

POPULATION DYNAMICS OF BREEDING SOUTH POLAR SKUAS OF UNKNOWN AGE

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SEVERAL authors have presented data and discussed various aspects of population dynamics of the two most southerly breeding forms of *Catharacta*, the South Polar Skua (*C. maccormicki*) (Eklund, 1961; Young, 1963; LeMorvan et al., 1967; Pryor, 1968) and the Brown Skua (*C. skua lonnbergi*) (Stonehouse, 1956; Burton, 1968; Purchase, *in* Carrick and Ingham, 1970). These studies have been either of short duration, based on few breeding pairs, or both. Breeding success in the extreme antarctic environment varies highly from year to year and also considerably within a region of dissimilar topography. Survival is less variable, but a large population must be studied to obtain accurate figures.

This study of individually marked skuas of unknown age took place at Cape Crozier (77° 27' S, 169° 14' E) on Ross Island, Antarctica during eight consecutive breeding seasons (November through February) beginning in 1961. It forms a base line for current studies on breeding skuas of known age. The South Polar Skua population at Cape Crozier consists of 950 to 1,000 pairs of breeding birds and an estimated 200 to 400 nonbreeders. Approximately 80 per cent of each group was banded. Six discrete breeding areas are dispersed along the inland periphery of a rookery of 175,000 pairs of Adélie Penguins (*Pygoscelis adeliae*) (Emison, 1968).

One breeding area of approximately 11 hectares (27 acres) was chosen at the beginning of the study for its relative freedom from human disturbance and for its isolation from other skua breeding areas. Topography varied from nearly level to a slope of 42 per cent. During 5 consecutive years of the study the mean number of breeding pairs was 110 (Table 4); 94 per cent of the breeders were banded and of these 55 per cent were sexed by copulatory position and/or by courtship feeding (Young, 1963). Breeding skuas on their territories were caught with a hand net when they dived at the observer's head (Austin, 1957). Breeding skuas away from their territories and nonbreeders were baited and noosed. The only banding casualty was a bird whose wing was broken when it was netted.

Three types of bands were used. All captured skuas were given a 25-mm (1 inch) tall aluminum band with the serial number imprinted vertically on two opposite sides of the band to facilitate reading with binoculars or spotting scope (Sladen, Wood, and Monaghan, 1968). This band was placed on the right tarsus of adult skuas and on the left

TABLE 1
MINIMUM DISTANCES BETWEEN ADJACENT NEST SITES IN ONE SEASON

Distance ¹ (m)	Number of nests	Per cent
1-10	15	14
11-20	58	53
21-30	25	23
31-40	9	8
41-50	1	1
51-60	1	1

¹ Range 4-53 meters, mean 19 meters.

tarsus of nestlings in conformance with recommendations of the Subcommittee on Antarctic Bird Banding of the international Scientific Committee for Antarctic Research. As part of a continent-wide scheme of area colors, a 10-mm tall yellow plastic band was put on the left tarsus of breeding adults to denote the Ross Sea sector of Antarctica. A 9-mm tall band of nickel alloy was placed below the yellow band on the left tarsus of study area breeders to distinguish them from other Crozier breeders. This band bore a three digit number imprinted three times in a horizontal position which further assisted in easy identification of individual skuas.

The possibility of band loss must be considered in any study of long duration that depends on individually marked birds. The specially-designed skua band, being 25 mm tall, is inherently stronger than the standard 11-mm band issued by the Fish and Wildlife Service. Very few bands were seen that had opened as much as 1 mm. These were replaced, as were nearly all original bands as the band design was improved. The two supplementary bands were a further check against band loss. Almost all breeding skuas in the study area were marked with yellow plastic bands, and about half were marked with nickel alloy bands. As none of these birds was seen without the tall band on the right tarsus, band loss during this study is assumed to be negligible.

