IS COOPERATIVE BREEDING IN BROWN SKUA (*Catharacta skua lonnbergi*) ON THE CHATHAM ISLANDS HABITAT-FORCED?

By E. C. YOUNG

School of Biological Sciences, University of Auckland, Auckland

ABSTRACT

Brown Skuas (*Catharacta skua lonnbergi*) on Rangatira (South East) and Mangere islands in the Chatham Islands group were studied over a period of 14 years (1978/79 to 1992/93 breeding seasons) to determine factors promoting cooperative breeding in this population. The size and composition of the breeding population and overall breeding success were remarkably stable. No significant differences in breeding success, density of territories or periods of individual occupation in different places on these islands were demonstrated that would demarcate optimal and marginal breeding habitat. Neither could it be demonstrated that the islands were saturated by breeding birds as required for a habitat-forced origin of cooperative breeding.

INTRODUCTION

The key role of habitat saturation by breeding birds has been a feature of ecological models of cooperative breeding since the 1970s (Brown 1974). Its significance is evident, for example, in the reviews by Koenig & Pitelka (1981) and Brown (1987), and in the environmental constraints model of cooperative breeding proposed by Emlen (1982). Indeed, this view is now so well established that Smith (1990) could conclude in his review of long-term studies of cooperatively breeding species that 'a principal cause of cooperative breeding is a critical shortage of suitable breeding habitat.' It is, however, only one of a long list of factors argued to favour delayed breeding and cooperation (see, for example, Table 5.1 in Brown (1987)) and recent literature offers a number of examples where habitat saturation did not appear to be a critical element (see review by Heinsohn *et al.* (1990)).

Part of the attraction of the habitat-saturation hypothesis is that it makes intuitive sense: in limited habitats surplus breeding birds of territorial species are 'forced' to become floaters - forming a nonbreeding group - or, in cooperatively breeding species, to stay with or join established breeders in cooperative groups.

This paper investigates whether habitat saturation in any of its various habitat-quality models (Koenig & Pitelka 1981; Emlen 1982; Stacey & Ligon 1987, 1991; Koenig *et al.* 1992; Walters *et al.* 1992) was a significant factor in the development of cooperative breeding in the population of Brown Skua (*Catharacta skua lonnbergi*) on the Chatham Islands.

Other aspects of the biology of this population are inconsistent with cooperative breeding. For example, although there is deferred breeding (in common with other skua populations), non-breeding birds (floaters) form typical skua 'clubs' (Furness 1987) instead of competing directly for territories. Moreover, in contrast to the common pattern of cooperative breeding in which there is significant philopatry, young skuas leave the natal territory as fledglings at the end of the breeding season and exhibit little natal philopatry when returning to breed 4-10 years later. Cooperatively breeding groups do not consist of closely-related family members (author's unpublished data).

The first requirement in this analysis was to determine whether all available breeding space on the islands was occupied by breeding birds; and hence whether the habitat was saturated as defined by Koenig *et al.* (1992), i.e. 'a syndrome of intense competition over territories that are rarely vacant'. In this respect, it was important to distinguish between the defended territory (different groups falling within Hinde's (1956) categories of breeding territory only or breeding-feeding territory have been described for these skuas by Young (1984) and Young *et al.* 1988)) and the area of suitable breeding habitat. Bare or grassed areas are the only places where skuas can nest on the islands and so can be considered skua breeding habitat. Skuas may forage for petrels within the forest, but they cannot breed there.

The second requirement was to assess the quality of breeding habitat. In particular, it was important to determine whether there was a wide range of quality, with a substantial area of marginal habitat. Food availability was an obvious measure of quality. However, Chatham Island skuas forage both on and off the territory and some very successful breeding units occupy territories without any food at all and forage throughout the breeding season on unclaimed, generally forested, areas. Food availability did not, therefore, seem to be a significant measure of the quality of the immediate nesting habitat in this population. Instead, breeding success and breeding group stability seemed useful indirect measures of habitat quality. Comparisons of breeding units in different places on the islands in apparently very different habitats might be expected to show whether habitat quality varied sharply. assuming the birds to be of similar age and breeding experience.

In saturated habitat, the size of the breeding population should be highly stable at carrying capacity. Rising, falling, or irregularly fluctuating breeding numbers would not support an hypothesis of habitat saturation. If the habitat were saturated, the territories should be of a uniform size at, or close to, the minimum closest-packing for the species. Wide variation in size, with territorial areas similar to or larger than those found in other populations of the species that were not breeding cooperatively would be another indication of unsaturated habitat. The stability of the number of breeding birds must be known to assess the alternative ecological constraint to habitat saturation proposed by Emlen (1982), that 'fluctuating, erratic environments' lead to fluctuating breeding numbers.

The records of territory occupation, identity of breeding birds, and breeding success reported here are for 14 years for Rangatira Island and 13 years for Mangere Island. Some of the information on breeding success for the skuas on Rangatira Island has been published by Hemmings (1989), but is used here to test a different set of hypotheses.

