THE OVERLAPPING BREEDING TERRITORIES OF SEVERAL SHORE BIRD SPECIES

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INTRODUCTION

The study of territory has been a popular interest for both ornithologists and mammalogists. Orians and Willson (1964) and Simmons (1951) review numerous papers describing the territories of individual species and the interspecific territories of closely related species "competing" for common ground. To date however, the literature indicates little interest in the way a specific area might be defended and exploited by a variety of territorial and nomadic species of birds. Studies have been made of the overlapping territories of blackbird (*Turdus merula*) and thrush (*Turdus philomelos*) in the Oxford Botanic Garden (Davies and Snow, 1965; Snow, 1958), of jaegers and owls of the Alaskan tundra (Pitelka *et al*, 1955); of the several species of tits in northern hemisphere woodland (Gibb, 1956; Hinde, 1952) and of the covey territories of partridges (Blank and Ash, 1956).

The present study is of a unique association of bird species on Rangatira Island (176°11'W, 44°22'S), in the Chatham Islands. Seven species shared the rocky coastline and held breeding territories there throughout summer.

The study area was at the landing place where a wide shore platform linked a narrow rocky point to the northern end of the island (Fig. 1). The platform provided a rich and varied feeding area for shore species. Its surface was a little above high tide level although covered with strong water flows during storms. Throughout summer it held a thick cover of *Ulva* and *Enteromorpha* and a diverse biota in the narrow trenches and slits that scarred its surface. The broken, rocky ridges and cliffs that bordered both sides of the platform provided good shelter for nesting, protected from the full force of the often severe wave action of this coast.

The observations were made over seven weeks during mid-summer of 1974/75.

THE USE OF THE SHORE PLATFORM DURING THE BREEDING SEASON

Birds of the following species nested around the platform or were commonly seen there: southern skua (*Catharacta lonnbergi*), black-backed gull (*Larus dominicanus*), red-billed gull (*Larus novaehollandiae*), white-fronted tern (*Sterna striata*), Chatham Island oystercatcher (*Haematopus chatha-*

