SOME IDEAS ON SPECIATION IN NEW ZEALAND PARAKEETS

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ABSTRACT

The distribution, speciation and probable evolution of New Zealand parakeets are outlined. Specific ecological adaptations keep closely related sympatric species separate. Examples are given of such ecological isolating mechanisms in Antipodes and Chatham Island parakeets. Occasionally, where man has drastically modified the environment, these barriers break down and widespread hybridisation occurs, as on Mangere Island, Chatham Islands. The existence of the very rare Chatham Island Yellow-crowned Parakeet *(Cyanoramphus auriceps forbesi)* is endangered by habitat changes and hybridisation.

INTRODUCTION

During the Antipodes Island Expedition of 1969, I studied some aspects of the ecology of the Antipodes Island Parakeet *(Cyanoramphus unicolor)* and the Antipodes Island Red-crowned Parakeet *(C. novaezelandiae hochstetteri)*. It was then suggested that comparable observations should be made of the habitat requirements of the two endemic parakeets at the Chatham Islands. The Chatham Island Yellow-crowned or Forbes' Parakeet *(C. auriceps forbesi)* is very rare and virtually confined to about 6 hectares of forest and scrub on Little Mangere Island, whereas the Chatham Island Red-crowned Parakeet *(C. n. chathamensis)* is more common and inhabits all four of the larger man-modified islands in the group.

I was able to visit the Chathams (Fig. 1) with New Zealand Wildlife Service expeditions in November 1970 and again in November 1973. During the 1970 expedition, rough weather prevented a landing on Little Mangere so it was not possible to observe anything of Forbes' Parakeets, except for a very few seen in much-altered habitat on adjacent Mangere Island. I was, however, able to study large numbers of Chatham Island Red-crowned Parakeets on South-East Island, and others of this species on Mangere. On Mangere, where both species were present, I was surprised to find many individuals showing various combinations of characters of both Yellow-crowned and Red-crowned Parakeets. These birds were judged to be hybrids.

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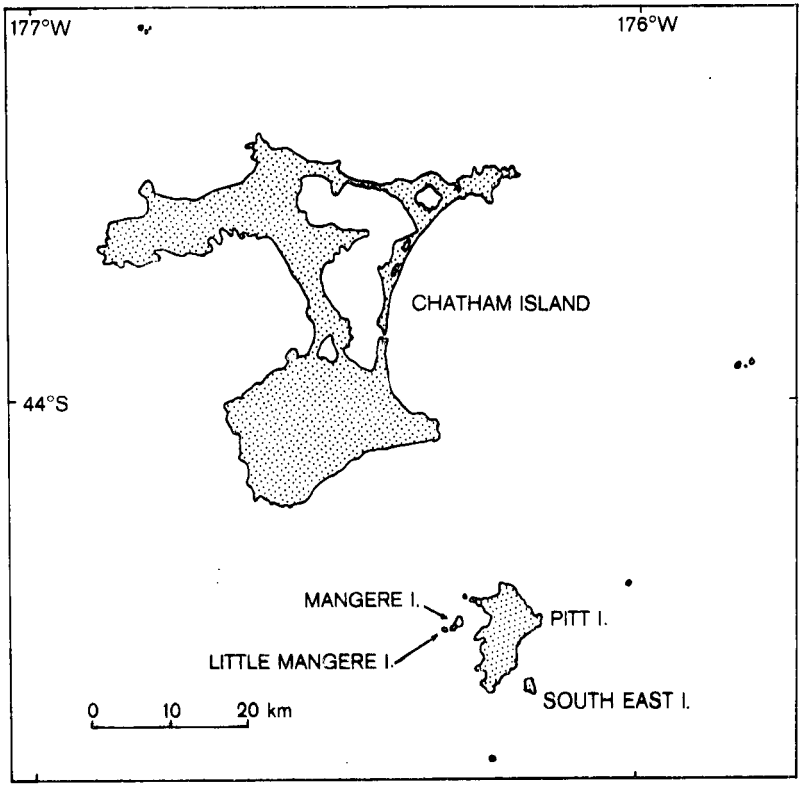

FIGURE 1 — The Chatham Islands, showing locations mentioned in the text.

During my second trip to the Chathams, in November 1973, I spent five days on Little Mangere and learned something of the habitat requirements of Forbes' Parakeets in their natural environment. And later, on the man-modified island of Mangere, I had a further look at the hybrid parakeets.

