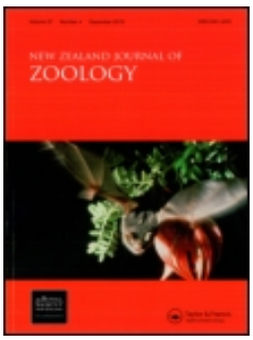

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Behavioural ecology of *lonnbergi* skuas in relation to environment on the Chatham Islands, New Zealand

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A population of *lonnbergi* skuas (family Stercorariidae) was studied over December and January 1974–75 on Rangatira Island, Chatham group (44°22'S,176°11'W). The main aim was to compare the behavioural ecology of these birds with that of *maccormicki* skuas of Antarctica, and to assess the moderating effect of environment on habits. The skuas held extensive territories along the coast and in inland areas clear of forest and bracken. Five of the 11 study territories were occupied by trios of adult birds. A major effect of the vegetation was to reduce contact between neighbours on the ground at territorial boundaries, and most territorial defence was by aerial display and attack. Eggs were laid from late September, and chicks began flying in late December and January. This breeding schedule is about 2 months earlier than for *lonnbergi* at Signy Island or for skuas in Antarctica, but falls on a trend line of latitude against egg-laying when all populations are considered. Seventeen chicks were reared on the 11 territories, a breeding success of 1.55 chicks per nest. This high success rate was attributable largely to success in rearing both chicks when two were hatched. This is seldom achieved in more extreme climates, and is apparently determined by the intensity of sibling competitiveness. It is hypothesised that this intensity is graded, and aggression by the older chick of the pair is provoked more easily by food shortage as environmental conditions become increasingly severe. The most important prey items recorded were adult petrels, especially broad-billed prion (*Pachyptila vittata vittata*) and white-faced storm petrel (*Pelagodroma marina maoriana*) captured on the ground at night. The skuas were mostly inactive during the day, and were not seen to fish or to chase or harass any other bird on or about the island. Southern blue penguins (*Eudyptula minor minor*), though very common on the island, were not attacked by the skuas. Skuas were not seen to attempt to dig out petrel or penguin nesting burrows. Of the differences in ecology recorded, only the presence of three adults on territories appears to be characteristic of *lonnbergi*; it has not been recorded for *maccormicki* or *hamiltoni*, and is either unknown or very rare in *skua*.

INTRODUCTION

Skuas are common throughout an enormous geographic range (the North Atlantic, southern regions of South America, subantarctic and Antarctic islands, and the coast of Antarctica), but vary so little in appearance that they are difficult to subdivide taxonomically. Early reviews of the group (e.g., Lowe & Kinnear 1930, Hamilton 1934, Murphy 1936, Falla 1937) concentrated largely on characters apparent in museum material, and have recently been challenged and amplified by ecological and behavioural studies in the field considering breeding range, interbreeding among forms, migration and dispersal, and the calls and displays of the behavioural repertoire (Perdeck 1960, Moynihan 1962, Swales 1965, Burton 1968a, b, Andersson 1973, 1976a, Parmalee *et al.* 1975, Watson 1975, Devillers 1977; and D. F. Parmalee, pers. comm.). These later studies point to a closer relationship among the forms of skuas and between skuas and jaegers than has previously been accepted, and to a great diversity and flexibility in their habits, depending on environment.

Further clarification of the systematics of the skuas depends on much closer study of their behaviour in relation to habitat conditions in the various regions, of which two seem particularly favourable for such studies. The first is the Antarctic Peninsula region, where there are several skua forms, and is being investigated by Dr D. F. Parmalee of the University of Minnesota (Parmalee *et al.* 1975). The second is the New Zealand region, which contains widely scattered breeding populations of skuas on the southern offshore and subantarctic islands. These islands provide a great range of habitats; on the northernmost ones skuas are living among dense, often luxuriant vegetation with numerous other bird species, whereas on those far to the south conditions are as barren as those of Antarctica.

Intensive work by numerous authors (e.g., Eklund 1961, Young 1963a, b, 1972, Reid 1964, 1966, Le

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Morvan *et al.* 1967, Spellerberg 1967, 1971a, b, Wood 1971, Müller-Schwarze & Müller-Schwarze 1973, Procter 1975) has given a good understanding of the ecology and behaviour of skuas in the Antarctic environment, with its restricted nesting areas and limited food resources of penguins and marine fish. Previous major studies of subantarctic populations of skuas by Stonehouse (1956) and Burton (1968a, b) have also been of southern populations living in a severe environment where most food was from seal colonies or penguin rookeries. It seemed important, therefore, to investigate the ecology of a population of Southern Hemisphere skuas in a temperate climate to obtain an appreciation of the impact of such an environment on behaviour, feeding, and breeding success. The present study, from 22 December 1974 to 30 January 1975, was of a small population of *lonnbergi* on Rangatira Island (South East Island; 44°22'S,176°11'W), one of the Chatham Islands group to the east of New Zealand. Although these birds are at the northern limit of the skua's breeding range in the Southern Hemisphere they experience similar conditions to those breeding further south about Stewart Island, since both places are on the subtropical convergence.

The main comparison was to be with the Antarctic populations of *maccormicki,* which were well known to me. From consideration of the differences in the environments and published accounts of uniformity of behaviour in contrast to variability and flexibility in ecology (e.g., Tinbergen 1959, Moynihan 1962, Burton 1970, Andersson 1973), I predicted that there would be substantial differences in behavioural ecology but only minor differences in the behavioural repertoire of calls and displays, despite the great distance between the two populations.

The study was aimed at investigating generally the breeding and feeding biology of the skuas, but more specifically:

1. the impact of the island's dense vegetation on both behaviour and breeding success;
2. utilisation of the rich and diverse food resources there, for comparison with published accounts and personal experience of skua behaviour in places with quite direrent foods; and
3. the impact of aerial predation by skuas on the behaviour and breeding success of other bird species on the island.

Short-term comparisons of small populations which seek to relate the sociality found to environmental parameters may be invalidated by insufficient notice being taken of the range of the behavioural scale evinced by the forms or species considered, in both qualitative and quantitative terms. The concept of "behavioural scaling" (Wilson 1975) means that it is important to know something of the histories of the populations and habitats being compared, so that possible responses to different or changing population densities can be appreciated, and for comparisons to be made at the same points of the annual cycle. For this reason the present study at Rangatira was made during the latter half of the breeding season, when chick rearing and territorial behaviour were predominant activities, and so could be compared directly with the Antarctic results. There is little information for Rangatira of recent population changes, but numbers have declined from a maximum some 35 years ago (Fleming 1939). This decline may have weakened the intensity of interactions among the birds for breeding sites.

The validity of comparisons between populations depends also on knowledge of the systematics of the various forms involved. Although skuas are variously ordered by different authors, there is no doubt that they are a closely related natural grouping within which comparisons are valid. The confused taxonomy of skuas of the family Stercorariidae has been well summarised by Devillers (1977), who outlines the nomenclatural history of the group and the preferences of the various authorities. Because it is not possible at present to resolve any of this confusion, it seems prudent here to refer to them merely as different forms. Clarification of their generic status as *Catharacta* or *Stercorarius,* or whether or not they are all specifically distinct, will depend on further systematic analysis and on resolution of the implications of interbreeding among them and of their wide-ranging migrations. The forms considered here are therefore *lonnbergi,* the brown or southern skua of the subantarctic islands; *hamiltoni,* of Tristan da Cunha and Gough Island; *maccormicki,* the Antarctic, South Polar, or McCormick's skua of Antarctica, including the Antarctica Peninsula; and *skua,* the great skua or bonxie of the northern Atlantic.