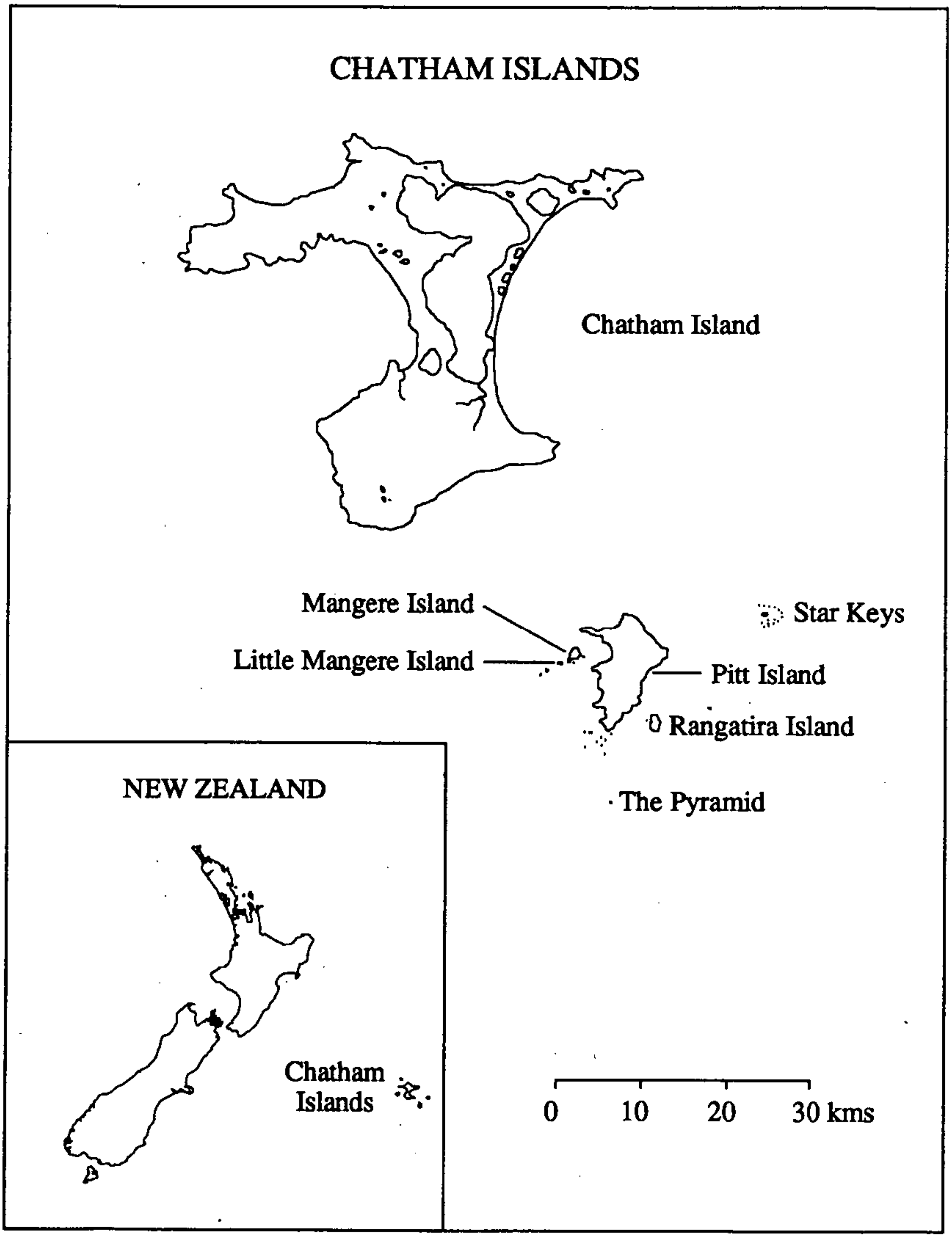

FIGURE 1 – Location of Rangatira and Mangere Islands within the Chatham Islands archipelago.

METHODS

Long-term study of cooperative breeding of Chatham Island skuas began in the 1974-75 austral summer on Rangatira Island (South East Island) (Figure 1) but the concerted banding efforts to produce a fully-banded and identified population did not begin until 1978-79 on Rangatira Island and 1979-80 on Mangere Island. In 1978-79, only the northern side of Rangatira was surveyed; in the following year all of Rangatira was surveyed as was Mangere except for the mountain plateau. From the 1980-81 season both islands were surveyed fully each year for breeding birds. Capture and recovery records showed that the skuas on Mangere and Rangatira islands, 12 km apart and separated by Pitt Island, form a single population.

Most data were collected during visits made to the Chatham Islands in December each year, when territories were mapped, the identity of all birds on territories confirmed, breeding success for the season determined and the adults and chicks banded. In December the oldest chicks were just beginning to fly and nearly all chicks were old enough to be banded. By the fifth year of the study (1982-83), almost all breeding adults had been captured and banded. After 10 years, most new birds coming on to breeding territories were already banded - as non-breeders on the 'club', as birds found at night by spot-lighting, or as chicks.

Nest sites were found and mapped easily, but because of the broken topography and dense vegetation, the boundaries of territories could only be accurately located in a few areas where the birds themselves marked these out on the ground. In this way the boundaries between 6 and 6A on the western side of Rangatira Island and most of the territories on the south coast were accurately mapped from observations of contact. Others had to be defined through flight patterns and where birds met and left flying intruders. Much of the report consists of comparisons of breeding statistics in different localities. The same localities and sets of territories shown in Figure 2 were used in each comparison.

Differences in breeding success and group stability were analysed by one-way analysis of variance (ANOVA). Significant results were then examined by Bonferonni least significance plots for individual significance (Lee *et al.* 1991).

RESULTS

Evidence for habitat saturation from the occurrence of unoccupied, apparently suitable habitat, and from data on population stability and breeding success

Habitat occupation by breeding skuas

Almost all the open ground on both islands was permanently occupied by breeding skuas. This was most obvious on Rangatira Island, where few places were free of skuas and there were only two areas in which skuas have been found in some years but not in others (12 and 13A/13B, Figure 2). Site 12 was occupied in the very first year of the study, but no other. Site 13A/13B was swampy ground and its occupation depended on water levels in spring. Similar swampy conditions forced trio 21 finally to abandon their