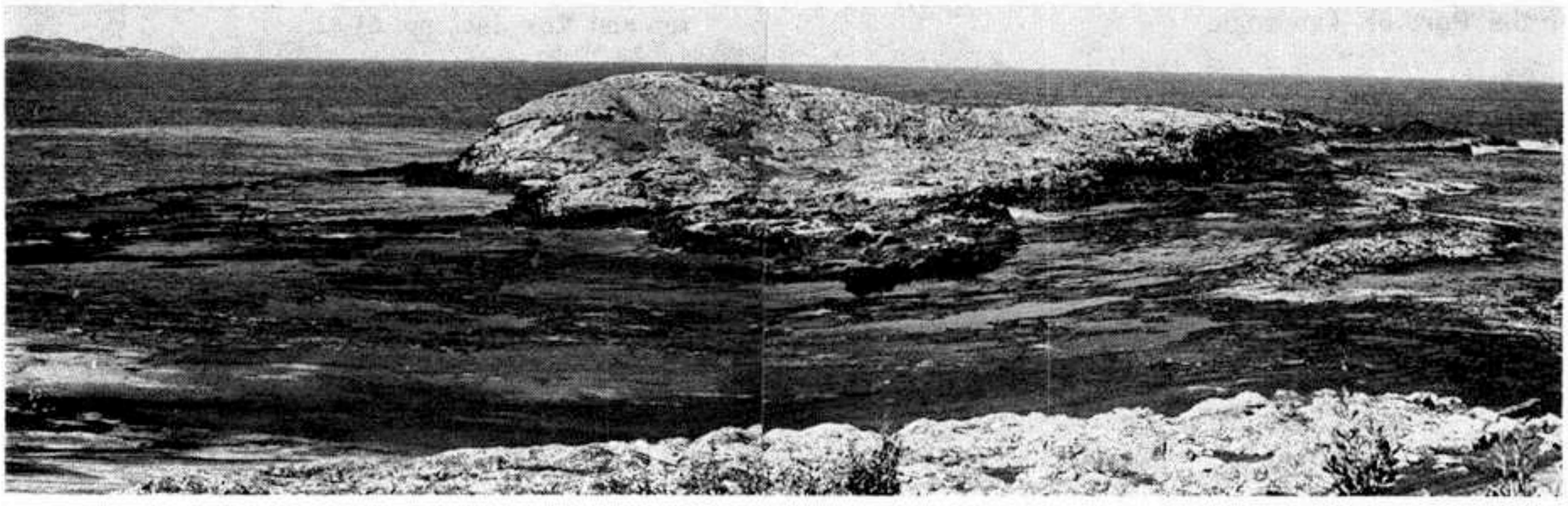

FIGURE 1. *The shore platform of the landing place on the north end of Rangatira Island. The view is from the main island looking north across the platform to the point. The landing place is to the right of the platform.*

mensis), New Zealand shore plover (*Thinornis novaeseelandiae*), New Zealand pipit (*Anthus novaeseelandiae*) and starling (*Sturnus vulgaris*). Many of the plovers and oystercatchers were banded. The territories and nest positions of these species are shown in Fig. 2. The limits of the territories were determined from observation of the movements of the birds and of territorial disputes.

These observations established that the platform was utilised as follows:

Southern Skua: Three pairs held territories extending on to this platform area (Fig. 2A). All however, nested and raised their chicks among vegetation on high ground well above platform level. Flights by the territory skuas at others were usually high in the air above the platform and no landings were seen there. These skuas fed at sea or at night on petrels captured inland away from the territories. Many skuas used the brackish-water pools on the inland edge of the platform for bathing but showed little interest there in other species.

In summary, the platform formed a buffer zone separating the nesting areas of the three pairs.

Black-backed Gull: Five pairs nested on the point along the edge of the platform and a further 12-15 pairs nested further out on the point. There were three other pairs on the coast at the western edge of the platform, giving eight pairs altogether with access to the platform from territories along its edge. The nesting territory was essentially no more than a few metres around the nest but defence shifted later as chicks moved from the nest into more sheltered positions. The platform was little used for feeding but later in the season gulls often accompanied fledgling chicks as they wandered across it to the sea edge. The gull nests on both sides of the platform were overlooked by skua pairs and the breeding birds were always vigilant to the possibility of skua predation on the chicks. One attack by skuas was observed in which a fledgling gull was killed.

Red-billed Gull: These gulls nested under overhangs or in caves on Rangatira Island and their nesting dispersion was determined by the occurrence of these sites. Only one pair nested in the immediate area of the platform. The nest, with a pair of eggs, was located in a shallow cave on the western edge of the platform but was washed out by exceptionally high seas during a storm. The pair soon abandoned the area. Red-billed gulls fed at sea, commonly with terns, at the turbulent upwellings close inshore. Little use was made of the platform.

White-fronted Tern: Two pairs nested here; one on the point and the other on an outcrop to the east