METHODS

The study was based on observation and measurement; no experimentation was attempted. Far less could be achieved here than was possible in Antarctica with the techniques advocated for skua studies there (Young 1970), because the vegetation often obscured the birds' behaviour and because the nests were so widely spaced that only one could be observed at a time. In addition, the birds on Rangatira did not become as quickly habituated to my working among them, and few observations could be made of undisturbed behaviour. This was especially frustrating in the study of their predation on petrels at night.

An outline of the breeding cycle of the skuas on Rangatira can be obtained from estimates of the ages of chicks from growth data to give hatching dates and, with knowledge of the incubation period, prob-

able laying dates. The growth of primary flight feathers was found to be a good indicator of chick age in *maccormicki* (Young 1963a, Reid 1966), and was used in the present study to age all chicks. Several pairs of chicks were measured at intervals throughout their growth to demonstrate that growth rates were uniform with age and similar for all chicks in the area. A rate of 0.5 cm per day was found for the longest flight feather, similar to that determined for *maccormicki*. Estimates of age obtained from this growth index were checked against descriptions of *lonnbergi* chicks of known age given by Stonehouse (1956) and Burton (1968a). For calculation of laying dates the incubation period was taken to be 30 days (Burton 1968a).

Routine observations were made of occupation of the territories to adult birds throughout the study period. During the day the birds were easily checked, but at night it was necessary to search to be certain that they were not on the territory or in the immediate area. Most of the checking for occupancy at night was carried out during moonlight. Under these conditions skuas flew readily at intruders, hovering above them or making tentative "swoop and soar" attacks (Burton 1968b). They rarely alarm-called at night, even when their chicks were handled, so this convenient indicator of parental occupation was not available at these times. Checks were made soon after sunset on the first night of a series and successively later on the following nights, so that the records together covered all night-time hours. The two series of night-time observations were on 2–6 January and 24–27 January.

Territorial boundaries were determined from the flight patterns of skuas in the area and locations of feeding places, and by noting where skuas met or left observers and where intruding birds elicited defensive behaviour. Because boundary zones of territories were too densely vegetated for skuas to walk through or land in there were no ground-based displays; the territory limits shown in Fig. 1 are therefore approximate only.

The chicks were banded soon after the study began to ensure that an accurate accounting could be kept of them in the difficult terrain. The adults were not banded. Because the territories were so large and the breeding groups so consistently referable to nesting areas, confusion of ownership or chick-adult groupings was improbable.

Feeding habits were studied by direct observation of the birds' movements and behaviour in relation to the possible food resources, and of the food brought to chicks. These methods have been used successfully in earlier studies of skuas feeding in various ways ranging from sea fishing and 'pirating' to predation and scavenging (Young 1963b, Bayes *et al.* 1964b, Burton 1968a, Andersson 1976b), and could be expected to be adequate for a general description in the present study also.

THE TERRITORIES

Seven of the 11 skua territories were strung out along the coast on the north and west of the island, and 4 were inland on an elevated, open flat beneath the steep bluff that effectively divides the island in half (Fig. 1). Because much of each territory was densely covered in tall plants, ground used by the birds was restricted to the roosts (usually on rocky outcrops), the shore platform, and the few clear areas in the long grass. None of the boundaries ran through open ground, and no ground-based territorial displays so characteristic of skuas elsewhere were seen; but flight attacks on intruding birds were common, and swoop and soar attacks (Burton 1968b) were pressed home determinedly, even fiercely, on man. The territories were centred on a high point with several roosts on which the birds loafed during the day, and from which they flew to repel intruders. The nest, chick resting places, and sites where the chicks were fed were close by but lower down the slope, so that they were overlooked from the roosts.

The coastal territories were backed by forest, mainly of *Olearia traversii*, and fell steeply across the more open marginal fringe along the coast to the shore platform and the sea edge. Roosts commanded a wide view of coast and sea. The western coastal margin occupied by territories 4–7 is shown in Fig. 2 *(upper)*. The four inland territories occupied an undulating flat well above sea level, bounded by the coastal forest on one side and the slopes of the bluff on the other. The flat was densely clothed by tall seeding grasses, of which Yorkshire fog (*Holcus lanatus*), browntop (*Agrostis tenuis*), and cocksfoot (*Dactylis glomerata*) predominated. Clumps of New Zealand flax (*Phormium tenax*) were scattered over the southern end, and a tall, impenetrable cover of bracken (*Pteridium esculentum*) closed off the eastern end along the edge of territory 11 (Fig. 2, *lower*). Skua activity in these four territories was restricted to the open slopes on the bluff above the flat and to the clear areas in the grass and along the edge of the forest.

The occupancy of territories on 20–22 November 1974, and again during late January 1975, is shown in Table 1. Five of the 11 territories contained 3 adult birds in November, through December, and at least up to mid January. None of the adults was banded, and nothing was known of their ages and previous history. The following could, however, be observed.

1. In November and December all three birds were invariably present during the day, when the birds were loafing on the territory and guarding chicks.

Late in January, when most chicks were flying well, both territorial defence and occupation declined. In at least two territories it seemed that the breeding group was reduced to a pair for a week or more from mid January before territorial behaviour lapsed entirely.

2. The three birds in all territories were similarly pigmented. There was no indication—from markedly darker pigmentation, for example—that one of the trio was a younger bird.
3. All three birds participated equally in the defence of the brood against man. They all met my visits with similar 'swoop and soar' attacks, and alarm-called for the whole period I was on the territory.

Observations of reproductive behaviour earlier in the season or observation of the feeding of young chicks by adults would have given some information on the composition of the group, but by the time this study began all territories contained chicks that were too big to be fed individually and were in any case being fed only at night. On 9 one chick did, however, approach and beg from all three adults in turn on one afternoon, but was not fed. Since all territories with three birds contained chicks, and two had two chicks each, it is certain that none of the trio was a chick of the breeding season being observed.

The breeding area was shared with other bird species, some of which were also territorial. Skuas were seen to chase out only Australasian harriers (*Circus approximans gouldi*) of these other species, and then only when a harrier flew close to the ground in a searching flight near the skua chicks. When observations began the skua chicks were too large to be preyed on by either red-billed gulls (*Larus novaehollandiae scopulinus*) or black-backed gulls (*Larus dominicanus*), the only other potential chick predators on the island, and birds of these two species were largely ignored in the territory.

During the day all birds of the breeding groups were usually to be found on the roosts. There was no difference between pairs and trios; in both, absences were sufficiently uncommon to be worth recording. A strikingly different situation obtained at night, when territories were often deserted by the adults, leaving the chicks unattended.