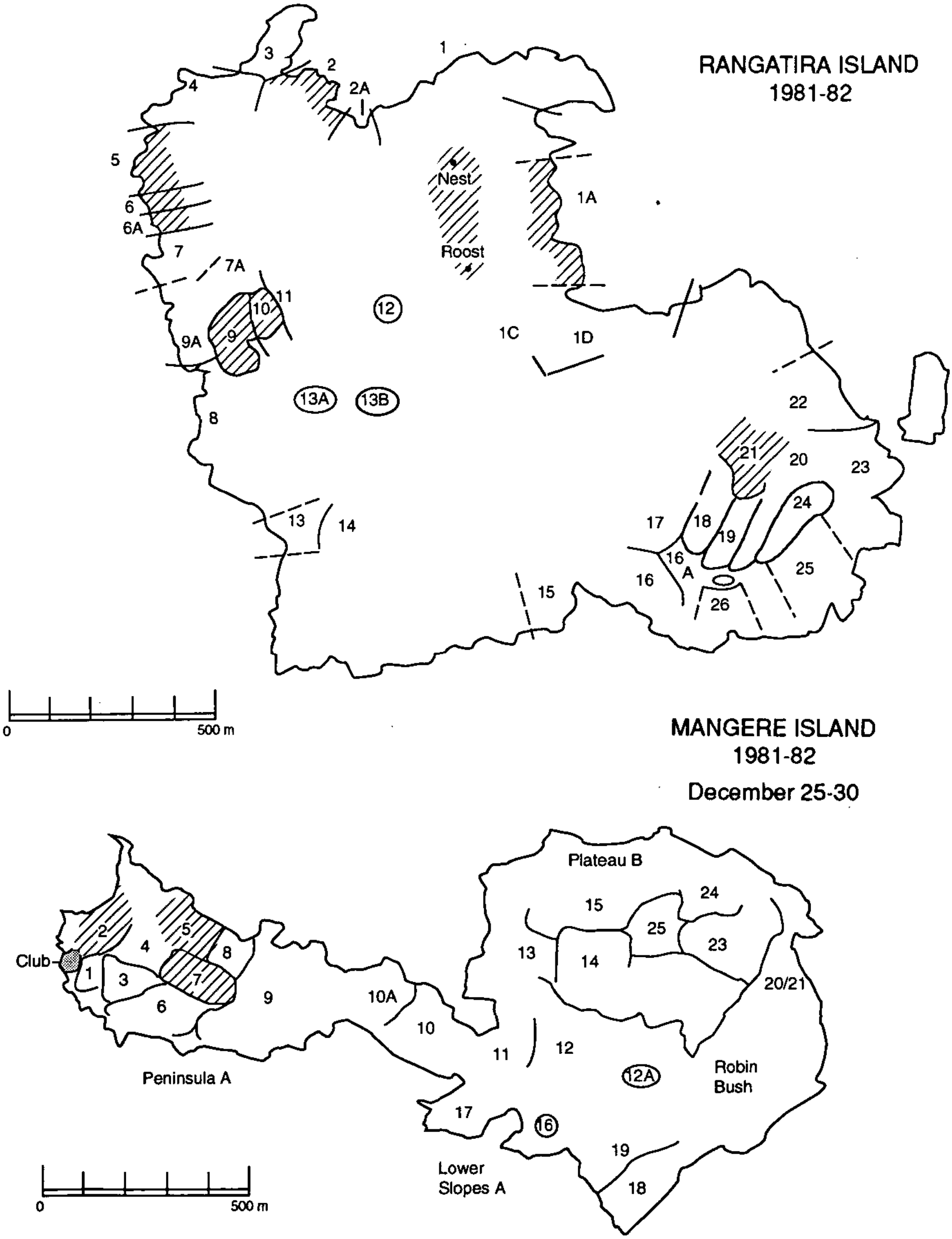

FIGURE 2 – (Part 1) Skua territories on Rangatira and Mangere islands during the 1981-82 and 1991-92 breeding seasons. Territorial boundaries marked out by ground display shown by complete lines, all other boundaries shown by broken lines. Territories occupied by cooperative groups shaded; all other territories occupied by pairs: mt, apparently empty ground. Sets of territories in each area used in the comparisons of habitat quality indicated by letters A & B on Mangere Island, A-E on Rangatira Island.

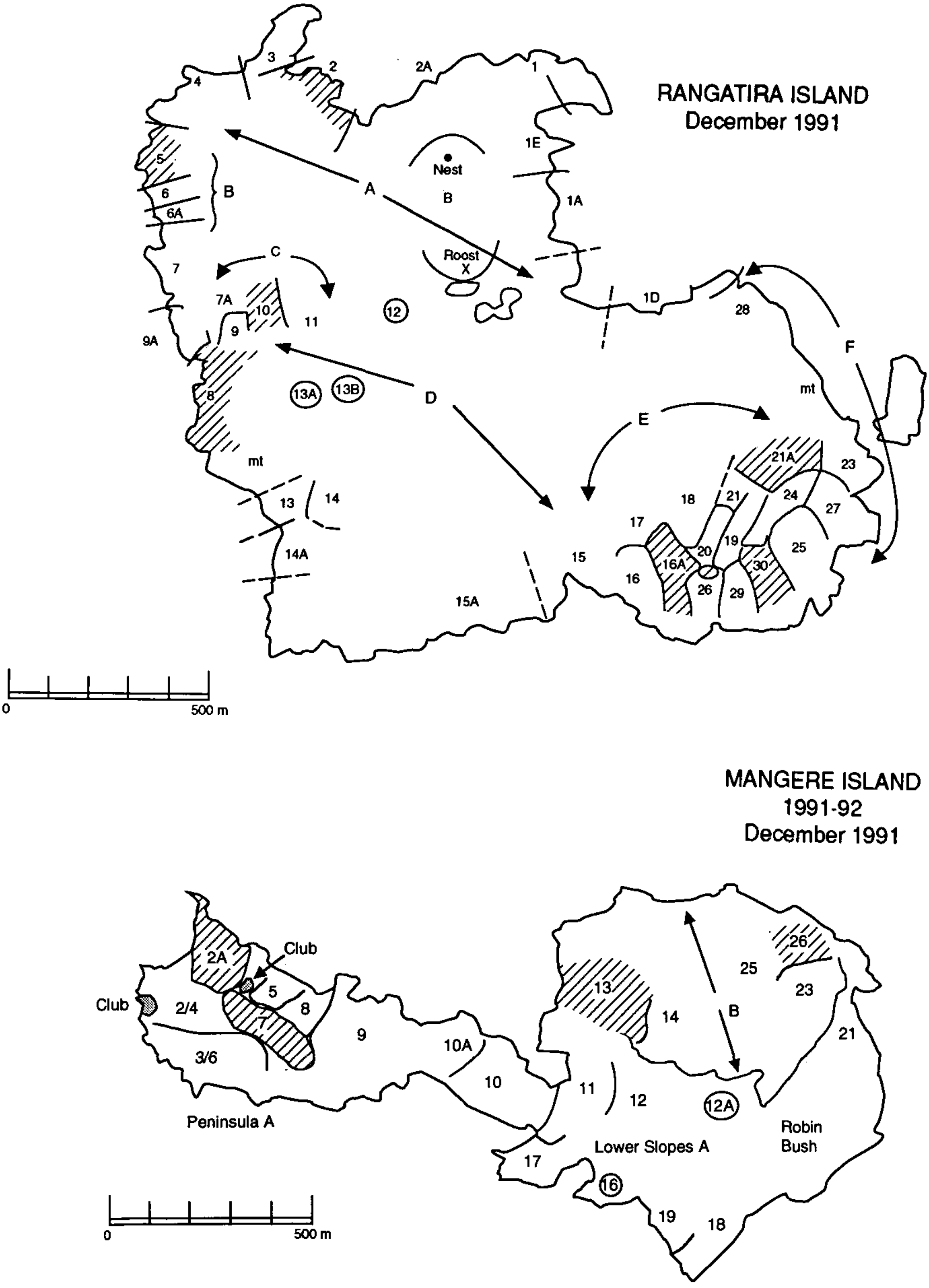

FIGURE 2 – (Part 2)

nest site and move on to bare, dry ground. Rangatira Island did not appear, therefore, to have marginal breeding ground in the way this is usually defined by relative quality. However, although breeding territories appeared to include all of the suitable habitat, it was clearly not occupied at maximum density. Over the years of this study, a significant number of new territories became permanently established on the island among those that were first mapped. In addition, the size of territories and nest spacing varied widely (see analysis of habitat quality below). A higher proportion of apparently suitable ground was unoccupied on Mangere Island. The most obvious gaps in the pattern of territories were site 16 (never occupied during these years despite appearing no different from the neighbouring headland occupied by pairs 18 and 19); site 12A, similar in all respects to 12, and the area abandoned by 19 to the north of 18. Moreover, some territories on the peninsula, merged (notably 2 with 4 and 3 with 6) so that they became occupied by a single pair in place of the initial two pairs. Even so, compared with the peninsula, the plateau appeared sparsely occupied, with very large territories in which the nests were widely separated along the perimeter. It was not occupied sporadically, however, as might be expected for a marginal area, and only once was a new territory formed temporarily. On Mangere, skuas did not occupy all the apparently suitable ground available.