PAIR BOND

Breeding skuas apparently do not remain paired during the winter, as single birds were seen reoccupying territories at the start of the breeding season. In early November, approximately 2 weeks after the first arrival and just prior to a rapid increase in numbers that coincided with the peak of laying in the Adélie Penguin rookery, partial counts showed 16 skuas paired (8 pairs) and 29 unpaired. Some of the latter were probably paired and their mates were away foraging. Of the unpaired birds whose sex was known, 10 were males and 2 were females, suggesting that males usually return to the breeding territory before

TABLE 2
CHANGES IN NEST SITES OF 47 PAIRS OF SKUAS IN TWO CONSECUTIVE SEASONS

Distance moved ¹ (m)	Number of pairs	Per cent
0-5	23 ²	49
6-10	12	25
11-15	6	13
Over 15	6	13

¹ Range 0-51 meters, mean 7.6 meters.

² 14 pairs re-occupied the same nest site.

females. Burton (1968) reported that in the Brown Skua successful breeders left the area several days apart at the end of the breeding season.

Skua pairs normally reunited each breeding season unless one bird failed to return. Thus of 267 pairs that were recorded in 2 consecutive seasons, only 4 pairs (1.5%) did not reunite. Five of these eight individuals found new mates the first year, one remained unpaired until the second year, and two were not seen again after the year of separation.

Skuas were prompt in replacing lost mates. In 27 pairs in which one bird failed to return, all survivors but one paired again the first year and produced eggs either the first or second years. Eighteen (67%) survivors paired with skuas that were unbanded, suggesting that the latter were breeding for the first time. Four survivors combined to form two pairs, four paired with skuas that had separated from their previous mates, and one paired with a skua that had previously bred outside the study area.

The ease with which skuas acquired new mates did not mean that they immediately became effective members of the breeding population, as will be shown in the discussion.

SITE TENACITY

Skuas show a high degree of site tenacity, breeding in the same territory year after year and often in the same nest scoop. Territorial boundaries were not plotted; data are based on the relative nest positions of adjacent pairs. In one season the mean distance between each of 109 nests and its nearest neighbor was 19 m (Table 1). The mean distance that 47 pairs moved from one season to the next was 7.6 m (Table 2), 14 (30%) of these pairs using the same nest scoops both years. Of 312 pairs that bred together in two consecutive seasons, only 4 pairs (1.3%) moved far enough to change the previous relationship of adjacent pairs (Table 3). These four moves averaged 32 m, almost twice the mean minimum distance between nests.

When a pair was broken by the disappearance of one bird, the survivor rarely moved farther than to an adjoining territory. Of 27 such

TABLE 3
CHANGES IN RELATIVE NEST POSITION OF ADJACENT BREEDING PAIRS

	1963-64	1964-65	1965-66	1966-67	Total
Number of pairs that had bred together for 2 or more consecutive years	67	76	87	82	312
Number of changes in relative position of nest site	2	1	0	1	4

survivors, 23 (85%) remained on their territories, including 3 that used the same nest scoops, while 3 moved to adjoining territories and only 1 moved farther. This skua was not recorded for two seasons and then was found breeding two territories away, a distance of approximately 35 m. Changes were too infrequent to be correlated with the bird's sex.

Because site changes within the study area were limited almost entirely to adjacent territories it is not surprising that changes between breeding areas at Crozier were very infrequent. Emigration from the study area was detectable by the supplementary metal bands put on about half the breeders. One instance of emigration was found, a movement of about 1,500 m. The bird's sex was unknown but it had bred for the previous 4 years, the last 2 with the same mate. The mate remained on the original territory, alone. Two females moved into the study area from distances of approximately 1,000 m. Their original mates were banded but were not recorded after the change.