This difference in the level of occupation between day and night was clearly demonstrated in records kept of searches made on territories 2–4 and 6–11 at

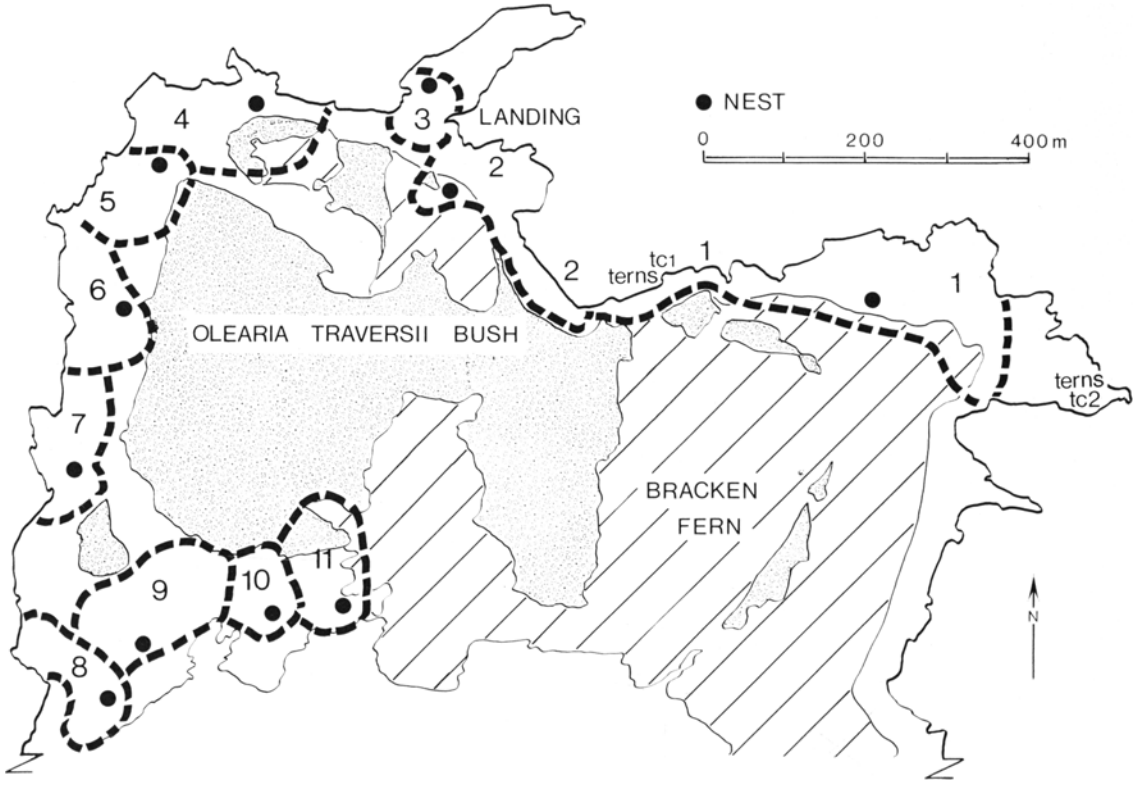

Fig. 1. Territories (1–11) of the *lonnbergi* skua population on the northern part of Rangatira I., Chatham group, Jan. 1975.

Fig. 2. Areas covered by *lonnbergi* skua territories, Rangatira I. (see Fig. 1): *(upper)* view northward from territory 7 across territories 6 and 5 to the steep bluff of territory 4; *(lower)* view westward from the roost of pair 11 at the eastern end of the flat to territory 8 and (far horizon) Pitt Island.

different times on four nights from 3 January. On average only 33% of the total possible occupancy occurred for the birds on these territories. None of the trio on territory 2 was found on any occasion, and only one bird of the pair on territory 3 was found once in the four nights.

Similar searches were repeated over four nights on 24–27 January. At this late stage in the breeding season most chicks were flying well, and territory occupancy during the day had lessened. Pairs with older chicks were away for most of the day, and were also away at night, but others with younger chicks behaved as they did earlier in the year, being on the territory during the day but absent at night.

BREEDING CYCLE AND SUCCESS

Skuas on Rangatira had a very high breeding success. In 10 of the 11 territories at least 1 chick was raised, and in 7 territories there were 2 chicks (Table 1). On average, each territory group (of two or three adult birds) raised 1.55 chicks to fledging, a breeding success of 77% assuming that each nesting group laid two eggs. Only three losses are recorded in the table. Trio 5 had a single egg on 22 November, but this—or the chick hatching from it—had been lost before I arrived on 22 December. Both fledgling chicks on territory 2 left or were killed on the territory on 19 January during a storm with very high seas and severe winds. It is not known whether they were blown away or struck by big waves pounding on to the beach, or flew off intentionally. These two fledglings had been flying for nearly 3 weeks by this date. Both were banded, but were not discovered subsequently in searches about the island.

It is possible to estimate laying and hatching dates for each brood. Egg laying occurred between 15 September and 25 October (mean *c.* 10 October), with chick hatching a month later (mean *c.* 10 November). First flights by chicks were governed by their maturation and by the favourability of the chick-rearing site for flight practice, and were after 7–10.5 (mean 9.3±1.0) weeks' development. They were first recorded for the year on 26 December (on territory 6), and most chicks were flying well by mid January. Chicks of pair 11, confined to a small clearing in long grass, did not begin flying until the grass collapsed and flattened towards the end of January, even though they were flight-mature much earlier. All chicks were still being maintained on their territories by the parents when the study ended in late January.

The two chicks of each pair were apparently reared together throughout their development. All four pairs discovered by J. R. Hay (pers. comm.) in November were together at the nest site, whether on open terrain or among long grass. In late December and January the two chicks of all study pairs were being reared together and apparently fed together at the same time. This occurred both where the chicks were closely confined to the nest area by bracken or long grass (as in territories 2 and 11) and where extensive open spaces enabled the chicks

Table 1. Dimensions and area of territories, nest spacing, and numbers of adult birds, eggs, and chicks of *lonnbergi* skuas on Rangatira I., Chatham group. Nov. 1974 and Jan. 1975

	THE TERRITORIES			OCCUPANCY BY *lonnbergi* SKUAS				
				20–22 Nov. 1974*	Early Jan. 1975		Late Jan. 1975	
No.	Dimensions (m; approx.)	Area (ha; approx.)	Spacing of nests (m)	Adults Eggs/chicks	Adults	Chicks	Adults	Fledglings
1	75 × 500	3.75	625	3 Nest not found	3	1	3	1
2	60 × 250	1.50	125	3 2 chicks	3	2	2	0
3	75 × 75	0.56	225	Territory not recorded	2	2	2	2
4	150 × 250	3.75	200	2 Nest not found	2	2	2	2
5	100 × 125	1.25	150	3 1 egg	3	0	0†	0
6	100 × 150	1.50	140	3 1 chick	3	1	2	1
7	75 × 175	1.30	325	2 2 chicks	2	2	2	2
8	75 × 175	1.30	100	2 2 chicks	2	2	2	2
9	100 × 200	2.00	160	3 1 chick	3	2	2	2
10	75 × 125	0.95	100	2 1 chick	2	1	2	1
11	100 × 150	1.50		2 2 chicks	2	2	0†	2

*Records by J. R. Hay (pers. comm.)

†Territory deserted by adults

to range freely (territories 3, 4, 7, and 8). Later, when the fledglings were flying readily, they usually flew on to neighbouring territories when disturbed by me. No obvious antagonism by the chicks or adults of the territory was recorded on these occasions.

FEEDING HABITS

This account of the skuas' feeding behaviour falls into two sections. The first deals with predation on a number of petrel species, and follows on from observations made by Fleming (1939). The second considers the possible utilisation of other food resources available to skuas on Rangatira Island.

