as feeding territories. Like Neilson, I gathered data on skua diets by recording foods regurgitated when adults fed chicks or mates and when adults or chicks were captured. Additional information came from direct observations of adult foraging activity.

Time budgets.—During observation periods at several skua nest sites, the behavior of each pair member was noted every 30 s using a metronome (Wiens et al. 1970). From these records hourly and daily time budgets were constructed for each individual and pair.

A total of 4,058 bird-hours of observations was made in the two seasons. Between 8 December 1979 and 22 January 1980, a field assistant and I documented the behavior of 4 South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed-species pair using 24-h sample periods. We obtained 50 bird-days of observations for South Polar Skuas, 14 for Brown Skuas, and 8 for the mixed pair. Between 27 January and 9 March 1980, when increasing darkness prevented 24-h observations, we watched each of the 7 pairs for 6 dawn-to-dusk periods. From 7 January to 6 March 1981 I made additional observations, using sample periods of 3–14 h. Eight South Polar Skua pairs, 2 Brown Skua pairs, and 1 mixed pair were sampled in the second season. The mixed pair, 1 Brown pair, and 4 South Polar pairs were observed in both years.

Some related behaviors were combined before time budget analysis. Grouped behaviors included resting (sitting, incubating, and brooding), foraging (procuring, transporting, and eating prey, and out of view off the nest territory), pairing (courtship and courtship feeding, copulation and attempted copulation), agonistic displays (long call, alarm call, bent neck, and wing raising), and agonistic encounters (running or flying displacement, swooping, aerial chasing, and fighting). Skuas were assumed to be resting during hours of darkness.

Assessment of foraging behavior presented special problems related to differences in observability of terrestrial and marine feeding. Total foraging time included periods when birds were off their territories and out of view as well as when they were feeding visibly (see Pietz 1986).

Breeding biology.—I divided the breeding season into (1) pre-egg laying, (2) incubation (after the first egg was laid), (3) brooding (after the first chick hatched), (4) postbrooding (after the first chick was no longer brooded regularly), and (5) fledging (when the first chick flew well enough to avoid capture). A sixth category (failed-nest) contained observations on pairs following loss of eggs or chicks.

Of the 4 South Polar Skua pairs observed in 1979–1980, 1 courted and defended a territory but failed to produce eggs. For comparison with the 3 breeding pairs, this pair's eggless season was divided into sections based on the average timing of incubation and brooding of the breeders.

In each season, breeding chronologies, egg sizes, chick growth rates, and reproductive success were documented for over 20 South Polar Skua pairs and for all Brown Skua and mixed-species pairs in the study area. Egg volumes were calculated from measurements of length and breadth, using the formula $V = (0.00048)LB^2$ (Furness 1983). Chicks were weighed and their tarsi and seventh and tenth primaries measured every 2–4 days.

Nest counts, fledgling counts, and notes on breeding chronology were recorded for the Adélie Penguin colonies. Approximately 14,000 Adélie pairs nested on islands in the study area.

RESULTS

Feeding habits.—The diets of skuas in the Palmer study area showed species-specific tendencies (Fig. 1). In both seasons, and in the seasons monitored by Neilson (1983), over 70% of the observed food items were fish for South Polar Skuas and penguin for Brown Skuas. Penguin accounted for less than 5% of the food records for South Polar Skuas, and fish accounted for less than 8% of the records for Brown Skuas. It should be noted that Neilson never observed fish in the Brown Skua diet, and 5 of 6 fish I recorded were attributed to chick feedings by a single Brown Skua female in one 24-h period. Furthermore, 3 of 4 observations of penguin in the South Polar diet involved only penguin skin and feathers. These meager meals presumably resulted from scavenging rather than predation.

For a mixed-species pair observed in both seasons, 45% of food records were fish and 50% penguin. Of the foods identified during chick feedings, all 5 of those brought by the Brown Skua female were penguin and all 5 brought by the South Polar male were fish.

Penguin in the diet was observed or assumed to be Adélie Penguin, as this was the only species

nesting close by. Skuas typically snatched penguin eggs and flew with them some distance from the colony, where they opened them and drank the contents. Small penguin chicks were swallowed whole at the site of capture or carried in the bill to the skua's nest. Large chicks, including those close to fledging, were dragged a short distance from the colony, killed, and eaten as described by Sladen (1958) and Young (1963b). Skuas often fed on large chicks over the course of several hours; they left only the feet, the bones of the legs and pelvic girdle, and the inverted pelt.