Breeding changes of greater distance were very rare. Approximately 1,800 Crozier breeders were marked with the distinctive yellow plastic band; only one such breeder was found during searches of all known breeding areas within 160 km of Crozier. This skua had moved 71 km to Cape Evans on the opposite side of Ross Island. It had bred at Crozier in 1962-63 and was found breeding at Cape Evans in 1967-68. It was not seen during the intervening four seasons. Immigration to Crozier was virtually impossible to detect as so few breeding skuas had been banded elsewhere.

These four movements demonstrate that skuas occasionally change breeding areas and that a missing breeder may not be dead. However the very small number of such moves makes this factor negligible in determining survival. Because two of the four skuas involved in these changes moved from territories near the hut and helicopter landing area, it is possible they were influenced by human activity, yet the number of breeding skuas in this area changed only slightly in 5 years, from 71 to 67 pairs. This fluctuation is no greater than was recorded in the study area (Table 4).

TABLE 4
BREEDING SUCCESS IN CAPE CROZIER STUDY AREA

Year	Breeding pairs	Fledged chicks	Fledged chicks per breeding pair	End of observations
1961-62	110 ¹	45	0.41	22 February
1962-63	121	73	0.60	2 March
1963-64	111	46	0.41	28 February
1964-65	107	33	0.31	19 February
1965-66	112	19	0.17	22 February
1966-67	98	12	0.12	18 February
1967-68	110 ¹	14	0.13	14 February
1968-69	110 ¹	53	0.48	16 February
TOTALS	879	295		

¹ 110 is the mean number of breeding pairs from 1962-63 to 1966-67. Counts were not made in 1961-62, 1967-68, and 1968-69

BREEDING SUCCESS

Table 4 shows the breeding success of skuas in the Cape Crozier study area. Figures are based on the ratio of fledged chicks per breeding pair, the most meaningful measure of productivity for the study because some pairs did not lay a full clutch of two eggs. A successfully fledged chick is one banded up to 3 weeks before fledging (chicks could not be banded at an earlier age because of the height of the band) and which was not found dead at a later date. Of 1,445 chicks banded in all breeding areas at Crozier, 74 (5%) were found dead the same or following season. Corpses were not difficult to find because of the absence of vegetation. Undoubtedly some were overlooked or were blown into the sea during storms, and certainly an occasional pair of skuas produced and lost its eggs before being recorded as a breeding pair. Including these small but unknown quantities would make skua productivity somewhat lower.

Annual breeding success varied fivefold over the 8-year period, from a minimum of 0.12 chicks per breeding pair to a maximum of 0.60 chicks. The mean was 0.34 per breeding pair. This wide range in annual productivity emphasizes the need for data from several breeding seasons.

The figures for breeding success given in Table 5 for Haswell Island, Windmill Islands, and Geologie Archipelago are much higher than those for Crozier, Cape Hallett, and Cape Royds. This is probably due more to observations being concluded before chicks were fledged than to a much higher productivity. Observations ended at Haswell Island on 5 January (Pryor, 1968) and at Windmill Islands in "the last week of January" (Eklund, 1961). Some of the least productive years at Crozier were caused by heavy losses of chicks during blizzards in late January when winds reached velocities of 60 to 100 mph for periods up to several days. Small, late-hatched chicks suffered proportionately higher losses

TABLE 5
COMPARISON OF BREEDING SUCCESS IN SOUTH POLAR AND BROWN SKUAS

Location	Breeding seasons	Breeding pairs	Chicks fledged ¹	Chicks per pair	Reference
South Polar Skua					
Cape Crozier	8	879	295	0.34	This study
Cape Hallett	3	472	204	0.43	Reid (MS)
Cape Royds	1	67	31	0.46	Young, 1963
Haswell Island	1	23	18	0.78	Pryor, 1968
Geologie Archipelago	4	66	75	1.13	LeMorvan et al, 1967;
					Isenmann (pers. comm.)
Windmill Islands	1	40	34	0.85	Eklund, 1961
Brown Skua					
Macquarie Island	1	40	46	1.15	Purchase, in Carrick and Ingham, 1970
Signy Island	3	65	77	1.18	Burton, 1968
South Georgia	2	6	6	1.00	Stonehouse, 1956