I found this striking example of natural hybridisation in a population of wild birds of great interest. It is also of considerable concern, in that it poses a possible — and novel — threat to the preservation of the last of the Forbes' Parakeets on Little Mangere Island, thus, perhaps, dashing hopes that they might eventually re-populate Mangere and other newly-reserved islands in the group.

In attempting to explain what is happening among the parakeets on Mangere Island, it is helpful to look first into the distribution, speciation, and probable evolution of New Zealand parakeets generally.

TAXONOMY AND DISTRIBUTION

In the New Zealand region live four species of parakeets of the genus *Cyanoramphus* (Fig. 2). They are the only New Zealand representatives of the very large and diverse sub-family Psittacinae. In Australia this sub-family is represented by 36 species in 17 genera including the rosellas and the Budgerigar. Common features of the group are that none of the birds displays an erectile crest and nearly all have smooth tongues (Forshaw 1973).

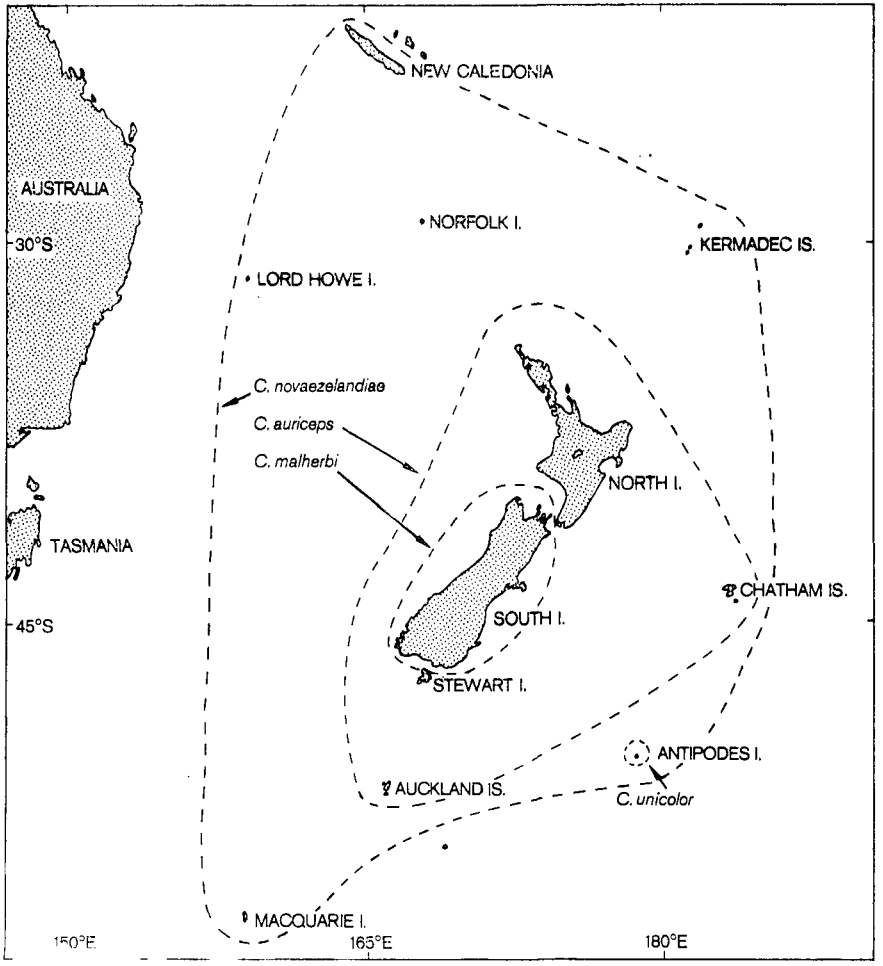

FIGURE 2 — The New Zealand region, showing the limits of distribution of *Cyanoramphus novaezelandiae, C. auriceps, C. malherbi,* and *C. unicolor.* Note: the Lord Howe Island and Macquarie Island parakeets are now extinct.

All *Cyanoramphus* species are small or medium sized parrots with long, pointed tails. Green in colour with blue on the wings, they may have crimson, yellow, and orange on their heads, and spots of the same colour on each side of the rump (Falla *et al.* 1970).