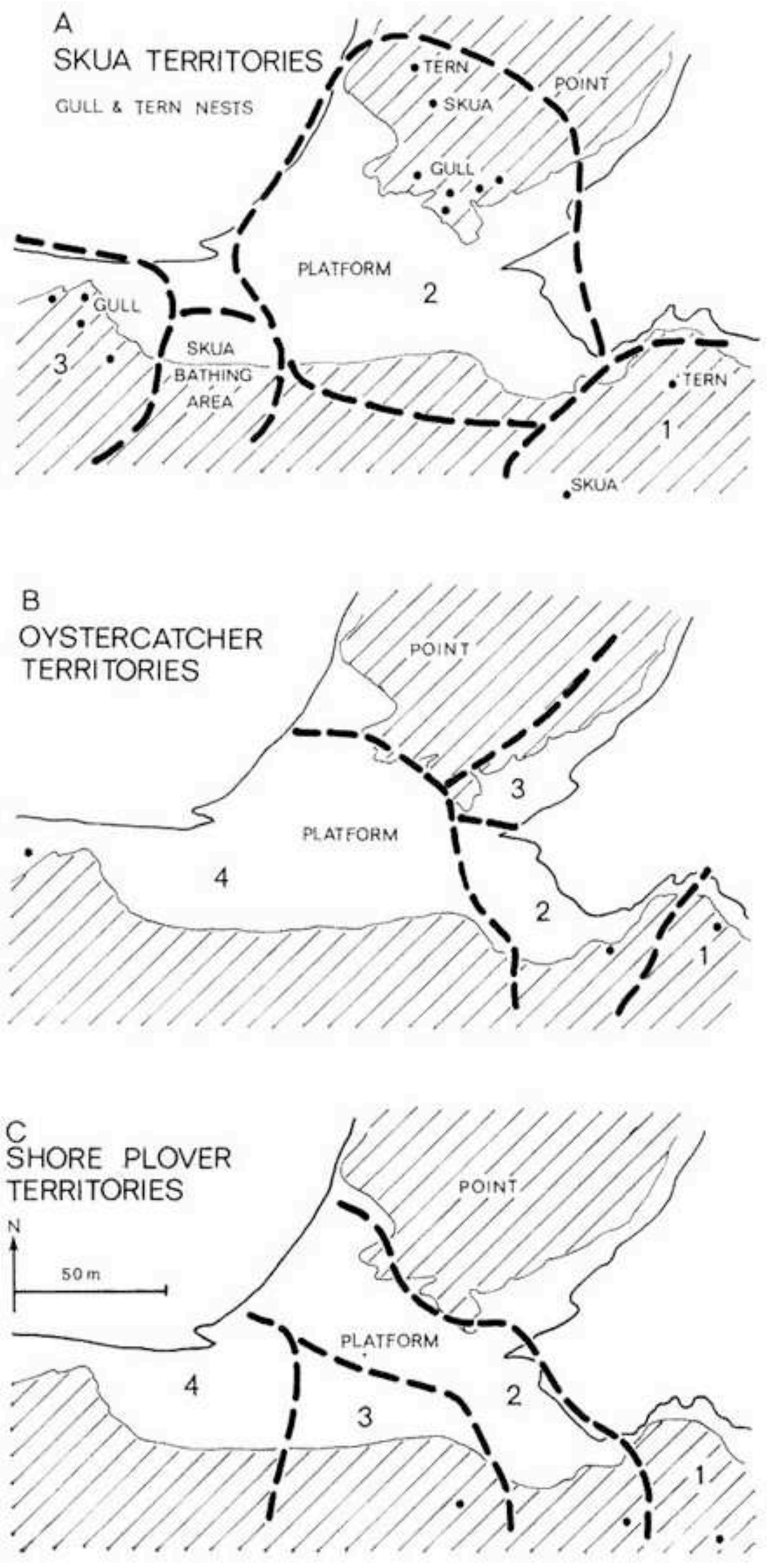

FIGURE 2. *The nests and territories of the species breeding on the shore platform at the landing place. A. Skua territories and nests and the nest positions of the gulls and the white-fronted tern. B. The territories and nest positions of the oystercatchers. C. The territories and nest positions of the shore plovers. The nest of pair 4 was approximately 150 m to the west of the platform. The rock outcrops and higher areas on the point and the main part of the island are hachured.*

of the platform. Both raised a single chick. They were extremely pugnacious in defence of the nest and chick and invariably pursued skuas and gulls in flight near them. The pair to the east of the platform also attacked oystercatcher pairs 1 and 2 and prevented them occupying or visiting the high ground of their territories.

A tern territory for conspecifics is only a small area about the nest and the pairs may be closely packed together in colonies. The area defended against other bird species, especially black-backed gulls and skuas, is however, far greater and both these species may be harried away from colonies or isolated nests for several hundred metres. They are in fact being chased away from the general area and not just from the nest.