¹ Not all chicks were known to fledge as observations were concluded on varying dates: Cape Crozier, see Table 4; Cape Hallett, 23 Jan. (2 years) and 5 Feb.; Cape Royds, 23 Feb.; Haswell Island, 5 Jan.; Windmill Islands, last week of January; Signy Island, end of breeding season.

of up to 75 per cent, apparently from exposure and from the inability of parents to forage normally. Accurate, comparable figures on breeding success should be based on data gathered through at least the middle of February with subsequent searches for late casualties.

Young (1963) noted that breeding success of South Polar Skuas at Cape Royds was lower than that of Great Skuas (*C. s. skua*) in the Shetland Islands. He postulated that this was partly due to the South Polar Skua's smaller territories from which second chicks were often driven by their older siblings during times of food shortage. The same relationship appears to be valid between South Polar Skuas at Crozier and Brown Skuas at Signy Island in the South Orkney Islands (Burton, 1968). Annual breeding success at Cape Crozier averaged 0.34 chicks for 8 years while at Signy Island the 3-year average was 1.18 chicks (Table 5). The mean minimum distance between nests in one season at Crozier was 19 m (Table 1) while at Signy Island it was approximately 190 m. Burton did not specify the number of Brown Skua pairs that successfully fledged two chicks, but the number falls between 14 (22%) and 38 (58%) of the 65 successful pairs in three breeding seasons. In five seasons at Crozier 15 (9%) of 168 successful pairs fledged both chicks. This percentage varied little from year to year.

Table 5 shows the great difference in productivity between South Polar

TABLE 6
SURVIVAL OF SKUAS WITH BREEDING EXPERIENCE

Year	Skuas with breeding experience	Number returning following year	Per cent survival
1961-62	35	33	94
1962-63	208	194	93
1963-64	222	202	91
1964-65	232	225	97
TOTALS	697	654 ¹	mean 93.8

¹ Includes 18 skuas that were not observed until the second year.

and Brown Skuas. In 18 seasons at 6 locations on the antarctic coast, South Polar Skuas fledged 0.42 chicks per breeding pair, while in 6 seasons on 3 subantarctic islands Brown Skuas produced 1.16 chicks per pair. The incidence of successful two chick broods is much higher in the Brown Skua. The correlation of territory size to breeding success is obvious; it may be but one of several factors affecting skua productivity.

ADULT SURVIVAL

Very few adult skuas die at Crozier. Over a 7-year period an average of eight dead skuas was found each season, an annual loss of less than 0.4 per cent of the breeding population (not all deaths were of known breeders). Most mortality, then, occurs during the nonbreeding season, March through October, when the skua is a pelagic wanderer.

This mortality is readily measurable because of the skua's strong attachment to its nest site. With very few exceptions, a skua that is missing from the vicinity of its previous breeding site can be assumed to be dead. As noted earlier, changes in breeding site were infrequent and could be recognized by the distinctive nickel alloy band put on about half of the breeders in the study area. Each year several skuas were not noted but were recorded the following season. These birds, whether actually missing throughout the season or not present regularly enough to be recorded, are considered as present in calculating survival.

The mean annual survival rate of skuas with breeding experience was 93.8 per cent, the annual rate varying over a 4-year period from 91-97 per cent (Table 6). This is one of the highest rates to be reported for any avian species and is comparable with survival rates of several of the larger Procellariiformes as summarized by Hudson (1966). That this high survival rate is not correlated with an expanding population is shown in Table 4 where the number of breeding pairs is relatively stable or, at most, declining slightly. No sex difference is apparent in survival; just half of the 32 skuas of known sex that disappeared were males.