Most of the fish in the skuas' diet were *Pleuragramma antarcticum* that averaged about 10 cm in length. Skuas fished by surface plunging and surface seizing (terms follow Ashmole 1971).

Apart from fish and penguin, no single food type accounted for more than 15% of the records for either skua species. These items, several of which were taken by both species, represented opportunistic predation, pirating, and scavenging. One pair of South Polar Skuas caught adult Wilson's Storm-Petrels (*Oceanites oceanicus*) that nested in its territory; another pair raided the nests of neighboring Southern Black-backed Gulls (*Larus dominicanus*). Other pairs preyed on eggs and chicks of Antarctic Terns (*Sterna vittata*). Both skua species foraged in a melt pond during a temporary abundance of fairy shrimp (*Branchinecta* sp.). The contribution of such items to the diet varied from year to year.

For some of the foods eaten by both species, the sources were very different. Krill (*Euphausia superba*), for example, sometimes were caught at sea by South Polar Skuas. Possibly they ate krill when fish were difficult to find, as appeared to be the case in February–March 1981. Sometimes skuas caught krill incidentally with fish (pers. obs.; at Signy Island, Hemmings 1984). Krill are an important prey of *Pleuragramma* (DeWitt and Hopkins 1977), and they are often found together. Krill have also been seen washed up on ice floes (Fraser pers. comm., Parmelee pers. comm.), where they can be picked off by skuas fishing in the area. Brown Skuas, on the other hand, generally found krill in the penguin colonies, where they were spilled by penguins feeding their chicks. Gulls and American Sheathbills (*Chionis alba*) are credited with startling penguins during chick feedings to promote krill spillage (gulls: G. Maxson pers. comm.; sheathbills: Sladen 1958, Jones 1963); presumably skuas use this ploy as well.

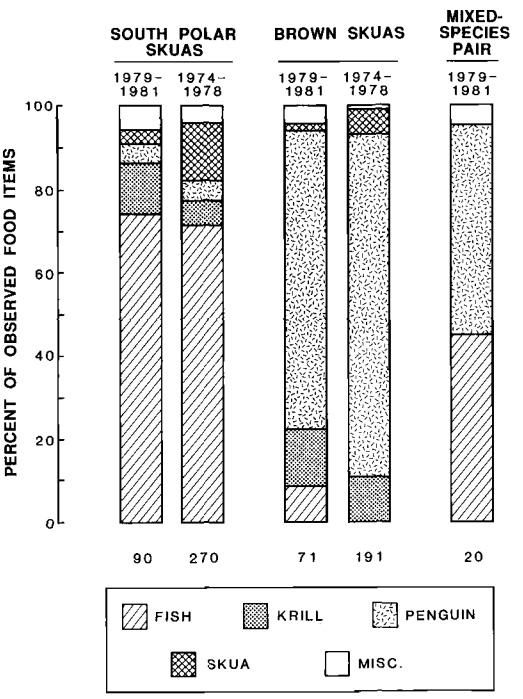

Fig. 1. Diet of South Polar and Brown skuas from records of direct feedings, courtship feedings, chick feedings, and regurgitations of food during handling. Percentages of each food type for 1979–1980 and 1980–1981 are compared with those calculated from 1974–1978 records (Neilson 1983). Total number of food records is given below each bar.

Kleptoparasitism was not an important means of obtaining food for either skua species at Palmer. However, during a period of heavy ice cover in 1979–1980, when little open water was available for surface fishing, South Polar Skuas chased and harassed Blue-eyed Shags (*Phalacrocorax atriceps*) in attempts to steal their catch. Maxson and Bernstein (1982) observed 38 such chases, 8 of which were successful, in less than 2 h. During the rest of the season, chase and success rates were lower; between 28 October 1979 and 11 March 1980, Maxson and Bernstein observed only 13 successful chases out of 280.

In some years gull fledglings provided a supplementary food source. Skua chicks require food from their parents well beyond the age of fledging, as late as March and sometimes April (Neilson 1983). After penguin fledglings left the Palmer area in mid-February, Brown Skuas still scavenged around the colonies on carcasses and krill, but they undoubtedly needed addi-

tional food sources. On several occasions adult skuas harassed fledgling gulls in the air. Remains of fledgling-size gulls were found on territories of both skua species. In other years at Palmer, Neilson (1983) observed that fledgling skuas also were taken late in the season. Given the highly variable reproductive success of gulls and South Polar Skuas at Palmer (Parmelee et al. 1978), this food source may not be available every year.