The terns fed on small fish and plankton taken directly from the sea and were often seen fishing on upwellings close to the shore. They were not seen on the platform.

Chatham Island Oystercatcher: The platform was divided among three territories and a fourth touched the eastern edge (Fig. 2B). A single bird defended much of shoreline of the point (Territory 3) but did not attract a mate at any time during the observation period. Territories 2 and 3 were small compared with other territories on the island. The territory of pair 1, for example, extended over 600 m of coast to the east of the platform and that of pair 4 for 300 m of coast to the west. These are more typical of the territories on the island.

The oystercatchers fed mainly on limpets *(Cellana strigilis chathamensis)* and chitons (mostly *Guildingia obtecta)* taken from the intertidal zone. Little feeding occurred on the wide flats of the platform itself. This area, however, was used extensively by the birds, during preening and loafing and in interminable territorial disputes. In summary the birds were invariably present on the territory with feeding, nesting and roosting occurring there.

Shore Plover: The platform was defended by three pairs of plovers (Fig. 2C). Territorial conflicts were common and much of the birds' time was spent in territorial defence. Pair 2 made especially long flights to chase off intruders settling in their territory on the far side of the platform some 200 m from their usual feeding and roosting area. Persistent intruders were generally able to stay on a territory for some hours but were chased continuously by the defending pair. Territorial defence was by supplanting flights and no fighting was seen. Starlings were also chased off the territory and even flocks of 20 or more were successfully forced away. In these encounters a series of short flights at individual birds shifted the whole flock.

Plovers spent nearly all their time on the platform area or on the rocks and flats bounding it. They spent little time in the intertidal zone of the sea edge. This zone was more attractive to both the pipits and starlings and was the main feeding area of oystercatchers.

The plovers appeared relaxed near oystercatchers even when their chicks were with them on the open platform. No interactions between these two species were observed.

Plovers responded agitatedly to both black-backed gulls and skuas coming on to the territory or flying across it. Their most common contact was with the gulls and few interactions with skuas were seen. Gulls flying low into the territory near the chicks were invariably met by plovers which flew a few metres ahead piping the alarm-call continuously. This very obvious and characteristic display to gulls, part distraction and part advertisement, alerted the whole area and chicks were quickly shepherded into shelter.

Territorial skuas were not often seen on the shore platform anywhere on the island and did not feed there except when attracted by dead or injured penguins. Plovers were apparently unconcerned by the proximity of groups of bathing and preening skuas at the pools on the upper shore line of the platform. The skuas at bathing pools were mostly loafing birds from territories and for this short period each day mixed together easily. They were certainly not foraging at this time.

Most plover feeding occurred along the edges of the shallow trenches which crisscrossed the platform. These held water even when the rest of the platform was quite dry. From close observation of feeding behaviour and from collections made from the places feeding occurred it was concluded that they were feeding mostly on the amphipod *Paracalliope,* which occurred abundantly in the *Enteromorpha,* and on smaller numbers of the isopod *Isocladus.* Two snails, *Littorina unifasciata* and *Zeacumantus subcarinatus,* were also abundant on the platform but did not appear to be taken by the plovers. When the platform was covered with running sea-water the plovers foraged for insects among the rocks and shore vegetation along the forest edge and took mosquito larvae *(Aedes chathamicus)* from brackish pools.