TABLE 7
BREEDING SUCCESS IN RELATION TO LENGTH OF PAIR BOND

Length of pair bond	Pairs	Successful pairs	Per cent of successful pairs
New pairs	36	2	6
Established pairs	266	53	20

DISCUSSION

Length of pair bond and breeding success are closely correlated (Table 7). Of 36 pairs of skuas that bred together for the first time (new pairs), only two (6%) were successful, although at least 23 birds had bred in a previous year with other mates. Chicks were fledged by 53 (20%) of 266 pairs that had bred together for a minimum of two seasons (established pairs). The majority (69%) of new pairs laid their eggs during the last one-third of the egg-laying period (Table 8), but the percentage of successful pairs laying in that period was only one quarter that of the earlier layers (Table 9). The process of pair formation in the aggressive, strongly territorial skua apparently may delay laying beyond the deadline for successful breeding in the short antarctic summer. Thus one of the criteria for successful breeding is not previous experience *per se*, but previous experience together.

When adult skua mortality data are applied to Lack's (1954: 93) formula for determining mean adult life expectancy, $(2-m)/2m$, where m = per cent of annual mortality, we find that Crozier skuas have a breeding span of approximately 15.6 years. A breeding success of 0.34 chicks per pair results in the average skua pair producing 5.3 fledglings during its lifetime. Only two of these fledglings need survive to breeding age, a survival rate of 38 per cent, to keep the Crozier population stable, provided there is no appreciable imbalance between emigration of Crozier-reared skuas to other colonies or immigration from other sites.

So far we have little data concerning dispersal of skuas whose natal areas are known. Pryor (1968) reported two South Polar Skuas breeding at Haswell Island that had been banded as nestlings at the Windmill Islands (Wilkes Station), 800 km away. A Hallett skua was found breeding at Cape Crozier (Sladen, LeResche, and Wood, 1968), 565 km distant, and another at Cape Evans (LeResche et al., 1970), 580 km away. The only known Crozier-reared emigrant is a skua seen breeding at Cape Evans, a distance of 71 km (LeResche et al., 1970).

Skua studies at Crozier show a breeding success rate of 0.34 fledglings per breeding pair, a 93.8 per cent survival during adult life, and a pro-

TABLE 8
TIME OF EGG LAYING IN RELATION TO LENGTH OF PAIR BOND

Time of laying	Established pairs		New pairs	
	Number	per cent	Number	per cent
17 November to 17 December	156	59	11	31
18 December to 31 December	110	41	25	69

jected 38 per cent survival from fledging to breeding age. The latter figure, as well as the mean age of first breeding, will be determined in present studies of eight age groups of South Polar Skuas.

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SUMMARY

The population dynamics of about 110 breeding pairs of individually marked South Polar Skuas of unknown age were studied at Cape Crozier on Ross Island, Antarctica, over eight consecutive breeding seasons. Skua pairs maintained their pair bond from year to year unless one bird failed to return, and reoccupied the previous territory. This strong attachment to mate and territory permitted observation of a large number of skuas over successive years.

Breeding success averaged 0.34 fledglings per breeding pair for 5 years. The annual rate varied widely from 0.12 to 0.60 chicks. Higher breeding successes reported elsewhere may have resulted from observations being concluded before chicks were fully fledged. The wider disparity of

TABLE 9
BREEDING SUCCESS IN RELATION TO TIME OF EGG LAYING

Time of laying	Breeding pairs	Successful pairs	Per cent of successful pairs
17 November to 17 December	167	46	28
18 December to 31 December	135	9	7

success between South Polar Skuas and Brown Skuas is partly due to the latter's larger breeding territories where two chicks are often fledged.

Length of pair bond and breeding success were closely correlated. The low rate of success of 36 pairs without previous experience together, 69 per cent of which laid eggs during the latter third of the 6-week laying period, suggested that behavioral difficulties in pair formation were partly responsible.

The annual survival of adult skuas with breeding experience averaged 93.8 per cent for 4 years, the highest year being 97 per cent. There was no difference in survival of males and females.

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