Cannibalism among skuas was difficult to distinguish from scavenging. In either case, the proportion of skua in their diets (eggs, chicks, and fledglings) varied among years (1–14% occurrence in food samples; Fig. 1), and probably depended on skua nest densities and the relative availability of other foods. During February 1981, when South Polar Skuas appeared to have difficulty finding food, there was evidence of sibling aggression and extensive "cannibalism." On one part of the study area, remains of skua chicks were found on 14 of 20 territories. Some chicks were eaten on their natal territory, others on neighboring territories; in most cases there were too few remains to identify individual chicks.

Territories.—Skua territories at Palmer were of two types. Every breeding pair defended the area surrounding its nest site. In addition, some Brown Skuas defended adjacent penguin colonies as feeding territories, from which they excluded other Brown Skuas, South Polar Skuas, and Southern Black-backed Gulls that tried to feed there.

During the two seasons at Palmer, 4 Brown Skua pairs maintained feeding territories containing roughly 700–2,300 penguin nests, 2 had territories with ≤300 nests, and 3 did not defend feeding territories. Holding a large feeding territory may not have conferred much advantage in this area, because the 5 pairs with small or no feeding territories foraged at least part of the time on another island <1 km away. This island offered a plentiful food supply, as there were 8,700 penguin nests and no skua feeding territories.

One would expect territory size and distances between nests to depend partly on territory type. As South Polar Skuas held only nesting territories and 6 of 9 Brown Skuas held combined nesting and feeding territories, it is not surprising that the closest nests were those of South Polar Skuas. On a peninsula where South Polar nest territories had been established for at least a decade, the closest nests were 12 m apart. On an island where 7 South Polar pairs were defending new nest sites, 2 nests were 2.5 m apart and a third was within 7 m. For Brown Skuas in this study, the closest nest of either species was 49 m away. In earlier years at Palmer, when Brown Skua densities were higher, their nearest neighbors were still >30 m away (Parmelee pers. comm.). In 1983–1984 Parmelee (pers. comm.) found a South Polar nest 15 m from a Brown Skua nest. He also noted nearly continuous aggressive interactions between the two pairs.

Time budgets.—Complete time budgets for individual South Polar and Brown skuas were given by Pietz (1984). Within stages of the breeding season, the two species did not differ greatly in time allocated to most behaviors. There were significant species differences, however, in the amount of time spent foraging and in agonistic encounters.

Foraging time, or time away from the nest territory, differed most strongly during the incubation/brooding period (Fig. 2); 3 breeding South Polar pairs averaged 6.6 h/day off the nest territory, and 3 Brown pairs averaged 3.2 h/day ($t_4 = 4.324$, $P < 0.02$). During postbrooding, South Polar foraging time remained the same (6.7 h/day); Brown Skua foraging time increased to 5.7 h/day (2 pairs), probably reflecting their increased searching and handling time as penguin chicks became larger and less abundant. Despite closer mean values for foraging, postbrooding data produced a statistically significant difference between species ($t_3 = 5.087$, $P < 0.02$). This could be due to very small standard deviations resulting from coincidence in the small sample.

Small sample size also made it difficult to evaluate the pre-egg-laying period. South Polar pairs foraged slightly more in this period (7.7 h/day) than in the rest of the season. Foraging time of the only Brown pair observed in this period (10.4 h/day) probably was not typical for the species. This was a recently formed pair that laid eggs 6 weeks after the median date for Brown Skuas that year.

Differences in male and female foraging time (Fig. 2) were evaluated statistically only for South Polar Skuas. In the pre-egg-laying period males did most of the foraging (91% of pair totals); females remained on the nest territory and received most of their food through courtship feedings (Pietz 1984). After eggs were laid, female foraging time increased to nearly match

that of males (46% and 48% of pair totals during incubation/brooding and postbrooding, respectively). Despite the fact that it produced no eggs, a fourth South Polar pair showed similar trends in male and female foraging time from early to late in the season (Fig. 2). An ANOVA test for the 4 South Polar pairs revealed significant effects of sex (log-transformed data, $F_{1,18} = 8.73$, $P = 0.008$) and of a sex/season interaction ($F_{2,18} = 7.31$, $P = 0.005$).

For Brown Skuas no clear male/female pattern in foraging time was evident; however, sample sizes were very small. Elsewhere, both Brown Skuas (Stonehouse 1956) and South Polar Skuas (Young 1963a) showed the pre-egg-laying foraging pattern described, where females were rarely away from the nest site and received most of their food from their mates.