One of these species — the Red-crowned Parakeet *(C. novaezelandiae)* — comprises eight currently recognised sub-species that were once found from New Caledonia, 1300 kilometres north of New Zealand, to Macquarie Island, 1000 kilometres to the south. Two of the sub-species — the Lord Howe Island Parakeet *(C. n. subflavescens)* and the Macquarie Island Parakeet *(C. n. erythrotis)* — are now extinct, having been exterminated by introduced rats and cats about the beginning of the present century. Of the six remaining, one *(C. n. novaezelandiae)* occurs on the main islands of New Zealand, its adjacent islands and the Auckland islands; while the rest are endemic island races belonging to New Caledonia *(C. n. saissetti)*, Norfolk Island *(C. n. cooki)*, Kermadec Islands *(C. n. cyanurus)*, Chatham Islands *(C. n. chathamensis)* and Antipodes Island *(C. n. hochstetteri)*.

The slightly smaller Yellow-crowned species *(C. auriceps)* has a more limited geographical range and comprises only two sub-species. One *(C. a. auriceps)* inhabits the main islands of New Zealand, its adjacent islands and the Auckland Islands; and the other *(C. a. forbesi)* is found in the Chatham Islands.

The still smaller Orange-fronted Parakeet *(C. malherbi)* formerly occurred in most parts of the South Island and possibly on the North and on Stewart Island. It is now presumed to be rare and the only recent records are from forest areas in North Canterbury and Nelson (Harrison 1970).

The fourth New Zealand species is the Antipodes Island Parakeet *(C. unicolor)*. This relatively large species lacks coloured markings and is confined to isolated Antipodes Island where it lives sympatrically with an endemic sub-species of the Red-crowned Parakeet.

About 3000 kilometres north-eastward of New Zealand, on Tahiti and Raiatea in the Society Islands, there were once two species congeneric with those in New Zealand and both extinct since the beginning of the nineteenth century. In the Tahitian species *(Cyanoramphus zealandicus)* crimson was replaced by brownish red and the forehead was black. In the other species *(C. ulietanus)* the entire head was dark brown (Forshaw 1973).

EVOLUTION

Speciation in birds is a consequence of long isolation, heritable variation, and natural selection. The process starts simply with the division of a single, interbreeding stock into two or more geographically isolated populations. The isolates will gradually accumulate genetic differences due to the genetic variability in the founders of each population, non-adaptive random "drift" and, most importantly, different selective pressures from their respective environments. In time, major divergence between the populations may create distinct

species with fertility, behavioural, and ecological barriers to successful interbreeding (Mayr 1947, Sibley 1961, Ford 1964). Thus speciation is a process involving time, geographic isolation, ecological divergence and selection.

The *Cyanoramphus* parakeets illustrate several evolutionary concepts. The first is speciation by geographical separation. For example, the various " allopatric " island sub-species of the Red-crowned Parakeet have, in isolation, each evolved in a slightly different way from a common colonising parent stock.

The second concept involves initial physical isolation followed by ecological separation. Examples of this are found when species that have evolved apart later come together geographically but remain distinct species; as have Red-crowned, Yellow-crowned, and Orange-fronted Parakeets on the New Zealand mainland. These " sympatric " species evolved from a common ancestral form, probably during the Pleistocene (about 20 000 - 2 000 000 years ago) when fluctuating ice and sea barriers favoured speciation in then isolated refuges.

Somewhat comparable are the parakeets at the Antipodes Islands, where the two species have resulted from separate invasions of the islands by the same generic stock (Fleming 1952); the first colonisers *(unicolor)* being a distinct species by the time of the second, relatively recent, invasion by Red-crowned Parakeets.

Chances for hybridisation occur where the ranges of two once separated but closely related species now overlap, though normally behavioural and ecological isolating mechanisms — such as different calls, different habitat preferences, niche differences in the same habitat, or different times of breeding — would keep them apart. All isolating mechanisms have a genetic basis although some behavioural components may be reinforced by learning. Specific habitat preferences rank as one of the most important restrictions upon hybridisation between different species (Mayr 1963). Usually hybrids tend to be eliminated from a population because they are less well adapted than either of the parental forms (Ford 1964).

The two Antipodes parakeets provide a good example of how ecological separation works. Although the two species occur together on all parts of Antipodes Island, they have different feeding habits (Fig. 3), breed at slightly different times, and nest in different sites (Taylor unpubl. and in Forshaw 1973). So, even though fertile matings between the two species have occurred in captivity (Mr C. D. Roderick, pers. comm.), hybrids are unknown in the wild.