A. Predation on Petrels

The skua territories were already littered with the remains of small petrels when observations began. The remains were identified and counted on some territories between 22 and 24 December. Only three species were represented – broad-billed prion (*Pachyptila vittata vittata*), white-faced storm petrel (*Pelagodroma marina maoriana*), and diving petrel (*Pelecanoides urinatrix chathamensis*). Most remains were of prions. Over 200 part-skeletons (usually only the linked wings) of this season were cleared from each of the four inland territories (numbers 8–11); 134 were cleared from territory 6, 34 from 7, 25 from 2, and 5 from 3 at the same time. White-faced storm petrels are swallowed whole, and the undigested remains are regurgitated as a single pellet some time later, not necessarily on the territory; counts of these could therefore give a misleadingly low total. These petrels were obviously commonly taken as food—for example, over 200 pellets were cleared at this time from territory 7.

Searches were made for petrel remains on the territories each morning from 31 December to 5 January, on 23 January, and again from 26 to 28 January to count the catches made each night.

Over the first period inland territories 8–11 averaged 2.0–3.3 prions each night, with a maximum of 6 on one night in each of pair territories 10 and 11. Over all territories, trio 3 gave the highest nightly average of 4.8, with 5 prions found on each of 4 nights. The remaining territories searched (3, 4, 6, and 7) yielded much lower totals, averaging from 0.7 to 1.8 prions each night. No prions nested on territory 3, and food was apparently captured and consumed elsewhere, because although the chicks flourished few petrel remains were ever found at the roost. Territory 4 was large, and on broken terrain that was difficult to search; I was never confident of finding all remains there. The skuas on territories 6 and 7 were scavenging on dead penguins at this time, and were presumably as a consequence less active predators. Seven diving petrels had been killed also, but had not been eaten. No attempt was made to find the regurgitated pellets of white-faced storm petrel remains. The birds in the four inland territories all had prions and storm petrels nesting in their territories, and the numbers of remains found there probably reflect predation rates that are usual at this time. This view is supported by the fact that when five or more prions were taken in a night several might be only eviscerated, the rest of the body being scarcely touched.

A similar intensity of searching discovered far fewer remains in late January. In total only nine prions, two storm petrels, and a scavenged penguin were discovered for the four nights checked.

All broad-billed prion remains collected between 1 and 5 January had fully developed wing feathers. These appeared to be adult birds, and conformed to descriptions for this species given by Richdale (1944). They had wingspans of about 65–67 cm, with a single wing length from the humerus socket to the tip of the 10th primary feather of 24.9–27.2 cm and an exposed length of the 10th primary feather of 10.3–14.2 cm. Moulting adults were present on the island late in January. Four birds excavated from burrows on 26–27 January had variably developed wing feathers, of which the outermost three were only partly grown and had a substantial length of vascularised sheath with a short vane. The feathers of one, for example, measured as follows: 8th feather 12.8 cm; 9th 10.5 cm; 10th 7.2 cm. All these birds flew off strongly, however, when released after examination.

The white-faced storm petrels taken were also adult. Measurement was more difficult, but the long length of flight feather projecting from the pellet confirmed their mature status.

Neither petrel egg shells nor the remains of petrel chicks were found on any of the places where the skua chicks were fed by their parents.

Four lines of inquiry pursued to determine where petrels were captured by skuas are described below.

Direct observation of skua foraging at night

Of six observations of skuas with prey between 2245 and 0300 h NZST, three were of skuas killing petrels and three of skuas plucking a warm, freshly killed petrel. In five instances the prey was a broad-billed prion adult, and in one it was a white-faced storm petrel adult.

When discovered these skuas were either in small clearings in taller vegetation or on the bare ground just at the edge of the forest. Observations made at the time suggested very strongly that the petrels had been captured on the ground at the places I found them, presumably between their flight and the burrow. Surprisingly, although two of the captures had been made during moonlight the other four were made in the dark, either after the moon had set or

when it was obscured by heavy cloud.

At night skuas were often found on small roosts dotted about their territories, or on the open slopes of the coastal platform, but none was found more than just within the edge of the forest, although searched for there regularly.

PETREL AVAILABILITY TO SKUAS

The ground backing the coastal skua territories and surrounding the inland territories is riddled with the burrows of nesting petrels and penguins—it is difficult to walk through the grass and shrubs and beneath the *Olearia* forest without collapsing them at every step. During the day these areas appear deserted; none of the birds are in flight, there is no calling, and neither chicks nor adults are to be seen at the burrow entrance. At night they are transformed – birds circle in noisy flight, the vegetation rustles and crackles with bird movement, and there is an impressive volume of calling in burrows, on the ground, and in the air. It becomes a rich foraging area.

Three species of petrel predominated in the coastal bush – sooty shearwater (*Puffinus griseus*), broad-billed prion, and white-faced storm petrel. Adults of all three species took flight in large numbers on many nights, though varying widely in abundance from night to night.

Only shearwaters were commonly seen at the burrow entrance or on the ground near it. Adult prions, diving petrels, and storm petrels were, however, very commonly seen at night in long grass, clambering through shrubs, or climbing in shrubs and trees. They were especially easily discovered when moving noisily through the long grass on the inland territories. On still nights their movement could be heard from 15–20 m, and was so obvious that they could be immediately tracked down. A count on 4 January, for example, disclosed 12 prions, 2 diving petrels, and 4 storm petrels on the ground in the long grass on a 300 m circuit across territories 9–11. All these birds were trapped in the grass, and presumably struggled through it until by chance they found clear areas, or shrubs to climb, which would allow them to take off. Of the 12 prions, 6 had clean, dry plumage and were apparently recent arrivals. They flew well when tossed into the air. Four were wet and bedraggled, with significant wear on the feather tips, but could still fly when released. The remaining two birds were heavily matted with burrs of the bidibid (*Acaena* sp.), and being unable to fly could not be expected to survive. Later in the season small numbers of prions were discovered in which the flight and tail feathers were so worn that little more than the shaft remained. They were unable to fly. Petrels in this condition would be easy prey for skuas.

DISTRIBUTION OF HEAPS OF PLUCKED FEATHERS ON TERRITORIES

The larger petrels were at least partly plucked by skuas when eaten, and patches of feathers could be found about the inland territories. Their distribution and association with burrows and petrel remains indicated that most were at places where petrels had been captured. For example, three prion carcasses, partly eviscerated and surrounded by feathers, and two other feather patches were discovered on a low mound of iceplant (*Disphyma* sp.) containing numerous prion burrows. This site was so distant from where the skua chicks were fed by the parents that the most likely explanation for it is that petrels had been captured and eaten there. Since the remains were so closely grouped together near the petrel colony, they provide good evidence also for the view that captures occurred on the ground near the burrows.

These patches of feathers were found only in areas containing petrel burrows, and none occurred in several of the coastal territories. Skuas in these must have foraged away from the territories and carried the ingested food back to the chicks.

EXCAVATION OF PETREL NESTING BURROWS

Although many thousand burrows in different situations were checked, no evidence was found to indicate that these skuas dug them out to reach nesting petrels or penguins. Nor were skuas seen inspecting burrow entrances, or standing guard over them.