Members of the mixed pair followed the patterns of their respective species and sexes. Before egg laying the South Polar male foraged an average of 10.0 h/day, and the Brown Skua female almost never left the nest area (0.02 h/day). After egg laying the female increased her foraging time to 2.3 h/day during the incubation/brooding period and then to 5.8 h/day during postbrooding. During the same periods the male's foraging time remained constant (8.9 h and 9.1 h/day).

Frequency of agonistic encounters was another aspect of time budgets related to feeding ecology. The frequency of low-energy agonistic displays (e.g. long calls and bent-neck displays used in territorial advertisement) did not differ significantly between South Polar Skuas and Brown Skuas with or without feeding territories (Fig. 3; t-test results for both years had P-values > 0.10). However, the frequency of high-energy agonistic encounters (e.g. aerial chases and fights used in territorial defense) was significantly greater for Brown Skuas with feeding territories than for South Polar Skuas (1979–1980: $t_3 = 3.412$, $P < 0.05$; 1980–1981: $t_5 = 7.548$, $P < 0.001$) or for Brown Skuas without feeding territories ($t_3 = 5.781$, $P < 0.05$). The frequencies in 1980–1981 varied more widely within groups than those in 1979–1980. This probably reflected fewer observation hours in the second year (Fig. 3). Nevertheless, frequencies of agonistic displays ranged from about 1/h to 3/h for pairs of both species in both years. Agonistic encounters ranged from 0.08/h to 0.33/h for all pairs without feeding territories (including South Polar, Brown, and mixed), and from 0.80/h to 1.75/h for Brown Skuas with feeding territories.

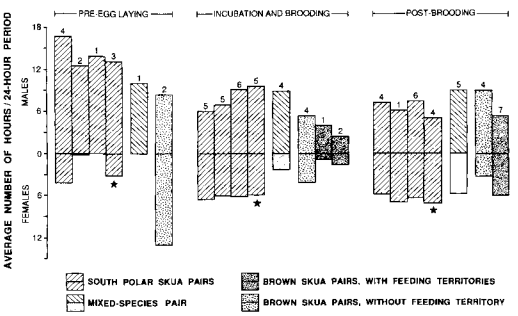

Fig. 2. Average foraging time of South Polar and Brown skuas during 3 phases of the breeding season. The male and female of each pair are represented above and below the abscissa, respectively. The number of 24-h or dawn-to-dusk observation periods is indicated above each set of bars. Stars indicate a South Polar pair that maintained a territory but produced no eggs.

Activity patterns.—During two months of the summer at Palmer the sun stays above the horizon for about 23 h/day. A short period of twilight occurs around 2400. Previously, I examined daily activity patterns of Brown and South Polar skuas during these months (Pietz 1986). South Polar Skuas exhibited maximum resting and minimum foraging activity during twilight; Brown Skuas appeared to rest and forage more randomly. Members of the mixed pair exhibited patterns similar to those of their respective species. Several hypotheses were suggested to account for these species differences in activity patterns; most related dietary differences and differential foraging abilities at low light levels (Pietz 1986).

Length of foraging bouts was related strongly to diet and feeding behavior. Foraging bouts averaged 13 min for Brown Skuas with feeding territories and about 1 h for those without. South Polars averaged foraging trips of 2–3 h when the sea was open and over 7 h during heavy ice cover (Pietz 1986).

Breeding chronology.—South Polar Skuas showed more between-year variation in hatching dates than did Brown Skuas (Table 1). For Brown Skuas, median hatching dates of first chicks differed by only 3 days between 1979–1980 and 1980–1981. Median hatching dates for South Polar Skuas differed by 12 days between years.

Clutch initiation dates were observed directly

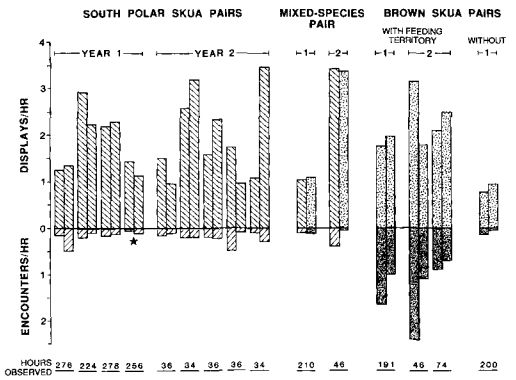

Fig. 3. Frequency of agonistic behaviors for individual South Polar and Brown skuas. Each set of 2 bars represents the male (left) and female (right) of a pair. Bars above the abscissa indicate frequencies of low-energy agonistic displays (e.g. long calls, wing raising); bars below the abscissa indicate frequencies of high-energy agonistic encounters (e.g. fights, chases). Star indicates a South Polar pair that maintained a territory but produced no eggs.

for most of the study birds in 1979–1980. For 1980–1981 most egg-laying dates were back-calculated, using mean incubation periods of 28 days for South Polar Skuas (SD = 1.47, n = 10 first chicks) and 30 days for Brown Skuas (Burton 1968).