FOOD HABITS AND TERRITORIALITY

Little is known of the ecological factors keeping Red-crowned, Yellow-crowned and Orange-fronted Parakeets apart on the New Zealand mainland, but marked differences certainly occur. Field observations suggest that the Yellow-crowned Parakeet is adapted to forest habitats, whereas the Red-crowned is a bird of more open country

and forest margins. Ecological barriers between the species are now difficult to determine on the mainland where the relative distribution of the three parakeets has been drastically altered by man's vegetational changes and introduced predators. On off-shore islands, however, the various effects of man on parakeet distribution are often isolated and can be more clearly assessed. Thus existing island situations are extremely useful in the study of ecological differences between New Zealand parakeets.

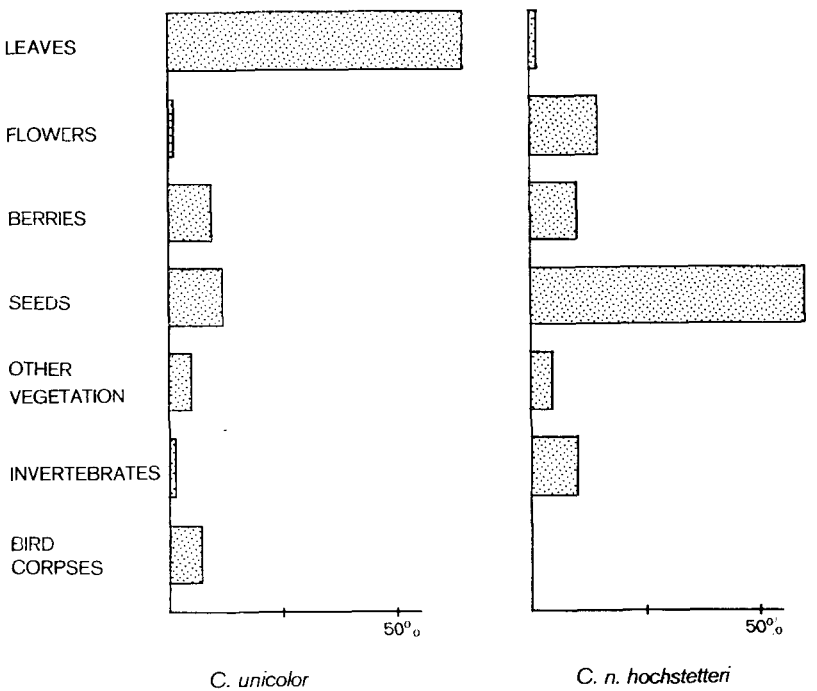

FIGURE 3 — Foods of the two Antipodes Island parakeets during February 1969. Percentages are based on 262 field observations of *Cyanoramphus unicolor* and 245 of *C. novaezelandiae hochstetteri.*

Preliminary studies of unbanded birds (Taylor unpubl.) suggest that each pair of Chatham Island Yellow-crowned (Forbes') Parakeets on unmodified Little Mangere Island restrict their activities to defended areas during the breeding season, and that in November a large proportion of their diet is made up of invertebrates — mainly caterpillars and scale insects — from the dense canopy of forest and scrub. Forbes' Parakeets were also commonly seen searching the forest floor for caterpillars dislodged from the canopy. They also eat substantial

amounts of flowers and seeds. In contrast, Chatham Island Red-crowned Parakeets on nearby South-East Island do not display territorial behaviour, eat an insignificant amount of invertebrate food, and take mainly leaves and shoots. Figure 4 summarises the differences in the October-November diets of the two species.