Population stability

The number of occupied territories, number of breeding adults, and numbers of chicks produced each year in this population varied little from year to year. Territories on these islands were occupied by single birds, pairs, and cooperative groups of 3-7 birds. The proportions of these different forms of occupation changed from year to year, but the size of the breeding population was remarkably constant. From 1981-82, by which time the surveys were generally very accurate, the population ranged from 132 to a peak of 144 birds in the 1983-84 season (Table 1). The low inter-annual variation was not because the same birds were present: the stability masked a considerable turnover of the breeding birds. The mean annual percentage turnover of breeding birds from one season to the next - replacements in pairs or groups, addition of new breeders, or loss of established ones - for the two islands taken together was 14.6% (range 10-22%, 228 of 1506 bird-seasons) in the 11 years from the 1981-82 season. Change did not differ significantly between years ($\chi^2_{10} = 13.99$, $p = 0.145$). On average, 10.3% (range 8.1-15.3%, 156 of 1508 bird-seasons through 11 seasons) of breeding birds were lost each year from the population. Only 12 birds changed territories. These were deleted from numbers 'lost' from territories in each year when calculating annual totals.

Chick production also varied little between years (Table 2). On Mangere Island, 17-30 chicks fledged each year (24.5 ± 1.08, mean $\pm$ SE), and 35-60 (45.2 ± 2.02) fledged on Rangatira Island. Total production for the two islands was 58-81 chicks (70.4 ± 1.76). There were no years of total breeding failure and in only four years, and only on Mangere Island, did mean chick production fall below 1.00 chicks/occupied territory. For the two islands, the highest production was in 1992-93, when 81 chicks were alive in mid December from 61 occupied territories (mean = 1.29 chicks/territory). Chick

TABLE 1 – Numbers of occupied teritories and numbers of breeding skuas on each island in December and total numbers for both islands.

Years	Mangere Island		Rangatira Island		Total for both islands	
	Territories	Skuas	Territories	Skuas	Territories	Skuas
1979-80	-	-	29	70	-	-
1980-81	25	53	30	72	55	122
1981-82	25	52	35	82	50	134
1982-83	23	48	39	93	62	141
1983-84	24	48	41	96	65	144
1984-85	23	46	37	92	60	138
1985-86	24	48	38	92	62	140
1986-87	23	48	39	94	62	142
1987-88	24	41	40	95	64	136
1988-89	23	46	40	91	63	137
1989-90	23	47	40	90	63	137
1990-91	21	44	40	90	61	134
1991-92	20	43	41	89	61	132
1992-93	19	41	43	91	62	132

TABLE 2 – The annual production of chicks on each island and total production. Numbers of chicks and mean number alive and likely to fledge per occupied territory.

Years	Mangere Island		Rangatira Island		Total production	
	Chicks fledged	Mean / occupied territory	Chicks fledged	Mean / occupied territory	Chicks fledged	Mean / occupied territory
1979-80	27 *	1.42	37	1.28	-	-
1980-81	29	1.16	35	1.17	64	1.16
1981-82	22	0.88	36	1.03	58	0.93
1982-83	24	1.04	45	1.16	69	1.13
1983-84	26	1.08	49	1.19	75	1.15
1984-85	30	1.30	40	1.08	70	1.17
1985-86	30	1.25	39	1.03	69	1.11
1986-87	26	1.13	48	1.23	74	1.19
1987-88	22	0.92	52	1.30	74	1.16
1988-89	21	0.91	50	1.25	71	1.13
1989-90	17	0.74	48	1.20	65	1.03
1990-91	26	1.24	40	1.00	66	1.08
1991-92	25	1.25	54	1.32	79	1.29
1992-93	21	1.10	60	1.39	81	1.31

* Partial count only for Mangere Island

production to fledging on these two islands was remarkably uniform, with the narrow range of 0.93-1.29 chicks/occupied territory over 13 years. Overall, 952 chicks were produced during the study, from 799 occupied territories, a mean of 1.19 chicks from each.

Variability in habitat quality - optimal and marginal habitat?

Variation in exposure to weather conditions, aspect, topography, and forest shelter caused different ecotypes on different parts of the islands. The summit of Mangere (286 m) has a markedly different climate and exposure from lower slopes on the peninsula. Similarly, the northern coast of Rangatira Island is backed by sheltering bush, and has a different microclimate from the exposed, wind-swept, and barren coastal slopes on the south of the island. Territories also varied; some contained burrowing petrels which could be exploited as food, and in others there was no food (Young *et al.* 1988). But did skuas perceive the apparently significant differences between various areas? For the birds, were some areas optimal and preferred and others marginal?

It was not possible to categorise territory quality by inspection, although - after long experience - it was possible to predict broadly that an area would be suitable. The best way to determine quality was taken to be measured by the success of the birds themselves; on average the most successful breeding units over time were probably in the best quality territories. Aspects of breeding biology in relation to rather wide habitat difference are considered in the following sections. For the analysis, territories on the two islands were partitioned into eight groups, each occupying areas on the islands with different aspect and habitat features. These groups of territories are indicated on the maps in Figure 2, and their habitats are illustrated in Figure 3.

Distribution and size of territories

The distribution of territories for both islands for two seasons, ten years apart, is shown in Figure 2. In many places the skuas did not come into contact on the ground, so the territorial boundaries at these points were usually poorly defined (broken lines on the map). Vegetation type was the major factor determining where skuas bred; they relied on open ground for nesting.

The two islands had very different vegetation. On Mangere Island there was a small area of forest below the cliffs on the eastern side (the 'robin bush'). Most of the island was covered by long grass, a legacy of the earlier pastoral farming. Skuas occurred throughout, and most of the open ground was defended in territories.

Forest or dense bracken (*Pteridium aquilinum*) covered most of Rangatira Island. Skuas were confined to the coastal margin, a central grassed valley (now appropriately called 'Skua Valley'), and the barren flats on the south coast known as 'the clears'. Skua territories occupied all of these areas.