For 4 other seasons at Palmer, mean clutch initiation dates for South Polar Skuas (Neilson 1983) were as much as 2 weeks earlier than I found. Over these 6 seasons South Polar Skuas exhibited a 4-week spread in mean initiation dates. For 3 other seasons Neilson reported mean initiation dates for Brown Skuas that fell within 4 days of my mean dates, resulting in a 5-season range of only 1 week.

Delayed nesting by South Polar Skuas in 1979–1980 (Table 1) coincided with evidence of food stress. In 1979–1980 heavy ice cover extended to the horizon from mid-November, when the South Polar Skuas arrived, through the second week of January. This made fishing very difficult, as indicated by the fact that foraging trips averaged over 7 h (Pietz 1986). During the same period in 1980–1981, open water occurred within 5 km of the nesting areas, and foraging trips were commonly under 1 h.

The relationship between food availability and breeding chronology was emphasized by the case of the mixed-species pair. Chick hatching dates of the mixed pair corresponded to those of South Polar pairs in both years (Table 1). Presumably, the Brown Skua female had to be brought into egg-laying condition by courtship feedings from her South Polar mate; thus, her egg-laying dates reflected the food supply of South Polar Skuas. In reports of nest-initiation dates for 9 other mixed-species pairs, only 1 nested earlier than was typical for South Polar Skuas of that year (Trivelpiece and Volkman 1982, Neilson 1983). The influence of food on breeding chronology was clearest in the case of a South Polar Skua pair with an artificially supplemented diet. In both years this pair, which received food from station personnel, laid eggs at the same time as the Brown Skuas. Their chicks hatched about a week before the next earliest South Polar pair and about 3 weeks ahead of the median date for South Polar Skuas. In a nearly identical occurrence on King George Island, a South Polar pair that fed at the station dump laid eggs nearly 3 weeks before any other South Polar pair (Trivelpiece 1980).

Given the temporal predictability of their food source, it is surprising that Brown Skua hatching dates were less synchronized within years than those of South Polar Skuas (Table 1). In both 1979–1980 and 1980–1981 this range was attributed largely to one late-nesting pair. Careful observation of these pairs throughout the season indicated that the late nests were not second nest attempts. At the end of the 1978–1979 season 60% of Palmer's breeding Brown Skuas died of avian cholera (Parmelee et al. 1979); thus, an unusual number of new pair bonds were formed in 1979–1981. This may explain the late-nesting pairs in my sample. In years before the cholera epidemic, Brown Skua pairs nested more synchronously than South Polar Skuas (Neilson 1983).

Breeding success.—Data from the 1979–1980 and 1980–1981 breeding seasons suggested that South Polar Skuas were more variable than Brown Skuas in number of nests initiated, proportion of two-egg clutches, and fledging success. This between-year reproductive variability was correlated with variability in the food supply. In 1979–1980, the year they experienced food stress at the start of the season, fewer South Polars initiated nests than in 1980–1981 (e.g. 11 vs. 19 in one sample area), and fewer had two-egg clutches (45% vs. 100%). In 1980–1981 food stress occurred late in the season and was correlated with lower fledging success (0.36 vs. 0.11/pair). Brown Skuas, feeding on a constant supply of penguins, fledged more young in both

TABLE 1. Hatching dates for Brown, South Polar, and hybrid skua chicks near Palmer Station, Antarctica, using the first chick hatched in each clutch.

Chicks of:	Median	Mean	SD (days)	Range	No. of clutches
Brown Skuas					
1979–1980	30 Dec	6 Jan	16.1	28 Dec–7 Feb	6
1980–1981	27 Dec	3 Jan	14.9	24 Dec–29 Jan	5
South Polar Skuas					
1979–1980	27 Jan	27 Jan	7.1	13 Jan–9 Feb	15
1980–1981	15 Jan	14 Jan	6.4	3 Jan–25 Jan	19
Mixed-species pair					
1979–1980	28 Jan				1
1980–1981	15 Jan				1
South Polar Skuas with artificially supplemented diet					
1979–1980	1 Jan				1
1980–1981	28 Dec				1

years (1.29 and 0.67/pair). Brown Skuas also showed less between-season variability in terms of numbers of nests initiated (7 and 6) and proportion of two-egg clutches (86% and 83%).