The section of pair 2 territory against the point was at a higher level than the rest and allowed this pair to feed there when the remainder was underwater. Their strong defence of this part was presumably related to its value as a feeding area: the

TABLE 1. *Summary of Characteristics of the Territories and of Links among Species.*

	Territory size	Nest site	Type of Territory			Months Territory defended	Interspecific Relationships		
			Large breeding area providing most of food (Hinde, Type A)	Large breeding area providing little food (Hinde, Type B)	Small Nesting Territory (Hinde, Type C)		Preyed on by:	Competes for food with:	Competes for nest sites with:
Southern skua	large	Exposed in short vegetation	+	+		mid-August–early February	—	black-backed gull (as scavenger)	dominant over others
Black-backed gull	small	exposed on rocky out-crops			+	August–early February	Skua	—	skua
Red-billed gull	very small	under cliffs or in caves			+	mid-November–late January	black-backed gull	tern	skua and black-backed gull
Tern	small	exposed on out-crops			+	mid-November–late January	skua and gulls	red-billed gull	skua and black-backed gull
Oyster catcher	large	exposed in shingle/sand near sea	+			?	skua and gulls	—	tern
Plover	large	hidden under shrubs or in burrows	+			?	skua and gulls	—	—
Pipit	large	hidden in grass	+			?	—	plover	—

chicks never visited it as it was too far away from protecting shelter.

Pipit: A single pair nested at the edge of the bush above the western margin of the platform and foraged along the sea edge. This feeding zone was rarely used by the plovers and the two species were seldom seen feeding closely together. When they did come into contact the pipit invariably gave way leaving the area to the plover. In this area the plover was the dominant and more aggressive bird of the two species.

DISCUSSION

The concept of territory as a defended area appears, at least for birds during the breeding season, to be as firmly established as ever. Even when unusual forms are discovered, as for example in antbirds (Willis, 1967), authors are now little inclined to abandon it, although its use may be specifically restricted or defined. The most recent reviews, e.g. Brown (1975), have supported retention of the concept in its initial form. Controversy has in fact shifted away from the generality of its occurrence to its function, and its supposed role in population regulation (Brown, 1969).

There is still some confusion about whether defence of the nest and chicks against birds of other species should be classed as territorial behaviour. Hinde (1956), in response to criticism that the conventional description did not state against whom the territory is defended, noted that the behaviour used in encounters with conspecifics, species of similar appearance and predators is similar (footnote p. 341) and so by inference would include this behaviour within the scope of the definition. Simmons (1951) however, in the first major review of interspecific territorialism, particularly limits the definition to cases where the territory as a whole is defended, not merely a specific part of it, and by way of example excludes competition for nest holes within territories. This usage was commended by Lanyon (1956) in discussion of the interspecific territories of meadowlarks. The problem of precise definition and of distinction between defence against predators and species with similar ecologies is not considered in the recent reviews by Brown (1964, 1975), Orians and Willson (1964) and Murray (1971).

There is merit in Hinde's view when nest defence of the terns is considered. For example not only did they defend the area from possible predators but they also defended it equally against plovers and oystercatchers, neither of which could be considered a direct threat to the nest or the chicks. Similarly, but less effectively, plovers attempted to protect the whole territory from pipits and starlings, and harassed gulls and skuas—showing similar responses to both competitors and predators.

Nevertheless, the pattern and organisation of territories resulting from the effects of this behaviour are clearly different from those resulting from behaviour to secure a breeding place at the start of the breeding season, when ground is first claimed and the territories become spaced out as though the populations are of the same species. Because of these differences (in the timing of the interactive behaviour in relation to the breeding cycle and in the effect on the spatial organisation of the territories) I would prefer to limit the definition of interspecific territoriality so that it applies only to situations where pairs with similar requirements compete for breeding areas. The special case of competition for nest holes is excluded. Competition between quite different species which has a strong element of predatory behaviour thus falls into the general category of predatory and brood defence behaviour. In contrast to territorial behaviour defensive behaviour only becomes intense after the eggs are laid or the chicks hatch and generally continues until the chicks are independent.

In view of the diversity now recognised in territories, it is noteworthy that the territories of the species using the platform during the nesting period conformed to three of the basic patterns described by Hinde (1956). Skuas had either Type A or B territories, the gulls and terns Type C and the oystercatchers, plovers and pipits, Type A.