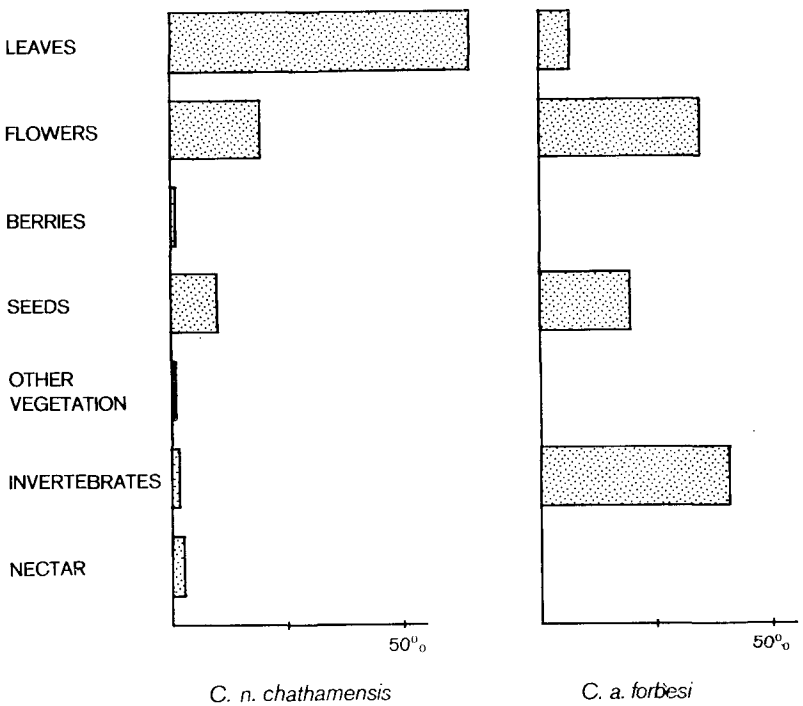

FIGURE 4 — Foods of the two Chatham Island parakeets during October-November 1970-73. Percentages are based on 465 field observations of *Cyanoramphus novaezelandiae chathamensis* and 64 of *C. auriceps forbesi.*

I interpret the feeding habits and territorialism of Forbes' parakeet as ecological adaptations to a forest habitat, which now effectively confine the breeding population to the remnant of unmodified forest and scrub on the top of Little Mangere Island (Fig. 5), and restrict the number of birds breeding there to about 10 pairs. That Forbes' Parakeets are comparatively poorly adapted to more open vegetation is further suggested by the apparent exclusion from any of their territories of the northern and eastern cliffs of Little Mangere. In November 1973, this habitat of scattered patches of scrub and herbs was left to a resident pair of Chatham Island Red-crowned Parakeets and a few others that visited from Mangere. No inter-specific territorial

encounters were observed, although red-crowned birds were not seen to enter the Forbes' Parakeet territories.

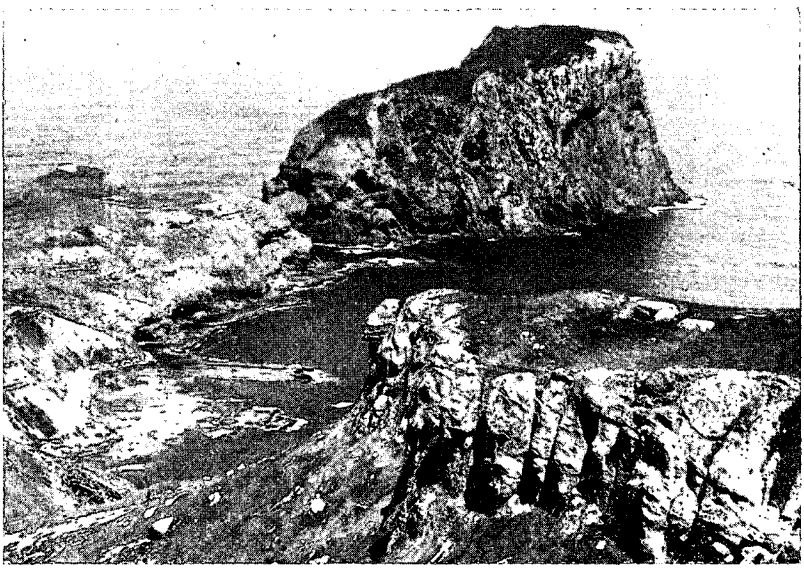

FIGURE 5 — View south-west from the summit of man-modified Mangere Island showing Little Mangere (right rear) with its cap of untouched forest and scrub. This small patch of bush is the last stronghold of Forbes' Parakeet and its preservation is essential if the species is to survive.