To test the long-term validity of these trends, I combined the data for all Brown Skua nests in the Palmer area and for all South Polar nests on one part of my study area with data collected at the same sites by Neilson in 1974–1975, 1975–1976, 1976–1977, and 1977–1978, and by Rimmer and Parmelee in 1983–1984. Combined data for these 7 breeding seasons confirmed the trends suggested above (Table 2). Fledging success over the 7 seasons differed significantly between species (paired $t_6 = 2.778$, $P < 0.05$). South Polar Skuas showed wider ranges in nest density, percentage of two-egg clutches, and number of fledglings/pair.

The most dramatic effect of food stress on nest initiation was recorded in 1977–1978, when South Polar Skuas experienced a total reproductive failure because of the persistence of heavy ice cover (Parmelee et al. 1978). Skuas had to fly so far to feed that they were absent from their territories for days. Consequently, only a few eggs were laid in the sample area and none hatched.

A more subtle indicator of food availability was egg size. At the beginning of the 1979–1980 breeding season, when South Polars had difficulty finding food, those that completed a two-egg clutch laid a significantly smaller second egg ($\bar{x}_{diff} = 4.13$ cm^3, SD = 2.09; paired $t_6 = 5.228$, $P < 0.002$). In 1980–1981 the same sample of birds showed no significant differences between first and second eggs ($\bar{x}_{diff} = 2.09$ cm^3, SD = 2.81; paired $t_5 = 1.822$, $P > 0.10$). Furthermore, paired tests across years showed that first eggs in 1979–1980 were smaller than first eggs in 1980–1981 ($\bar{x}_{diff} = -6.57$ cm^3, SD = 3.01; paired $t_5 = -5.356$, $P < 0.005$), and second eggs of 1979–1980 were smaller than second eggs of 1980–1981 ($\bar{x}_{diff} = -8.45$ cm^3, SD = 2.96; paired $t_5 = -6.981$, $P < 0.001$).

The sample of Brown Skua eggs of known laying order was not adequate to compare with the South Polar Skua results. Therefore, I calculated volumes and attempted paired tests on measurements given by Stonehouse (1956) and Bonner (1964) for Brown Skuas on South Georgia (54°S, 37–38°W). Neither data set ($n = 5$ and 10 clutches, respectively) yielded a significant difference in the volumes of first and second eggs. In larger samples, differences in first- and second-egg volumes can be detected in both species. When the Bonner and Stonehouse data were combined, the paired t-test revealed a slightly significant difference ($\bar{x}_{diff} = 4.34$ cm^3, SD = 7.64; $t_{14} = 2.203$, $P < 0.05$). Likewise, for my expanded data set of South Polar Skua nests from 1980–1981, the paired t-test indicated a slight difference between first and second eggs ($\bar{x}_{diff} = 1.99$ cm^3, SD = 3.48; $t_{15} = 2.285$, $P < 0.05$). Nevertheless, these differences were statistically much less significant than those for 1979–1980 or between years.

Food availability ultimately affected chick survival at Palmer. During February 1981, a pe-

TABLE 2. Average annual productivity for South Polar and Brown skuas near Palmer Station, Antarctica. Tabulations include data for 1979–1980 and 1980–1981 (present study), and for 1974–1975, 1975–1976, 1976–1977, 1977–1978 (Neilson unpubl. data), and 1983–1984 (Rimmer and Parmelee unpubl. data). Values are means ± SD, with ranges in parentheses.

	South Polar Skuas	Brown Skuas
No. of nests in sample area	14 ± 6.0 (2–20)	9 ± 1.9 (6–11)
Percentage of 2-egg clutches	88[a] ± 22.1 (45–100)	91 ± 6.6 (83–100)
Percentage hatching success	86[a] ± 7.6 (77–95)	90 ± 10.8 (73–100)
Fledging success (fledglings/pair)	0.8 ± 0.7 (0–1.7)	1.4 ± 0.4 (0.7–1.8)

[a] Excludes 1977–1978 season, in which South Polar Skuas initiated only 2 1-egg nests in the sample area, and no eggs hatched.

riod of food stress for South Polar Skuas, chick mortality was high. On one island, for example, at least 13 South Polar chicks from 8 nests were still alive at the end of January; by 17 February they were all dead. Sibling aggression in skuas is triggered by hunger (Procter 1975) and can be an important direct or indirect cause of chick mortality (Young 1963a, Reid 1966, Spellerberg 1971). During the 1980–1981 season I first observed signs of sibling aggression in February. Two pairs of sibling chicks had feathers plucked from their heads in the days before their deaths. One of these pairs, 4–6 weeks old, showed successively severer wounds to the head, neck, and back in the 2 weeks before they died.