Four prion burrows were excavated by hand to determine how easily skuas might be able to reach adults or chicks on the nest and to see what soil disturbance would show from such attempts. The burrows were in short grass and tunnelled into a deep, loose soil bed. Their openings, partly obscured by trails of iceplant pulled into the burrows, were 7.0–9.0 cm wide and 4.0–7.0 cm high. They were from 55 to 105 cm in length, and angled down into the ground so that the nest at the end was roofed by 11–30 cm of soil and the floor of the nest lay 23–35 cm below ground level. The soil disturbance caused by digging—a deep trench tunnelling from a large mound of bare, loose soil—demonstrated that similar excavations by skuas would have been immediately obvious. Similar, though less substantial, upheavals would result from attempts to dig out storm petrels or from attempts to break into the roof of the burrow directly over the nest.

B. POSSIBLE UTILISATION OF OTHER FOODS

The following food resources could be exploited by the skuas breeding on Rangatira Island.

1. FOOD SCAVENGED FROM FARMS ON PITT ISLAND

The sheep flocks on Pitt Island are separated from Rangatira by a narrow strait 2.1 km wide. Although

they are within easy flight range, no evidence of skuas feeding there at this time was gained from watching skua flight or checking food remains at the nest. Although harriers were regularly seen to fly across the strait, and flocks of starlings (*Sturnus vulgaris*) were conspicuous in flight to and from the roosts on the island, no skua flights across here were recorded. At other times of the year, especially during lambing, skuas do scavenge on the farms and are considered a pest equal to the black-backed gull (W. Gregory-Hunt, pers. comm.). The nesting areas of the gulls on Rangatira (but not of skuas) were littered with wool, lambs' tails, and docking rings, testifying to their scavenging habits.

2. FEEDING ON MARINE FISHES

Many hours were spent on Rangatira searching the sea around the island through binoculars for skuas fishing or returning from more distant fishing grounds. However, few were observed at sea, and none appeared to be fishing or searching for fish. Nor did they ever join the mixed feeding flocks of red-billed gulls and white-fronted terns (*Sterna striata*) that fished regularly on turbulent upwellings near the island. Moreover, skuas were rarely absent from territories during the day, when feeding on surface-shoaling fishes could be expected to take place, and on the few occasions a skua was watched returning to the territory after some hours away it did not feed the chicks. No fish remains were found on any feeding area. It is doubtful whether any fishing occurred at this time, though the possibility of fishing at night cannot be discounted.

3. PIRACY (KLEPTOPARASITISM) ON OTHER SEABIRDS

In the Northern Hemisphere the great skuas chase a variety of sea-feeding birds, forcing them to disgorge food (Perry 1948, Meinertzhagen 1959, Andersson 1976) which is then appropriated in flight. Only red-billed gulls and white-fronted terns were available as equivalent 'prey' species of Rangatira Island skuas. These two species fed all round the island throughout the day, singly or in large mixed flocks. Although they regularly fished in full view of skuas on roosts, not once during many hours' direct observation were they visited or flown over by skuas. Nor were skuas seen to chase birds of either species as they returned to their nests. Indeed, over land, skuas were themselves harried by terns defending their nesting colonies.

4. PREDATION ON OTHER SHORE BIRDS

Skua territories along the shore contained gull and tern breeding colonies and breeding pairs of the Chatham Island oystercatcher (*Haematopus chathamensis*), New Zealand shore plover (*Thinornis novaeseelandiae*), and New Zealand pipit (*Anthus novaeseelandiae novaeseelandiae*). There is little evidence that skuas preyed on these birds, which collectively were too few to form a significant part of the skuas' food even had they been preyed on intensively. Nevertheless, their reactions to skuas flying near them showed that they were alert to the risk of skua predation, and their contact here with a recognised aerial predator is of interest.

The relationships between skuas and these other shore birds were as follows.

BLACK-BACKED GULLS. Gull nests were on bare rock outcrops, and were fully exposed to the weather and to possible aerial predators.

In territories 2, 3, 4, and 6, where they nested within 50 m of skua roosts and both nests and chicks were overlooked at all times, they were at most risk from skua attack on this island. Only one attack on a gull chick was seen. The male of pair 3 flew down from the roost to catch a 30-day-old chick by the head after it had strayed 15 m from the nest. The disturbance of the attack immediately attracted five adult gulls, which chased the skua out and prevented it from carrying the dead chick away.

In general, adult gulls were not attacked on the ground or in flight, and fledgling chicks were not harried in the air even though they sometimes flew about the skua roosts. In their early flights, however, fledglings were invariably accompanied by an adult, which would fly at skuas passing near them or flying over them when they had landed.

RED-BILLED GULLS. Nests of these gulls were spaced out singly or grouped in loose colonies of up to 10 nests on rock outcrops close to the shore. All nests discovered on Rangatira were sheltered under rock overhangs, in shallow caves, or in erosion holes in the outcrops of soft sandstone. No nests were found in exposed positions.

Skuas were never seen near the nests, and although they could perhaps take eggs, chicks moved even further into shelter soon after hatching and could then be taken only with difficulty. It is doubtful, therefore, whether live eggs or chicks of this gull are often taken.

WHITE-FRONTED TERNS. Tern nests were on outcrops about the coast, commonly in places occupied earlier in the season by nesting black-backed gulls. Most nests were in the open on bare rock, but several were found on narrow ledges and in shallow caves on the rock faces. Two colonies of approximately 25 and 150 nests each occurred in skua territory 1, but nests were dotted elsewhere all about the coastline. Red-billed gulls were not attacked by breeding terns, and were able to stand on the colony fringes with impunity. Mixed nesting groups of red-billed gulls and terns occurred at several places.

Tern eggs and chicks suffered heavy mortality in

this year, apparently through predation. In the smaller of the 2 colonies noted above, 11 chicks hatched from 23 nests but none survived to fledging. Direct observation of this colony left the impression that either the black-backed gull pair roosting above it or the several pairs of red-billed gulls nesting among the terns were responsible for this mortality. Skuas were never seen to fly near the colony nor to deviate from their flight paths along the coast to investigate it. It is doubtful whether any skua gained food from the tern colonies.

OYSTERCATCHERS. These birds were too few in number and too widely spaced around the island to be a significant food resource for skuas; there were only 10 pairs on the coastline of the study area. Nests were found for six of eight nesting pairs; five were exposed on gravel at the seashore and one was in a small, shallow cave.

No evidence was gained from direct observation or from the egg and chick survival of pairs that skuas preyed at all on these oystercatchers.

SHORE PLOVER AND NEW ZEALAND PIPIT. Both species foraged on the shore platform within skua territories and about the skua 'club' at a brackish pool near the landing on the north end of the island. No contact between the skuas and these species was seen. Shore plovers accompanied gulls which flew across their territories, but since no skuas were seen in similar flights it was not possible to observe whether they elicited the same behaviour from the plovers.

DISCUSSION

This study was envisaged as having two main aims. First, to consider the place of the skua within the island's ecosystem, and especially its impact on the behaviour and breeding habits of the other shore bird species, most of which breed elsewhere in the New Zealand region in the absence of skuas. Second, to compare this skua population with others, especially with a view to assessing the significance of environment to the birds' behaviour and ecology.