By spacing out a population, territorialism allows for individual food exploitation and prevents interference in foraging and over-exploitation near nest sites — distinct advantages to a species whose prey is cryptic and dispersed. By comparison, flocking is most typical of species with diets including items such as seeds and berries that occur in scattered patches of local abundance. Foraging in flocks allows improved efficiency in food finding for the individuals in them. A good example of how differences in territoriality correlate with contrasts in ecology is John Crook's work on the social organisation of several closely related species of African weaver birds *(Ploceinae)*. He found that dispersed breeding and territorialism went with insect eating and dense forest habitats, while flocking, and a lack of territories, was correlated with more open environments and seed or fruit eating habits (Crook 1965, Lack 1968).

HYBRIDISATION

In nature, however, ecological barriers between closely related species sometimes break down and widespread hybridisation occurs.

I know of two examples of this in wild populations of New Zealand parakeets. One is at the Auckland Islands where hybrid Red-crowned x Yellow-crowned Parakeets have been recorded on some of the much modified islands in Port Ross as well as at Ranui Cove and Musgrave Peninsula (Dr C. A. Fleming, pers. comm.). But perhaps better documented is the Mangere Island situation mentioned earlier. This island, of 113 hectares, has a long and varied history of modification by fire, and grazing by sheep, goats and rabbits. Cats were also introduced. From original dense forest that supported rich and varied endemic bird populations, including both Forbes' and Chatham Island Red-crowned Parakeets (Fleming 1939), it was modified to a sward of English grasses (Fig. 5). Only small patches of coastal scrub and forest were left on the cliffs and among boulder piles (Ritchie 1970). Native forest birds virtually ceased to breed on the island.

Fleming (1939) was told that in earlier times, when Mangere was forested and *forbesi* the most common parakeet there, some of these would regularly join flocks of red-crowned birds on visits to Pitt Island to feed on *Disphyma* flowers and *Acaena* fruit. But, apart from these seasonal visits to the Pitt Island coast, the Yellow-crowned Parakeet was scarcely known away from the Mangere Islands. When Archey and Lindsay (1924) spent 17 days on the then almost completely deforested Mangere Island in 1923-24 they found some Red-crowned but no Forbes' Parakeets. Later, Red-crowned Parakeets also disappeared from the island (D. V. Merton & B. D. Bell unpubl.). Of the introduced mammals, the goats and rabbits were killed or died out many years ago, and the cats disappeared in the 1950s. The sheep were destroyed by the Wildlife Service in 1968 after the island had been made a Flora and Fauna Reserve.

In relatively recent times, parakeets have recolonised the island. Red-crowned Parakeets were apparently absent and Forbes' Parakeets were rare visitors to Mangere in 1961, but by 1968, Wildlife Service parties visiting the island reported parakeets, particularly Red-crowned, as more numerous (Merton & Bell unpubl.). From counts in November 1970, I estimated there were about 60 parakeets on Mangere Island. Eight percent were classed as *C. a. forbesi,* 32% as *C. n. chathamensis,* and the remaining 60% were easily recognised as obvious hybrids in the field. By 1973, the total parakeet population of Mangere Island was estimated at about 100, of which 6% were classed as *forbesi,* 47% as *chathamensis,* and 47% as hybrids.

The hybrids varied considerably (Fig. 6). Some differed superficially from Red-crowned Parakeets only by having an orange upper edge to the red crown. Intermediates had a narrow red front, a large orange crown, and small reddish-orange patches behind the eyes and on the rump. At the other end of the range were " Forbes'-like " birds with yellow crowns and high pitched calls, but with faint yellowish-orange spots behind the eyes.

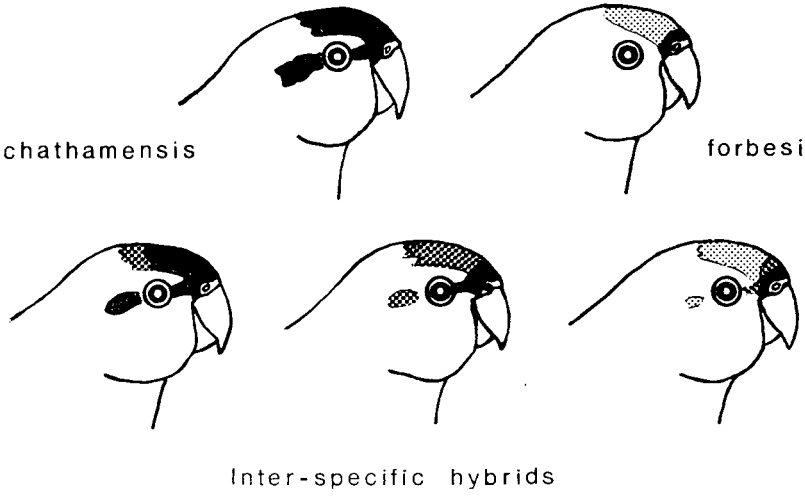

FIGURE 6 — Heads of Mangere Island parakeets showing *Cyanoramphus novaezelandiae chathamensis, C. auriceps forbesi,* and three inter-specific hybrids.
Colour key: Black = red, heavy stipple = orange, light stipple = yellow.