Open-ground areas suitable for breeding on the islands were not equally occupied and the size of individual territories and nest spacing varied widely. On Mangere Island, the territories were closest packed on the western

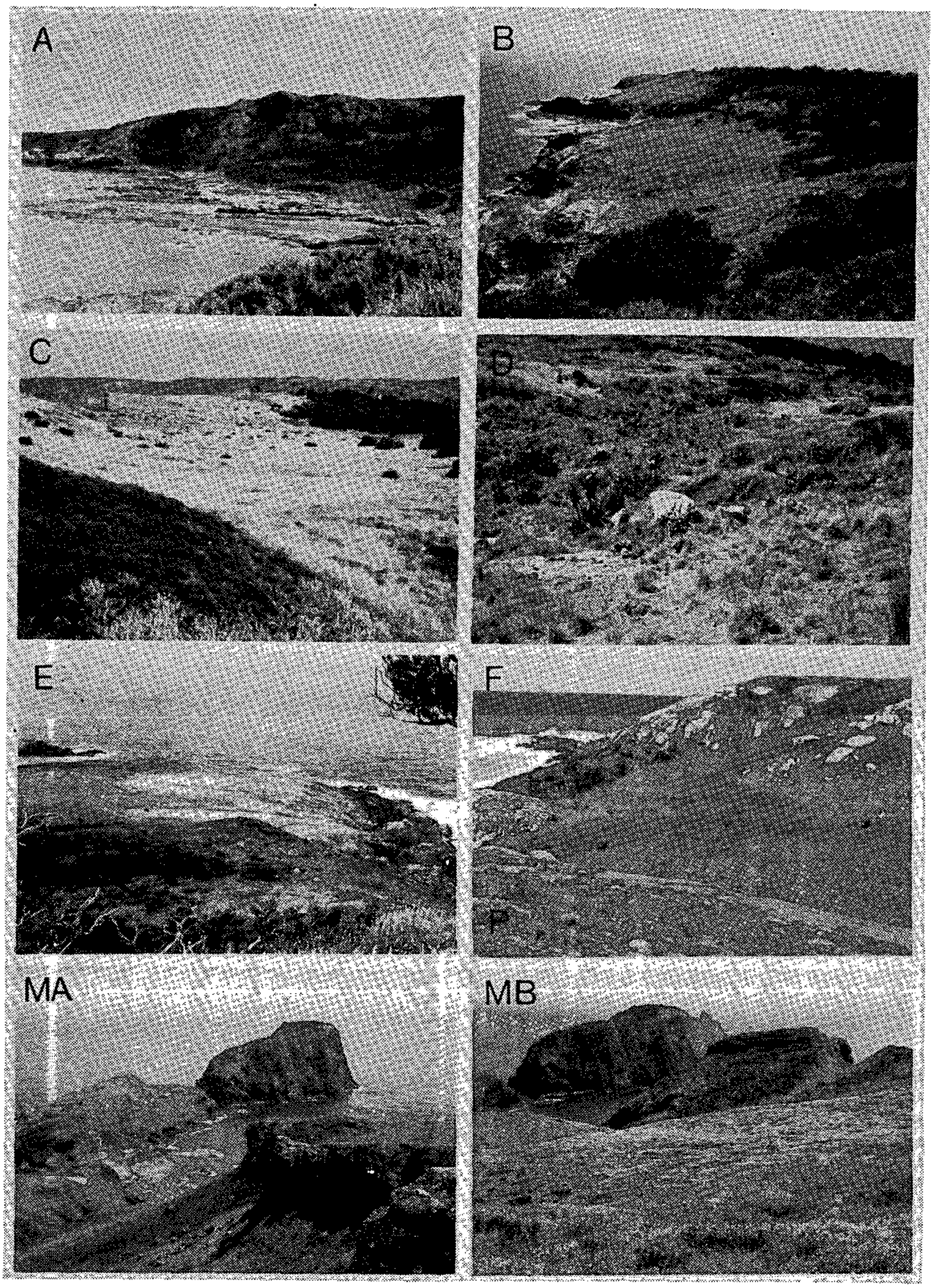

FIGURE 3 – Photographs of the different sectors used in the comparisons of habitat to establish whether optimal and marginal breeding localities occur on the islands. Habitat areas on Rangatira Island: A, sheltered north and east coasts; B, sheltered west coast; C, sheltered inland valley (Skua Valley); D, south-western slopes and cliffs; E, exposed, barren southern coast (the 'clears' photographed from the island's summit; F, east coast slopes. Habitat areas on Mangere island: MA, peninsula and lower slopes photographed from Mangere Peak, Little Mangere Island in the background; MB, mountain plateau.

peninsula - a low, gently-rounded point bounded by cliffs on each side. The largest territories on the island were on the summit plateau. On Rangatira Island, territories were aggregated in a small pocket of coastal shelf on the west of the island, in Skua Valley, and on the south coast. Elsewhere on Rangatira, territories were widely spaced around the island, on the narrow ribbon of open ground between the shore and forest.

The distribution of breeding birds and the disposition of territories remained remarkably constant throughout the study. The stability was doubtless influenced by topography and vegetation patterns, but was presumably also derived from the skuas' perception of what were suitable and desirable breeding places.

As noted earlier, most of the open ground of each island was permanently occupied. If marginal areas did exist, they could not be identified merely by checking occupation. Other assessments of biology were required to distinguish between more and less favourable areas on these islands. In the following analyses, different sectors of the islands are compared for three aspects of skua breeding that could be expected to distinguish breeding area quality: density of breeding birds; span of occupation by individual birds; and breeding success. In addition, the distributions of cooperatively breeding groups are compared, which may indicate areas where competition for breeding space was most intense.

Density of breeding birds

The densities of territories in different areas are compared in Table 3. It was not possible to measure breeding density uniformly well by territory area throughout the islands. Many groups occupied lengths of coastline without neighbours or boundaries on the inland side, so their inland margins were largely undefined. Their areas could not be measured accurately, although distance to the forest edge provided a consistent measure of their depth. Because precise areas could not be obtained for comparison, size of all territories to be compared was recorded as length of coastline and, for inland territories, as longest dimension. This length gave a consistent measure of size.

In general, the skuas had very large territories that extended over as much as 500 m of coastline, but the lengths did not differ significantly between islands (length in metres, mean $\pm$ SD: Rangatira Island, 189 $\pm$ 116, $n=38$; Mangere Island, 205 $\pm$ 68, $n=23$; one-way ANOVA, $F_{1,59}=0.35$, $p=0.55$, n.s.). An overall measure of nest spacing for each island was not appropriate because the different nesting areas were usually far apart. Nest spacing (distance from each nest to its nearest neighbour) is shown instead, within each of the habitat areas compared.

Small concentrations of territories were noted in three places: on the western beach (pairs 5 to 7) and on the 'clears' (pairs 16A-21, 26, 29) on Rangatira Island, and on the tip of the peninsula on Mangere Island. These groupings scarcely modified the general nest spacing of about 150 m, in territories averaging about 200 m long (Table 3). Territory sizes in these areas, measured as coastline or greatest length, varied significantly (one-way

TABLE 3 – Nest spacing and size of territories in different parts of the two islands. Data are mean and standard deviation for each group of territories.