THE PLACE OF SKUAS IN THE ISLAND'S ECOSYSTEM

The main changes affecting the skua population on Rangatira since Fleming's study in the 1937–38 summer (Fleming 1939) have been the protection afforded by the island's new status as a reserve, and removal of the sheep. The removal of sheep has taken away a possible food resource, and has allowed revegetation to occur, thereby limiting open areas available to skuas for breeding and restricting contact between neighbouring pairs on the ground. The population on the island during the present breeding season was estimated to comprise some 70 adults. There was a maximum of 22 territories, some of them containing three adult birds, plus some 10–20 resident, non-breeding birds. This number is less than half that present in 1937. Fleming (1939) considered that at that time the numbers had been increased artificially through association with the sheep flock, and that he was then observing an unnatural situation.

Apart from their important impact on the smaller petrels taken as prey, skuas appeared not to greatly affect the behaviour or breeding habits of other bird species, some aspects of whose interrelations have been described earlier in a paper on overlapping territories (Young 1976). It might have been hypothesised that the presence of as important an avian predator as this skua would have some effect on the timing and synchrony of the breeding seasons of these birds, on their nesting dispersion, on tendencies towards nocturnalism and cryptic behaviour in nest-site selection, and on the behaviour of chicks.

The general conclusion from the study was that although all these species reacted strongly to skuas intruding closely on the nest or chicks, they were already well adapted to the presence of the other avian predators there (the two gull species and the Australasian harrier), and that skuas added only marginally to this presence. The nesting habits of the oystercatcher and red-billed gull are, however, sufficiently different here from those of mainland populations to merit further study. All red-billed gull nests found on Rangatira were in caves, on overhanging cliffs, or in small holes in rock outcrops, and none was exposed to birds in flight. This is a quite different nesting habit from that of the same species around the mainland coast, where colonies cover outcrops and shingle ridges. The Chatham Island oystercatcher was thought to nest under cover, possibly to avoid predation by skuas (A. J. Baker, pers. comm.), but only one nest of the six nesting pairs in the study area was in fact in a cave; the others were exposed on seashore gravel. It is not possible at present to decide whether these differences are species-specific to the Chatham Islands or induced by skuas. Comparative study on the islands lacking skuas would provide decisive evidence one way or the other.

In all other respects—the timing of the breeding season, where the species overlapped with skuas; the occurrence of both colonial and widely spaced nesting; and the adults' diurnal habits and the strongly cryptic habits and camouflage of the chicks—the biology of these birds appeared to be similar to that of mainland populations.

COMPARISON OF HABITS OF RANGATIRA ISLAND SKUAS WITH THOSE OF OTHER POPULATIONS

The behavioural ecology of *maccormicki* skuas during the summer in Antarctica is now rather well

known, with numerous records of territorial and reproductive behaviour and of their relations with the Adélie penguin (*Pygoscelis adeliae*). These observations have covered several different breeding situations – birds with and without access to the food resource of penguin colonies, and birds nesting singly, in widely spaced, loose colonies, or in tightly compacted ones. They all have one feature in common, however: they are of birds on barren flats or basins which, because of the severe climate, lack vegetation or terrestrial food resources. Recently studies of comparable detail have been made of *skua* in the North Atlantic and of several populations of *lonnbergi* on subantarctic islands. These latter studies are of skuas in a less extreme climate; the territories contain some vegetation, and colonies commonly occur in association with those of nesting seabirds, which are preyed on.

The different populations of *lonnbergi* range from Antarctic to temperate climates, and in the southern part of this range may be associated with penguin colonies, as for *maccormicki*, though in the northern part only with shore birds and petrels. The population of *lonnbergi* on Rangatira Island is nearly the most northerly known, so its biology can be expected to be more like that of *hamiltoni* and *chilensis* than that of *maccormicki*, and its feeding ecology quite different from that of *maccormicki* and *lonnbergi* populations associated with breeding colonies of penguins.

Territories, territorial behaviour, and occupation

Skua territories on Rangatira were like those described in other accounts of *lonnbergi* (Stonehouse 1956, Burton 1968a) and of populations of *skua* (Perry 1948) and *maccormicki* (Young 1963a, Spellerberg 1966). Skuas in general have nesting dispersions ranging from fairly close spacing in favoured sites to solitary nesting in others, and this variety may occur within a single breeding location, as at Cape Bird (E. C. Young, unpubl. data) or Cape Royds (Young 1963a) on Ross Island, Antarctica, for example. Although *lonnbergi* populations are described as having widely dispersed nests, as on Rangatira, one high-density breeding population is known on Bird Island, South Georgia. This concentration has been attributed to attraction to a superabundance of breeding petrels on the island (Tickell 1962, Bonner 1964).

Skuas universally defend territories through a combination of ground displays and aerial displays and attacks. These are apparently characteristic and uniform throughout the genus (Burton 1968b), and form a major part of the birds' activity in Antarctic populations (Young 1963a, Spellerberg 1971a). Although territories were vigorously defended against neighbours on Rangatira, because of the long vegetation this was achieved almost exclusively by aerial display, flight attacks, and the territorial advertising displays of "long call complex" and "bent neck" (Burton 1968b). No contact between neighbours on the ground at boundaries was seen—indeed, it seemed scarcely possible. This gap in the behaviour pattern was therefore directly attributable to environmental features, and was certainly predictable, knowing how dense the ground cover was on the island.

The occurrence of trios of adults on territories, on the other hand, appears at first sight quite unrelated to the Rangatira habitat. Although this breeding system had been noted previously on Rangatira (Fleming 1939, Falla *et al.* 1966; B. D. Bell and D. V. Merton, pers. comm.), its high incidence there (on 5 of 11 territories) was nevertheless remarkable.

Trios of adults on territories have been recorded in almost all field studies of *lonnbergi*. Burton (1968a) records that on Signy Island one trio persisted for several years, and another formed in one season—two instances in about 100 pairs each year over 7 years. Although none was noted by Stonehouse (1956) on the nine territories he observed over two seasons on South Georgia, a trio was found by Bonner (1964) on neighbouring Bird Island and two trios were recorded there from among *c.*500 pairs in 1976 by Dr J. Croxall (pers. comm.). However, no trios were recorded on Heard Island by Downes *et al.* (1959) among *c.*95 pairs included in their account of breeding behaviour.

Trios at nests seem to be especially common in the island populations about Stewart Island, New Zealand, and have been recorded at a high proportion of nests by Guthrie-Smith (1925), Stead (1932), and Richdale (1965a, b). Richdale, for example, found 8 at 12 nests on Big South Cape Island, and concluded that "three adults at a nest is by no means unusual in the Stewart Island area". Indeed, Guthrie-Smith claimed that his companions believed it to be the normal condition. Trios were less common on The Snares islands in 1974–75, when only 3 occurred in 27 territories surveyed (H. A. Best, pers. comm.).

In summary, there is apparently a marked difference in the incidence of trios between the 'southern' *lonnbergi* populations (on Heard, South Georgia, Signy, and Bird) and those around New Zealand. This difference may be related to environmental factors, since the former populations are all from severe environments with little or no vegetation, and are often associated with penguin colonies, whereas the latter are from more temperate ones. It would be interesting to learn whether trios occur also on Macquarie, Campbell, or the Auckland Islands, which are in the New Zealand region but have rather severe

climates.