During periods of food stress both parents sometimes left the nest territory to look for food. This exposed chicks to potential danger from weather and predation. Joint absences from the nest territory were very rare for successfully breeding parents (Neilson 1983, Pietz 1986). Of the joint absences that I observed, 2 coincided with deaths of South Polar Skua chicks. One was a 4-day-old chick exposed to rain, snow, and 15 km/h winds for more than 3 h [chicks of this age require brooding to survive unfavorable weather (Spellerberg 1969)]. The other chick, about 4 weeks old, was killed by an adult on an adjacent territory when the chick approached it, begging for food.

DISCUSSION

In antarctic and subantarctic regions, most penguins breed at traditional colony sites. Their ability to fast during incubation allows nonincubating pair members to forage at great distances from the nest colony and, thus, overcome locally unfavorable feeding conditions. These characteristics make penguins a spatially and temporally predictable food source for skuas.

The availability of marine food sources, on the other hand, is affected by the skuas' ability to gain access to them. Ice cover and storms can prevent skuas from feeding (Parmelee et al. 1978, Neilson 1983). South Polar Skuas appeared to have difficulty obtaining food at sea during February 1981. Yet this was a period in which neither ice cover nor storm activity increased markedly. Prey movements, either horizontally or vertically, may have been the problem. *Pleuragramma* and krill swarms apparently move in ways that skuas find spatially and temporally unpredictable.

Neilson (1983) and Trivelpiece and Volkman (1982) found that Brown Skua nesting was closely timed to that of Adélie Penguins, thus ensuring a plentiful food supply. It also allowed them to nest earlier than South Polar Skuas in most seasons. In only 1 of the 7 years examined at Palmer (1974–1975) did South Polar Skuas nest as early as was typical for Browns. Early nesting may increase chick survivorship. Wood (1971) and Neilson (1983) found that chicks of late-breeding South Polar pairs suffered higher mortality rates than those of early-breeding pairs. The main mortality factor they cited was late-season storms; chicks apparently suffered from exposure and from the inability of parents to forage normally.

Young (1963b) suggested that higher fledging success observed in Brown Skuas was partly related to their having larger territories. Larger territories presumably make it less likely that chicks will wander into neighboring territories, where they might be attacked. My observations at Palmer support this idea. However, Hemmings (1984) found that South Polar Skuas had higher fledging success than Brown Skuas for 2 seasons on Signy Island, despite having smaller territories. Territory size possibly is critical only in years of food stress. Furthermore, territory size and nest distances need not be correlated. As Burton (1968) pointed out, territories may be over 1 ha in size yet, because of topographical features of the area, nests may be grouped together near mutual boundaries.

Another factor that may affect fledging success is the energetic cost of different foraging

strategies. Feeding at sea requires more search time, but feeding on penguin eggs and chicks requires more handling time. Trivelpiece et al. (1980) noted significantly greater fledging success for Brown Skuas that defended feeding territories. Yet, I have shown that Brown Skuas with feeding territories spent more time fighting and chasing other birds.

Actual energy costs of the differences in agonistic behavior and foraging time are difficult to assess. Foraging at sea has not been observed often enough to determine the proportions of time spent sitting on the water, surface plunging, and flapping, gliding, and hovering above the water. The cost of feeding on penguins and defending this food resource from other birds may include an increased risk of injury in addition to energy demands. The risk of injury, however, is probably small relative to others to which skuas are exposed [e.g. during fights for mates (pers. obs.) and long-distance migration (Parmelee et al. 1977)]. I never observed an injury related to foraging.

The higher fledging success associated with feeding on penguins at most sites was not restricted to interspecific comparisons. At Cape Royds on Ross Island (77°27'S, 169°14'E), South Polar Skuas that fed mainly on penguins fledged more chicks than those that fed primarily at sea (Young 1963a). It appears that both skua species should prefer to feed at penguin colonies.