Locations	Nest spacing (m)	Length of coast or longest dimension (m)
Rangatira Island *		
A. Sheltered north and east coasts	284 ± 80 (n = 7)	308 ± 133
B. Sheltered west coast	120 ± 65 (n = 4)	115 ± 77
C. Sheltered inland valley	111 ± 35 (n = 5)	175 ± 29
D. South-west slopes and cliffs	182 ± 126 (n = 5)	263 ± 171
E. Exposed, barren south coast	97 ± 35. (n = 11)	137 ± 62
F. East coast slopes	189 ± 132 (n = 4)	151 ± 74
Mangere Island †		
A. Peninsula and lower slopes	135 ± 55 (n = 15)	204 ± 79
B. Mountain plateau	136 ± 58 (n = 8)	207 ± 47

* A. 7 territories, 1D to 7; B. 4 territories, 5 - 7; C. 5 territories, 7A - 11; D. 5 territories, 8 -15A: E.11 territories, 16 - 29; F. 4 territories, 22,23,27,28.

† A. 15 territories, 2 - 21, minus 13 - 15; B. 8 territories, 13 - 15, 22 - 26.

ANOVA $F_{7,53} = 3.589$, $p = 0.003$). In paired comparisons by Bonferroni confidence intervals only two areas were significantly different: the territories along the north coast of Rangatira Island (coast length, 308 ± 133 m (mean ± SD)) were larger than those on the western beach of the same island (115 ± 77 m).

A similar variability in density of occupation was demonstrated by the spacing of nests within each area (Table 3). Not surprisingly, nests were more widely spaced along the north coast, where the territories were significantly larger, than elsewhere on the islands (one-way ANOVA $F_{7,49} = 5.30$, $p < 0.001$, Bonferroni least significance plot).

The significant differences between these areas of the islands were not sustained when all territories on the north and south of Rangatira Island and the peninsula and mountain areas of Mangere Island were grouped and compared for either nest spacing or longest dimension. Mean dimension for north and south coasts on Rangatira Island were 215 ± 125 m ($n = 19$) and 163 ± 102 m ($n = 19$), respectively. For the peninsula and plateau of Mangere Island they were 203 ± 79 m ($n = 15$) and 207 ± 47 m ($n = 8$), respectively.

With the exceptions noted above for Rangatira Island, the skuas did not appear to pack tightly into some areas and occupy others only lightly. On the contrary, they appeared to occupy all the open ground areas of these island at similar densities. Both the largest and smallest territories in 1992-93 were on the northern side of Rangatira Island.

Period of occupation of territories by individual birds, and maintenance of pair and group identity

Breeding group stability is significant for two reasons. First, if stability varied in different places on the islands, it may indicate different perceptions by the skuas of favourability for breeding, or variable survival; second, breeding group stability may reflect on overall breeding success and long-term productivity. Individual territories on these islands persisted apparently independently of the procession of birds that occupied them. This was derived, in part, from the geography of the habitable areas, and partly because new birds could occupy established territories before neighbours encroached. Very few birds changed territories after first-breeding. The tendency for territories to persist meant that there were two possible indices of stability in the make-up of the breeding population.

The first, the numbers of different birds over the years on a territory, was the appropriate index for comparing the use made of the breeding areas and for discriminating between optimal and marginal habitats. For a pair in unbroken occupation for 13 years this index would be 13 (i.e. $26 \div 2$); for the same territory occupied by 6 different birds it would be 4.5 ($26 \div 6$). Because the calculation is based on the product of birds and seasons, pairs and cooperative groups could be brought together for comparison within a single series. Table 4 shows the mean occupation span (average time individuals were in territories) for the same sets of territories used for comparing nesting densities and breeding success. Mean number of seasons skuas were on territories in these years in the different localities ranged from 4.68 to 7.70 years Differences in occupation times among localities were not significant (one-way ANOVA $F_{7,49} = 0.65$, $p = 0.71$).

The second possible index for assessing stability of the breeding group was the length of time individuals were associated within pairs or groups. This is the appropriate index for establishing relationships between breeding group stability and reproductive success and is considered below.

Breeding success in different habitat areas on the islands

Skuas on these islands consistently produced a full clutch of two eggs each year and had high breeding success. Few relaid. The breeding success over 12 years did not differ significantly among the eight areas (ANOVA $F_{7,51} = 0.82$, $p = 0.573$); when the areas were grouped together for the plateau and peninsula on Mangere Island and north and south coasts of Rangatira Island, respectively (ANOVA $F_{3,55} = 0.46$, $p = 0.707$); or when whole islands were compared (ANOVA $F_{1,57} = 0.5$, $p = 0.447$) (Table 5). Some pairs had, however, consistently poor or consistently high breeding success. For example, pairs 1 and 5 on Rangatira Island had only 9 chicks each in 14 years (0.64 chicks/year) and pair 7 had 10 chicks in 14 years (0.71 chicks/year). At the other extreme, pair 2A produced 20 chicks in 11 years (1.81 chicks/year) and pair 26, 21 chicks in 11 years (1.91 chicks/year).

TABLE 4 – Mean occupation span of individual birds within territories during 11 years in different places on Rangatira and Mangere islands. Mean and standard deviation.

Locations	Mean occupation span (seasons / bird)*
Rangatira Island	
A. Sheltered north and east coasts	7.37 ± 3.83
B. Sheltered west coast	7.70 ± 1.21
C. Sheltered inland valley	6.86 ± 3.54
D. South-west slopes and cliffs	6.02 ± 0.98
E. Exposed, barren south coast	6.43 ± 2.64
F. East coast slopes	4.68 ± 0.71
North coast as a whole (n = 20 territories)	7.01 ± 2.97
South coast as a whole (n = 16 territories)	6.00 ± 2.21
Mangere Island	
A. Peninsula and lower slopes	7.00 ± 2.84
B. Mountain plateau	5.88 ± 1.80

*The number of bird-years divided by the numbers of different birds occupying the territory. Pairs and cooperative groups are both included. The number of territories in each area is shown in Table 3. The occupation spans were not significantly different for the places shown (one-way ANOVA $F_{7,49}=0.65$, $p=0.71$) nor were the differences significant when the means for the north and south coasts as a whole on Rangatira Island were tested (one-way ANOVA $F_{3,53}=0.74$, $p=0.53$).

TABLE 5 – The average breeding success of skuas in the different parts of the islands from records for all seasons the territories were occupied.

Locations	Mean number of chicks / season *
Rangatira Island	
A. Sheltered north and east coasts	1.29 ± 0.39
B. Sheltered west coast	1.09 ± 0.48
C. Sheltered inland valley	1.00 ± 0.35
D. South-west slopes and cliffs	1.32 ± 0.28
E. Exposed, barren south coast	1.35 ± 0.32
F. East coast slopes	1.03 ± 0.32
Mangere Island	
A.Peninsula and lower slopes	1.18 ± 0.47
B. Mountain plateau	1.07 ± 0.39

* Breeding success in each area includes both pairs and breeding groups. The mean shown is for the overall production of each territory usually for 11 - 13 years but some shorter spans to 7 years have been included.