Trios are either unknown or very uncommon at the two extremes of the skuas' range. They may occur rarely in *skua* populations. Although not recorded in the original studies of Perry (1948), Perdeck (1960), or Bayes *et al.* (1964a), nor in the general review of the species by Bannerman (1963), their occurrence may be indicated in the statement by Witherby *et al.* (1941) that sometimes three eggs are found in a nest. Confirmation of their occurrence in one area comes from W. J. Plowden-Wardlaw (pers. comm.), who found trios at each of four nests he discovered on Mousa in the Shetlands. The situation is clearer for *maccormicki* in Antarctica. No trio has been recorded by Eklund (1961), Young (1963a and pers. obs.), Reid (1964), Le Morvan *et al.* (1967), Spellerberg (1971b), or Wood (1971) among the many hundreds of pairs studied closely by them over several seasons. Because of the barren terrain and exceptionally favourable opportunities for observing birds it is most unlikely that they would be overlooked in this region.

There is a suggestion in these records that the occurrence of trios in skuas is related overall to climate (broadly to latitude), the incidence increasing progressively as one moves from the poles to the equator. This does not, however, seem to hold for skuas as a whole, irrespective of the situation within *lonnbergi*, since many *skua* nest in conditions comparable with those of *lonnbergi*, and no trios were recorded by Swales (1965) in a large population of *hamiltoni* on Gough Isand (40°10'S), which, with Tristan da Cunha, is one of the northernmost skua breeding areas in the Southern Hemisphere.

The sex of the birds making up trios has rarely been determined. The *lonnbergi* trio described by Bonner (1964) was found by dissection to comprise one male and two females, and a trio at Signy was also thought to contain two females because four eggs were laid in one year (Burton 1968a). In contrast, a trio shot by Stead (1932) off Stewart Island "proved to be two males and a female, one of the former being a young bird". Four trios of *skua* shot in the Shetland Islands by W. J. Plowden-Wardlaw (pers. comm.) were also found to comprise two males and a female.

Little is known of the age or previous history of the birds of any of these trios, though the records of egglaying (Bonner 1964, Burton 1968a) confirm that some at least were composed entirely of mature birds. As far as is known none of the trios observed at Rangatira during the present study laid more than the two eggs expected of pairs. Little is known either of the individual roles of these birds in breeding, though equal participation in territory defence is well catalogued (Guthrie-Smith 1925, Bonner 1964, Richdale 1965a, and this paper) and Guthrie-Smith has observed a trio sharing incubation and chick feeding.

Clearly, further study of this interesting and unusual phenomenon is merited, so that the identity of the birds and their role in breeding are established and the significance of trios within the otherwise monogamous suborder Lari can be fully assessed. It has interest also from the viewpoint of the possible evolutionary routes leading to communal and colonial breeding in birds, as expressed by Brown (1974), for example.

Feeding

Skuas are well recognised as being generalised and opportunistic feeders. They obtain food during the breeding season variously by scavenging, by predation on other bird species or small terrestrial mammals or marine fishes, and by piracy on other seabirds. (When at sea over winter they presumably feed by fishing and piracy alone.) Within this broad pattern the different populations appear to exploit the most readily available food resources, with good evidence that cultural or learned behaviour differences may determine how different pairs or breeding groups may act (Bayes *et* al. 1964b).

In general, however, differences in the feeding behaviour of different populations can be expected to reflect differences in the foods present—formalised as the "profitability of hunting" hypothesis (Curio 1976). Skuas in Antarctica feed on marine fishes or at penguin colonies; those in the subantarctic on penguin colonies, fish, the offal of seal colonies, and petrels; and those further north and in the Northern Hemisphere on fish, other bird species, and food scavenged or captured on land. This trend line in the feeding pattern is therefore determined mostly by food availability in the different areas, and cuts across the geographic ranges of the different skuas.

The study of feeding by skuas on Rangatira was restricted to a 7-week period at the height of the breeding season, and thus considered only a small segment of their annual feeding ecology. It corresponded with an abundance of breeding petrels—notably sooty shearwaters, broad-billed prions, and white-faced storm petrels—and with the breeding season of the little blue penguin. Because of the variety of foods available at this island, interest centred on food selection. The skuas in fact largely ignored the foods available to them during the day through scavenging at sea or through predation or piracy on any of the other seabirds. They concentrated instead almost exclusively on the adults or fledgling chicks of just two of the several common petrel species seen in the breeding area.

Although one can be fairly certain that these skuas were not attacking gulls or terns or pirating food from them at sea, since such activity would

have been very obvious, one cannot be as certain that they were not fishing directly themselves. All that can be offered is the negative evidence that skuas were never seen during the day to be fishing or searching for fish at sea, and no fish or squid remains were found on territories following possible nocturnal foraging. Their lack of interest in white-fronted terns as a prey species for piracy is noteworthy, because *hamiltoni* skuas certainly chase this tern for food on Gough Island (Swales 1965).

The sooty shearwater appeared not to be attacked by skuas on Rangatira, although it was very common and was often seen at night in skua areas. Nor were shearwaters taken by this skua population in 1937–38 (Fleming 1939). This seems to be an example of cultural influence on feeding, since shearwaters are preyed on elsewhere (Stead 1932, and J. R. Hay (pers. comm.) for Little Mangere I., Chathams). Concentration on one or a few of the possible prey species has been described by Stead (1932) for the different skua populations around Stewart Island, and its evolutionary and ecological significance in skuas and other predators has been considered by Bayes *et al.* (1964b) following their observations on the selection of different prey by *skua* pairs in the Faeroes.

The limited prey range observed on Rangatira is unusual for skuas. In the populations on Signy Island and South Georgia they not only preyed and scavenged in penguin colonies but took chicks and adults of the South Georgian prion (*Pachyptila desolata*), snow petrel (*Pagodroma nivea*), and Wilson's storm petrel (*Oceanites oceanicus*) as well. These petrels were caught on the ground outside their burrows, but prions were also excavated from burrows in soft ground. The skuas also fed on debris washed ashore and on dead seal pups (Stonehouse 1956, Burton 1968a). A similarly wide range of diet is recorded from Heard Island, where the food taken followed a regular sequence beginning with scavenging during seal pupping and shifting to penguins and petrels as the breeding cycles of these birds developed (Downes *et al.* 1959).

There is only one other record of *lonnbergi* skuas concentrating largely on petrels. This is of the population on Bird Island, South Georgia, where the food taken by *c.*200 skua pairs consisted mainly of South Georgian prions and diving petrels (Tickell 1962, Bonner 1964). As on Rangatira, skuas caught the petrels at night on the ground near the burrows.

The counts of prey remains and the observations on feeding and of obviously very hungry chicks during January allow rough estimation of the total numbers of petrels taken. It is estimated that by mid January each territorial group had taken on average 200–300 broad-billed prions and probably similar numbers of white-faced storm petrels. No other petrels were taken in significant numbers. After mid January few prion remains were found, reflecting the end of this bird's breeding season and the departure of the chicks (Richdale 1965b). This food resource appeared not to be replaced effectively, and the amount of food provided by parents in late January failed to satisfy the chicks. During the day, adults on the territory were doggedly pursued by begging chicks, and the most pervasive sound on the coastal strip was the 'hunger calling' of fledgling chicks. Many called continuously throughout the day, were clearly desperately hungry in the evening, and were still calling the following morning, even though some feeding may have occurred. How skuas obtained food during this period is not known.

Although Tickell (1962) considered that prions were by far the most important prey of skuas on Bird Island, his estimate of 50 prions plus a smaller number of diving petrels as a seasonal total for a skua pair is insufficient for their nutrition, and these skuas must also have been feeding elsewhere.