These observations give rise to many questions. For example: Why is this widespread hybridisation occurring on Mangere ? Why — despite ecological separation — doesn't it happen more often elsewhere ? And, most importantly, what are the implications of hybridisation on management for the continued existence in a pure form of the now very rare Forbes' Parakeet ?

The phenomenon of hybrid swarms is well known to plant ecologists. They occur when the barrier between two sympatric species breaks down so completely that the parent species are replaced locally by an interbreeding population forming a continuous bridge between the two parental extremes. Inter-specific hybrid swarms are nowhere near as common with vertebrates, though they have been recorded in birds, amphibians and fish, but not in mammal populations (Mayr 1963).

My explanation of what has happened at Mangere is that with the disappearance of cats, parakeets were able to recolonise the much modified habitat. Unlike the smaller yellow-crowned species on the main islands of New Zealand, Forbes' Parakeet is about the same size as the Chatham Island Red-crowned Parakeet; and a very few birds of both species would have recolonised together. Both these factors would favour hybrid matings. The much modified environment of Mangere, being so different from the preferred habitat of either species, gave the parental forms no real survival advantage over hybrids.

The first generation hybrids would breed among themselves as well as backcrossing with parental types as further birds reached the island from outside. Numbers of backcrosses and second generation hybrids — each with inherent individual differences and requirements (Anderson 1949) — survived in the mixed up environment. And, of considerable significance, the parakeet population on Mangere was able to expand rapidly with the sudden increase in leafy vegetation and seeds that followed the removal of sheep in 1968.

In plants, hybrid swarms are associated with widespread and drastic modification of the habitat — usually either by geological forces, or by fire or other disturbances caused by man. To quote from plant geneticist Edgar Anderson (1949): "The production of hybrid swarms is limited to particular times and places at which man or nature may have 'hybridized the habitat' . . . as the previous ecological balance is restored, recombinations closely resembling the original parents will be those most likely to survive. The commonest end result of a hybrid swarm will be the introduction of a comparatively few genes from one species into the germplasm of another."

THE FUTURE

By analogy with plant ecology, the highly disturbed environment is the key to understanding the present parakeet situation on Mangere Island. But what of the future? The re-afforestation of Mangere is now being hastened by planting to provide more forest habitat for Black Robins *(Petroica traversi)*, Forbes' Parakeets and other rare Chatham Island birds. I suggest that while the habitat slowly reverts to forest, first generation hybrids and those back-crossed towards Forbes' Parakeets will be selected against. In the mid-term the only parakeets to breed successfully on Mangere may be those of near original red-crowned or pure red-crowned stock. On Little Mangere, Forbes' Parakeets should be able to hold their unmodified stronghold — despite Red-crowned Parakeets on the cliffs and the occasional occurrence of hybrid birds. In the long-term, when Mangere Island is once more covered with dense scrub and forest, Forbes' Parakeets should be able successfully to re-colonise this habitat, to which they are ecologically adapted.

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SHORT NOTE

UNUSUAL NEST SITES OF HOUSE SPARROW AND PARADISE DUCK

On 17 November 1974, while surveying a square for the Mapping Scheme in the upper Lindis (Geordie Hills station) area, I came across two unusual nest sites. The first was that of a House Sparrow in a small matagouri bush, about 2 m from the ground, and right adjacent to, and almost touching, a nest of a blackbird. Both nests were occupied. It was in open tussock country with no large trees or buildings anywhere near, and about 2000′ (710 m) above sea-level.

About 2 km away, in an adjoining square, two local men pointed out to me a small old musterer's hut, no longer in use by the station, with about a foot of ' starling straw ' on the floor, in the middle of which a Paradise Duck had built her nest and apparently successfully hatched a clutch of about ten. The walls and roof were well inhabited by Starlings. Only the door was open.

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