TABLE 6 – Impact of replacement of birds in pairs / groups on breeding performance in the following years and the initial success of newly formed pairs.

Effect of the replacement of one bird in established breeding groups recorded for the same group before and after the replacement of one adult.

	Years before replacement			Years after replacement		
	3	2	1	1	2	3
Total no.chicks / season (no. of breeding groups)	31 (23)	47 (34)	43 (34)	22 (34)	33 (29)	17 (14)
Mean no. chicks / season	1.34	1.38	1.26	0.65	1.14	1.21

Success of newly formed pairs over their first three breeding years

	Years		
	1	2	3
Total no.chicks / season (no. of breeding groups)	19 (21)	16 (15)	10 (11)
Mean no. chicks / season	0.90	1.07	0.91

TABLE 7 – The breeding success of pairs and cooperative groups during runs of seasons without changes in pair or group identity.

Locations	Mean numbers of chicks each season / occupied territory *
Rangatira Island	
A. Sheltered north and east coasts	1.31 ± 0.50
B. Sheltered west coast	1.06 ± 0.58
C. Sheltered inland valley	1.40 ± 0.48
D. South-west slopes and cliffs	1.48 ± 0.30
E. Exposed, barren south coast	1.47 ± 0.31
F. East coast slopes	1.10 ± 0..31
Mangere Island	
A.Peninsula and lower slopes	1.49 ± 0.31
B. Mountain plateau	1.31 ± 0.37

*Numbers in each category listed as territories as these contain both pairs and cooperative breeding groups. The means shown are for chick production on each territory during unbroken pairing sequences longer than 4 years. The means shown are derived from the products of between 36 to 101 season x breeding group records. The production in the various areas measured in this way was not significantly different (one-way ANOVA $F_{7,45} = 1.08, p = 0.39$).

Table 6 shows breeding statistics following changes within the birds of a pair (A), or when measured from first breeding of a newly established pair (B). Production in the same territory following a change in the pair fell from a mean of 1.26 chicks/pair to 0.67 chicks/pair in the first year, but recovered to normal levels two years later. The decline in chick production in these pairs resulted mainly from the failure of some pairs to produce any chicks at all. In the years before replacement, 79-86% of pairs produced chicks. In the first season following replacement only 47% of pairs were successful; in the year after the success rate had reached 70% of pairs, and in the year after that 85%. The success of birds in the replacement season was significantly below that of all other years when pairs were scored for success (with chicks) or failure (without raising chicks) ($\chi^2_5 = 19.04$, $p<0.001$).

The breeding success statistics of 21 newly-formed pairs (neither bird previously breeding) show that productivity was relatively high even in the first season (Table 6(B)). The success rate of these birds in their first year (recorded again as with or without fledglings) was not significantly different from that in later years ($\chi^2_2 = 0.58$, $p = 0.713$).

The moderate impact on chick production of changes in identity of birds on territories suggests that the low frequency of changes in breeding birds recorded in this study had little impact on the overall breeding statistics. This was confirmed by re-calculating the breeding success statistics using runs of season in which there were no changes in the breeding birds (Table 7). The overall breeding success for each habitat area measured in this way differed little from that measured for the entire period a territory was occupied, irrespective of the number of changes in occupying individuals over this time.

Distribution of cooperatively breeding groups

On Rangatira Island, most cooperative groups were on the north coast (8 as against 1 on the south coast) in 1979-80, the first year of the study. There were almost equal numbers in the two localities ten years later (4 as against 3), but the differences in numbers on the two coasts were not significant. Cooperative groups occurred equally on the peninsula and mountain plateau habitats on Mangere Island.

DISCUSSION

Charles Fleming and Graham Turbott visited these islands during the 1937-38 summer and provided the first detailed account of the islands' vegetation and ornithology (Fleming 1939). Rangatira and Mangere islands were both still grazed by sheep at this time. Farming favoured the skuas by providing food (sheep carcasses) and by maintaining open grazed areas (used for nesting). Breeding petrels, the staple food of breeding skuas on both islands, seem to have been abundant. Fleming observed that White-faced Storm Petrels (*Pelagodroma marina*) burrowed in every 'soil-covered square yard' on Rangatira Island - in the open and under the forest. The Broad-billed Prion (*Pachyptila vittata*) and Sooty Shearwater (*Puffinus griseus*) were also abundant. It is not known to what degree the farmers persecuted the skuas (because of the skuas' vigorous territory defence and their depredations on cast sheep and new-born lambs), but birds were certainly shot (Graham Turbott, pers. comm.). Fleming (1939) estimated that there 'were at least 150 adult birds present' on Rangatira Island. This is about the same number as at present, if nonbreeders in the 'club' are included. He did not give numbers of skuas for Mangere Island. Sheep were removed from Rangatira Island in 1961 (Ritchie 1970) and Mangere Island in 1968 (Veitch & Bell 1990), allowing bush, flax, bracken, and vines to spread widely.

Breeding skuas have been displaced from most inland sites on Rangatira Island and only Skua Valley (occupied by groups 7A-11) offered substantial open ground away from the coastline during this study. In time, this area will be covered with regrowth which will exclude breeding skuas.

Breeding population stability of skuas and their use of habitat on Mangere and Rangatira islands was studied to examine the hypothesis that cooperative breeding is habitat-forced (Koenig & Pitelka 1981). The two islands contained most of the breeding skuas on the Chathams; most of the remainder were on Star Keys and Little Mangere islands. As both of these appeared to be fully occupied, neither could be considered marginal habitats for the Chathams population as a whole.

At the start of the study on Rangatira Island, the northern half seemed to contain the most favourable skua habitat on the island because it was warmer, and the cliffs and forest sheltered it from the southerly gales. Moreover, nearly all cooperatively breeding groups occurred there at that time, with concentrations of cooperative groups in the northeast corner (trios 1, 1A, 1B, 2) and on the west coast (trios 5, 6, 6A). By the end of the study, proportions defended by cooperative groups in the two halves of the island had changed dramatically - about half were then on the supposedly less suitable and less favoured southern coast. Not least, this change in the distribution of the cooperative groups emphasises the benefit of longer term studies.

Breeding population stability

This study showed that the Chatham Islands Brown Skua breeding population numbers changed little over 14 years and they produced a rather constant number of chicks each year. The records nevertheless demonstrated significant turnover of individuals within the population. The environment for most birds was apparently benign, characterised by only small fluctuations in climate, habitat, or food availability. No widespread breeding failure was recorded in any year, although some individual pairs and groups did fail consistently over several seasons. The good success of pairs in their first year of breeding was also evidence of favourable breeding conditions. Other studies of skuas have shown that newly-formed pairs are generally less successful than established ones. In Great Skuas (*C. skua*), for example, Furness (1984) found that first-year breeders fledged chicks from 50% of their eggs as against 69% for birds with 2 year's breeding experience. The difference between naive and experienced breeders was even more pronounced in the South Polar Skuas (*C. maccormicki*) studied by Ainley *et al.* (1990).