In the absence of Brown Skuas, South Polar Skuas not only feed on penguins but also defend penguin colonies as feeding territories. Such territories have been described for allopatric populations of South Polar Skuas at Cape Hallet (72°19'S, 170°13'E; Trillmich 1978) and at Cape Royds (Young 1963a, b), Cape Bird (Young 1972), and Cape Crozier (Müller-Schwarze and Müller-Schwarze 1973) on Ross Island. Only 33 km from Palmer on the west coast of Anvers Island, South Polar Skuas nest adjacent to and feed on penguins in the absence of breeding Brown Skuas (Parmelee pers. comm.). I do not know if these South Polars defend feeding territories.

At Palmer in 1981, 2 yr after 60% of the breeding Brown Skua population died of fowl cholera (Parmelee et al. 1979), a few pairs of South Polar Skuas nested adjacent to small penguin colonies on one island. At least one pair attempted to defend the penguin food resource. None of these pairs succeeded in raising chicks, possibly because they were nesting there for the first time and started very late in the season. By 1983–1984 South Polar and Brown skuas successfully nested adjacent to these penguin colonies, but only the Brown Skuas appeared to use them as a food source (Parmelee pers. comm.).

Assuming that South Polar Skuas would prefer to eat penguins, what prevents them from doing so where they nest sympatrically with Brown Skuas? The limited number of penguin nests at Palmer (approx. 13,000–14,000; Maxson and Bernstein 1980, Pietz unpubl. data) suggests that skuas must compete for access to this food source. Brown Skuas weigh more, and have longer legs and heavier bills than South Polars (Neilson 1983, Pietz unpubl. data). Although direct observations of interspecific interactions during territory establishment have not been reported, larger size probably gives Brown Skuas an edge in aggressive interactions. Where they are in sufficient numbers, Brown Skuas apparently can monopolize the penguin food resource.

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100 Years Ago in The Auk

From "The Present Condition of Some of the Bird Rookeries of the Gulf Coast of Florida" by W. E. D. Scott (1887, Auk 4: 272–284):

"Wednesday, June 2 [1887]. Leaving the little town of Pinellas early this morning we rounded Point Pinellas, and again were cruising northward in the direction of Tarpon Springs. About three miles from the extreme end of Point Pinellas, in Boga Siega Bay, is the group of islands that once formed what is known as Maximo Rookery. These islands are so close together, being only divided by shoal and narrow streams of salt water at high tide, that practically they form a single low island. This is at least two hundred acres in extent, and is covered with a dense growth of the several kinds of mangrove and forms a point particularly attractive to birds either as a roosting or breeding place. I had been here six years before, and it fairly teemed with bird life then. Every tree and bush on this large area contained at least one nest, and many contained from two to six or eight nests whenever the size of the tree permitted. A perfect cloud of birds were always to be seen hovering over the island in the spring and early summer months, and conspicuous among them were Brown Pelicans, Man-o'-war Birds, Reddish Egrets, Florida Cormorants, Louisiana Herons, American Egrets, Snowy Herons, Little Blue Herons, Great Blue Herons, and both kinds of Night Herons. I have tried to give them in the order of their abundance, though it is difficult to say, in such an immense congregation, which species predominated. Beside, in comparatively smaller numbers, and yet by hundreds, were White Ibises and Rosy Spoonbills. So far as I was then able to determine, all these species bred here save the Roseate Spoonbill and Man-o'-war bird, the latter being present to prey on the Pelicans and Cormorants, taking from them, whenever possible, the food intended for the young birds. It was truly a wonderful sight, and I have never seen so many thousands of large birds together at any single point.

"We anchored the sloop just off the island and I went ashore to see what birds I might find. From the water, as we approached, only a few Cormorants were to be seen, possibly seventy-five in all, and though I spent several hours looking over the various parts of the island I found no other large birds breeding—absolutely not a single pair of Herons of any kind; five or six Louisiana Herons feeding on a small sand flat at one of the extremities of the island were all the Herons observed in the vicinity.

"When I previously visited this point A. Lechevallier had located on the mainland about three-quarters of a mile away; here he had built a house and was killing birds on the island for the feather market. He or his assistants had then been there a little over a year, and I am told by persons living near, whom I have every reason to believe, that it took these men *five* breeding seasons to break up, by killing and frightening the birds away, this once incomparable breeding resort. Of course there were other plume hunters who aided in the slaughter, but the old Frenchman and his assistants are mainly responsible for the wanton destruction. He regarded this as his particular preserve, and went so far as to order outsiders, who came to kill Herons and other birds, off the ground. The rookery being destroyed, he had now given up his residence here."