Aspects of Breeding Biology and Breeding Success

The study period corresponded with chick rearing by the skuas, and little is known of their egg-laying and incubation behaviour. Although egg laying occurs very early in summer compared with its timing in populations further south, it falls on to a trend line when dates are plotted against latitude for the different *lonnbergi* populations, and cannot be considered exceptional (Young 1977). The breeding success of 1.55 chicks raised per nesting pair or trio for the skuas in the study area on Rangatira in this year is appreciably higher than any recorded in other studies of skuas so far. Wood (1971) has summarised breeding data from recent studies for both *maccormicki* and *lonnbergi*, recording a range of 0.34–1.18 chicks raised per breeding pair with a tendency for greater success in the more northerly populations. To this series can be added the records for *lonnbergi* from Heard Island, where Downes *et al.* (1959) recorded 35 chicks (including 10 pairs) at 30 nests, a success rate of 1.16 chicks per nest. There are fewer records of comparable detail for *skua*. One record (Perry 1948) from Noss, Shetland Islands, is of ". . . 114 (34 pairs and 50 singles [*sic*] . . ." from 113 pairs of birds, an overall success of 0.98 chicks raised per nest.

Young (1963a) attributed the poor success in chick rearing of skuas at Cape Royds, Antarctica, to a range of factors, of which the early loss of the younger chick after its eviction from the nest, unfavourable weather (affecting the chicks directly or through its effect on parental interest or foraging behaviour), and predation were the most important. Of these, the one with the greatest impact was the loss of younger chicks of pairs through their eviction

from the nest area by the older chick, because two chicks hatched in most nests. A great improvement in rearing success could therefore be expected in populations in which chicks were more tolerant of competition (for food?) and could remain together at the nest, or in which the parents were better able to rear the two chicks apart. Both strategies can be seen in the different populations of skuas studied, though clearly the second simply overcomes a difficulty arising from lapses in the first.

At the extremes of the skuas' range—in Antarctica and in the North Atlantic—the chicks are seldom reared together on the nest area or fed together; intolerance and displacement of one is normal. Pairs of *maccormicki* chicks were occasionally reared at Cape Royds (Young 1963a, Spellerberg 1966) and at Cape Bird (pers. obs.), but by exceptional parents which managed to keep the two chicks apart yet within the territory. At Cape Crozier, Wood (1971) found that only 15 of 168 successful pairs fledged both chicks. Poor survival of pairs of chicks is not necessarily a specific characteristic of *maccormicki*, and Le Morvan *et al.* (1967) contrasted their records of high survivorship of pairs at Pointe Geologie on the periphery of the Antarctic Continent (60°40'S, 140°01'E) with other records for this form from further south. (It was not recorded for this population whether the chicks were reared together or separately.) In the more temperate environment of Shetland, Perry (1948) recorded 34 pairs of chicks in the total of 114 fledging. In all these populations the chicks were reared separately at different places on the territory. The alternative—and presumably more primitive—strategy in which the chick pair remain together, at least through early life, is known from both Rangatira and Signy (Burton 1968a) in populations of *lonnbergi*, but other studies of this form have ben insufficiently detailed for comment on this aspect.

On the basis of these records of chick rearing, there is some evidence of a difference in behaviour which might be taxonomically based. The variation in response to competition between the chicks, however, seems more likely to be related to climate and vegetation cover and to differences in food availability. Two previous studies have pointed to the importance of food abundance for high breeding success. Le Morvan *et al.* (1967) attributed the high success of rearings of two chicks in their study of *maccormicki* to abundant and regularly available food for chicks. Bonner (1964) gave the same explanation for *lonnbergi* when contrasting the general habit of skua pairs to rear two chicks on Bird Island, where prions and diving petrels abound, with single-chick rearings on South Georgia, only 45 km away.

Procter's (1975) experiments on nutrition and aggressive behaviour in *maccormicki* chicks were addressed specifically to this problem. From these he concluded that "the nutritional condition of the chicks regulates aggressive behaviour", and that this mechanism for moderating chick survival was adaptive.

The different situations of chick-rearing behaviour and breeding success found in different populations thus seem to fall within a gradation of behaviour within the species-group. At one end of the series, in populations having a locally abundant and easily obtainable food resource, the two chicks are brooded and fed together and little or no sibling rivalry develops. At the other, the chicks are less tolerant of competition and establish a fierce sibling competitiveness from which fighting may be triggered soon after hatching by even very temporary food deprivation. The first condition is exemplified by the Rangatira population, the second by that in the most severe Antarctic environments. For breeding success in populations where fighting occurs and the younger chick is evicted from the nest area the critical considerations then are parental response, the size of the territory (which will or will not allow both chicks to be contained within it), and the degree of visual isolation and security from predators of the two chicks afforded by vegetation. Where the parental response is adequate and the other factors are advantageous both chicks are likely to survive and be reared to fledging. Where the adults are unable to adapt their behaviour to support the two widely separated chicks, or to prevent the older from harassing the younger, or where any of the other factors are disadvantageous, the younger chick is soon lost and the post-hatching breeding success of the population is effectively halved.

In summary, the overall high breeding success at Rangatira comes from rearing both chicks. Skuas universally have a high egg-hatching success, and the big differences in overall breeding success come from variations in chick rearing. Even so, success on Rangatira was markedly greater than for the only other *lonnbergi* population for which there are detailed figures (Signy Island – Burton 1968a); but this latter population was living in a far more rigorous climate closer to that experienced by populations of *maccormicki*.

CONCLUSIONS

The foregoing discussion has compared aspects of the feeding and breeding behaviour of the Rangatira Island population of *lonnbergi* with other populations of skuas as described in the literature and from personal experience of *maccormicki* in Antarctica. It has attempted to place the Rangatira population on a series of trend lines of skua behaviour reflecting the island's geographic position and the special or

general features of its environment, in order to assess which of these skuas' characteristics are environmentally dependent and which may well be species-specific and largely independent of environmental influences.

It is concluded from this analysis that most of the features of behaviour and ecology initially found unusual in this population on Rangatira—especially in comparison with *maccormicki* populations—fall within trend lines for the species related broadly to latitude, or can be related to special features of the habitat. In the first category fall such features as breeding season, breeding success, lack of intense sibling competitiveness, and the general pattern of feeding habits. In the second category are the absence of ground-based territorial behaviour, because of the luxuriant vegetation, and, perhaps, the uniformly large territories and the selection of prey.

Once these aspects of its biology have been accepted as having a major environmental component, then only the occurrence of trios at nests seems to be a taxon-specific feature of this form. Trios have so far not been recorded in *maccormicki* or *hamiltoni*, and occur rarely—if at all—in *skua*. However, even in this feature some environmental influence may be significant, for a much higher proportion of trios occurs in the populations of *lonnbergi* in the New Zealand region than in others nearer Antarctica.

Although there is undoubted scope for using behavioural and ecological characters in the taxonomy of skuas, as advocated by Mayr (1958) and others, the selection and weighting of the individual behavioural traits to be used and a thorough knowledge of environmental effects on the ecology, obtained through large-scale comparative study, are of critical importance. Further studies of *lonnbergi* populations aimed at taxonomic clarification should initially concentrate on detailed ethograms of the behavioural repertoire. The present study has demonstrated so close a relationship between environment and habits that few if any of the characteristics recorded were of value in ordering this form's taxonomic position.

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