It was not possible to use presence or absence of food in the territory as a measure of habitat condition. None of the territories on the south coast flats of Rangatira Island, (territories 16A-25 of group E) contained petrel burrows, yet some of the breeding units there were among the most successful. The overall conclusion is that the islands provided extremely favourable breeding conditions for skuas. Unfortunately, there are no other long-term studies of Brown Skua breeding with which to compare the results.

The remarkable population stability across seasons found in this study indicated that the islands provided stable breeding conditions for these birds. It is highly unlikely, therefore, that cooperative breeding in this population has arisen because of variable or fluctuating habitat conditions. Of the constraints to breeding considered by Emlen (1982), variable or fluctuating conditions were suggested as an alternative to habitat saturation in stable conditions.

Habitat saturation and the occurrence of marginal areas

The important question to ask when considering the significance of ecological factors in relation to cooperative breeding in the present study is: To what extent were the islands saturated by breeding birds, or at least so extensively occupied that only marginally suitable areas were available for new breeders? This question is basic to tests of the habitat-forced hypothesis of Koenig & Pitelka (1981) or the more general ecological constraints model of Emlen (1982).

It was examined in four ways. First, were apparently suitable areas on the islands not occupied; second, were territories uniformly closely-packed; third, were there identifiable marginal areas that were occupied only during some seasons of high population or for short periods; and fourth, were there marginal areas recognisable through different levels of breeding success? In addition, differences in territory spacing between populations might well be instructive. As very few birds changed territories during this study, it was not possible to separate the contribution to breeding success of individual and pair quality, and habitat quality.

Little, if any, suitable empty ground existed on Rangatira Island, but it was less certain that none existed on Mangere. Some large open areas on the lower slopes there remained unoccupied throughout the study, and part of the plateau seemed so weakly defended that it must also have been available for occupation by new breeders. Only one part of this large central area (14A) was ever taken up, and that for a single year only. In addition, several territories remained empty for some seasons and others, notably 2-4 and 3-6, merged, so that two pairs came to occupy the same ground held earlier by four.

On this evidence, it appeared that the island was not so saturated with breeding pairs that new birds could not establish there. Moreover, in other places on both islands the territories were so large that their farthest limits were indefensible and new pairs and groups were able to establish among them. Examples of this were 2A (between 1 and 2), 1E (between 1 and 1A), and subsequently 1F (between 1E and 1A) on the northeast corner of Rangatira Island. This coast appeared to be fully occupied by the original pairs when first surveyed yet it seemed that new pairs established there without difficulty.

The relative size of territories observed also suggested that the habitats were not saturated. In a saturated habitat, a rather uniform size scaling down to the lower end of the range for this species might be expected. Instead, the territories exhibited a very wide size range, measured by nest spacing, area, length, or length of coastline; few on these islands could be considered small for this species.

Furness (1987) distinguished two groups of skua populations based on function of territory: populations in which birds feed away from the territory at sea or kleptoparasitically in which the territories are small; and those where birds are restricted to feeding within the territory, in which territories are larger. The Brown and Tristan da Cunha skuas belong in the second category, with territory densities of 5-100 pairs km^{-2}, i.e. with territory areas of 1000-20,000 m^2.

There were no such distinctions in territory size based on foraging place in the Chathams' skuas, which all had territories of much the same size (10,000-30,000 m^2) whether containing food or not. Chathams' skuas feed exclusively on land when breeding (Young *et al.* 1988). On some Southern Ocean islands, nests of Brown Skuas can be quite closely packed, almost as close as for the South Polar Skua. Hemmings (1984) found nest spacings of less than 50 m on Signy Island and Osborne (1985) recorded an overall spacing of 50-100 m for his study areas on Bird Island, South Georgia. No areas on Rangatira and Mangere islands consistently exhibited such close packing of territories.

Much of the work presented here was an attempt to elucidate possible preferences by skuas for different areas on the islands (by analysis of territory size, span of occupation, and breeding success) to demonstrate, if possible, the existence of favoured (optimal) areas compared with marginally suitable ones, within the total area occupied by the birds. None of the analyses showed any differences among the several topographical and geographic areas that are apparent within these islands, nor did they discriminate between the two islands. Of greater significance is that they did not demonstrate any difference between birds nesting on the northern side of Rangatira Island, in sheltered habitats containing many breeding petrels which were exploited for food, and those on the south of the island, where most territories were barren, and which the skuas had to leave to feed on common ground or, less commonly, along the edges of other territories at night. It is, therefore, extremely doubtful whether there were optimal and marginal areas on these islands that were exploited and occupied differently by the skuas. As noted, on average, skuas in the groups of territories in the different areas identified in this study seemed to perform equally well.

The conclusion from this review of skua distribution and breeding biology was that these islands, although seemingly full occupied by breeding birds, were not 'saturated' in the way this term is used in the ecology of cooperatively breeding species (e.g., Koenig *et al.* 1992). Nor did there appear to be areas of marginal suitability. On the contrary, a few breeding birds were spread throughout the open areas on both islands, in territories extending to the forest edge, or along the coastline, but few came into such close contact that much defensive territorial behaviour occurred on the borders. New pairs were able to establish territories in the ill-defined zones between breeding units.

Finally, it should be noted that the only way to test these views on the degree of habitat saturation would be by experiment, but this is not permitted on these nature reserves. In the absence of experimental evidence, the views on habitat saturation are simply considered opinion. A thorough test would be a large-scale experiment involving removal of breeding birds, to see to what extent cooperative breeding is retained in the population when breeding space is abundant. At the same time, more non-breeders - which are presently 'floaters' in the 'clubs' - progressing to breeding status, would support an hypothesis of behavioural or ecological constraint to breeding. Although clear in theory, ethically the experiment cannot be countenanced.

ACKNOWLEDGEMENTS

This research has been possible only through the cooperation of the administrators responsible for the islands, at first the Lands and Survey Department and latterly the Department of Conservation, in giving permission to work on the islands and in providing support and facilities. Accommodation on Chatham and boat transport was provided by local residents. Without their help and cooperation also none of this research would have been possible. Over the years many students and colleagues have been involved with the field work. I acknowledge especially Murray Douglas, Peter Jenkins, Tim Lovegrove, Alan Hemmings, Elsa Flint, John Tyrrell, Craig Millar, and Bob Furness. To all of these people my grateful thanks. The research was supported by grants from the Auckland University Research Committee and the University Grants Committee. I am grateful for helpful comments on this paper by Mick Clout, Craig Millar, and Greg Sherley.

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