The study was concerned firstly with intraspecific competition between the pairs in each species, and secondly, with interspecific competition among the resident and nomadic species. The territorial behaviour between the pairs of each species has been described in the general account and need not be considered here, except to note that it was intensive and ubiquitous for all species (allowing numerous observations of territorial display and aggressiveness) and to stress that the pairs established territorial boundary lines and not simply zones of changing dominance.

The relations between the different species were more complex: not only were they sharing the available nesting and feeding areas but they were also linked in a predatory-prey hierarchy requiring alertness and defence by the smaller species to protect the eggs and chicks. A summary of the characteristics of the territories and of the interspecific links is shown in Table 1.

The different species had different feeding ecolog-

ies during the breeding period. Four species fed mostly or entirely away from the territory: skuas preyed on the smaller petrels, black-backed gulls scavenged around the coast and on nearby Pitt Island, and the red-billed gulls and terns fed at sea, often together over upwellings. The remaining three species fed on the shore platform and the intertidal zone and were seldom absent from the territory. Even so their feeding habits were clearly distinct. The oystercatchers concentrated on chitons and limpets from the intertidal zone; the pipits foraged for smaller food in the intertidal zone and among the short vegetation along the forest edge and the plovers concentrated almost entirely on food taken along the edges of the small pools on the platform or from the bare rock and brackish pools of the higher shoreline.

Nest site preferences were similarly diverse and only the black-backed gulls and terns shared the same requirements. However, all species nested close to the shoreline on short vegetation, shingle or rock. Skuas nested on grass or herbs on the upper shore clear of forest and their territories covered the lower shore zones favoured by the others. By contrast, black-backed gulls nested on the summits of outcrops so close to the shore that they lacked vegetation. Red-billed gulls and terns also nested on outcrops and ridges. On Rangatira the gulls occupied sites in caves and erosion holes or under overhangs on cliffs whereas terns nested in the open with their exposed nests often sited on the high points of outcrops earlier occupied by those of black-backed gulls. Oystercatcher nests were found on fine shingle of the shore among low shrubs and, once, in a shallow cave. All were close to the sea edge. The eggs were protectively coloured and the nest scarcely discernible from its surroundings. Plovers and pipits nested away from the beach in covering vegetation and had quite different requirements from the other species.

Skuas and black-backed gulls began breeding at the same time early in the season and their chicks fledged together in late December and January. The main breeding season of red-billed gulls and terns was however, much later in the year with egg laying in November and December but because of faster growth their chicks also fledged in late December and January.

The differences in the timing of the breeding seasons means that the very pugnacious defence of the nest and chicks by the terns, which affects skuas, gulls and oystercatchers especially, appears quite late in the summer, beginning at the end of December and becoming most intense for 2-3 weeks after the chicks hatch in early January.

In addition to these links in feeding and nesting requirements the species were also linked in a hierarchical order of predation on eggs and chicks running down from the skuas through the two gulls to the terns, oystercatchers and plovers none of which were predatory. The young chicks of all these species were protectively coloured and patterned and were extremely difficult to see or discover once settled or hidden. This facility for hiding was so well developed in oystercatcher and plover chicks that searching for them was unprofitable unless they had been very precisely located beforehand.

Older chicks were more easily visible and more active and were apparently at greater risk from predation. They were certainly assiduously guarded right through fledging.

In conclusion, the arrangement of territories found on the shore platform at Rangatira results mostly from intraspecific competition for a breeding area in which to nest and rear young and less importantly from interspecific competition. Pairs of the different species holding large breeding and feeding territories (skuas, oystercatchers, shore plovers and pipits) occupied over-lapping areas. Their ecologies were apparently not sufficiently similar for interspecific territorial patterns to be established. However, the selection of nesting sites by gulls and terns, and probably also oystercatchers, was influenced by that of the nesting and roosting areas of the skuas and each other. Skua nesting deprived other species of nesting sites on the higher slopes and later in the year the persistence and pugnacity of breeding terns restricted the use of some areas by gulls, oystercatchers and plovers. Only in this behaviour could elements of interspecific territoriality be recognised.

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