Notornis, 2003, Vol. 50: 27-35

The orange-fronted parakeet (*Cyanoramphus malherbi*) is a distinct species: a review of recent research into its taxonomy and systematic relationship within the genus *Cyanoramphus*

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Abstract The taxonomic status of the endangered orange-fronted parakeet (*Cyanoramphus malherbi*) has been the subject of much debate since this endemic New Zealand parakeet was first described in 1857. The debate in the late 1800s and again over the past 30 years has been lively but inconclusive. We provide a summary of this debate and the most recent research into the taxonomic status of this parakeet based on mitochondrial DNA (mtDNA), assortative pairing, bill morphology, vocalisation, and comparative ecology. Based on all available scientific and historical data, we conclude that the orange-fronted parakeet is a distinct species.

Kearvell, J.C.; Grant, A.D.; Boon, W.M. 2003. The orange-fronted parakeet (*Cyanoramphus malherbi*) is a distinct species: a review of recent research on its taxonomy and systematic and systematic relationship within the genus Cyanoramphus. *Notornis 50(1)*: 27-35.

Keywords orange-fronted parakeet; *Cyanoramphus malherbi*; taxonomy; *Cyanoramphus*; conservation

INTRODUCTION

Controversy has surrounded the orange-fronted parakeet (*Cyanoramphus malherbi*) since Souancé first described the bird in 1857. His description is classically elegant and he obviously considered the orange-fronted parakeet a separate species, but he states that the habitat (site of collection) was unknown. This was not an auspicious beginning for a new species, but an indication of the taxonomic turmoil to come. The taxonomic status of the orange-fronted parakeet, whether as a true species or simply a colour morph of the yellow-crowned parakeet (*C. auriceps*), has been the focal point of this controversy (Holyoak 1974; Taylor *et al.* 1986; Turbott 1990).

Early descriptive evidence supporting the orange-fronted parakeet as a distinct species came largely from studies bill size, morphology, colour and distribution (Buller 1869a; Salvadori 1891). The debate over bill size, and its significance, has continued to the present day (Holyoak 1974; Nixon 1981; Taylor 1998; Young & Kearvell 2001). In the first study to deal with the genetics of the problem, Taylor *et al.* (1986) investigated the head colour of both orange-fronted and yellow-crowned parakeets (*C. auriceps*) through cross-breeding experiments. They established that head colour between these 2 taxa appeared to be under a single gene locus control, best explained by Mendelian dominant/recessive inheritance. As no intermediate head colours were detected, they concluded that both yellow-crowned and orange-fronted parakeets were of the same species and that the latter was a colour morph of the former.

The genus *Cyanoramphus* is endemic to the South West Pacific and has suffered from a lack of taxonomic identity because of an inability to accurately distinguish each of its species. The ability to describe the genetic uniqueness of a species has become a vitally important aspect of conservation policy making, but it has only been in the last 20 years that the genetic techniques required to resolve the phylogeny of such a complex and apparently actively speciating genus

Received 11 February 2002; accepted 18 October 2002

(Boon 2000) have become generally available. Earlier work involving analysis of variation at allozyme loci (Triggs & Daugherty 1988) and sequence data from the mitochondrial 12S rRNA gene locus (Evans 1994) have failed to satisfactorily resolve the taxonomic issues in the genus.

As the debate over taxonomy progressed, the conservation status of the orange-fronted parakeet declined to a point where only ~150-500 individuals were estimated (Boon *et al.* 2000) to remain in 2 allopatric populations (South Branch Hurunui and Hawdon Valleys). Unlike the kakapo (*Strigops habroptilus*), the New Zealand parakeets are generally unknown to the public, yet 2 species are recognised by the International Union for the Conservation of Nature (IUCN) as "endangered" (Table 1), as "vulnerable", and as "near threatened", respectively (McClelland & Stattersfield 2000). Within the genus *Cyanoramphus* as recognised by Boon (2000), only 1 of 10 extant species is classified as not threatened (Table 1). However, even this species, the New Zealand red-crowned parakeet, is now all but extinct on both the North and South Islands of New Zealand and survives only on offshore islands. The remaining 4 members of the genus are already extinct.

Clearly it is crucial for species status of the rare and declining orange-fronted parakeet to have its taxonomy confirmed or refined. This paper summarises the results of research on the orange-fronted parakeet since 1995 and reviews the significance of the results for the taxonomic status of the parakeet and its future conservation. We also attempt to clarify certain aspects of the historical background of the parakeet.

Table 1 A classification of the genus *Cyanoramphus*, reproduced in part from Boon *et al.* (2001), with permission. All species occur only in New Zealand territory unless stated as Australia (Aust) or New Calidonia (NC). When known, status based on Department of Conservation (*) classification (Molloy *et al.* 2001), or when unknown or no official status (#), based on most recent data. Taxon classified with IUCN=†; [1], further genetic work in progress; [2], no genetic work undertaken; 3, new classification. The mtDNA of the Macquarie Island parakeet indicates that it is a distinct species closely related to *C. hochstetteri*; the Macquarie I population was described first, so its name has precedence; 4 , classification unchanged.

Classification	Present status[5]
New	
Orange-fronted parakeet (*C. malherbi*)[1]	**Nationally critical*†**
Forbes' parakeet (*C. forbesi*)[1]	**Nationally endangered*†**
Macquarie Is parakeet (*C. erythrotis*) Aust	**Extinct**
Reischek's parakeet (*C. e. hochstetteri*)[3]	**Sparse***
Norfolk Is parakeet (*C. cooki*) Aust	**Endangered†**
New Caledonian red-crowned parakeet (*C. saisseti*) NC	**Sparse#**
Unchanged	
Yellow-crowned parakeet (*C. auriceps*)	**Gradual decline*†**
Antipodes Is (green) parakeet (*C. unicolor*)	**Sparse*†**
New Zealand red-crowned parakeet (*C. novaezelandiae*)	**Not threatened***
Chatham Is red-crowned parakeet (*C. n. chathamensis*)[4]	**Sparse***
Kermadec Is parakeet (*C. n. cyanurus*)[2]	**Sparse***
Lord Howe Is parakeet (*C. n. subflavescens*)[2] Aust	**Extinct**
Society parakeet (*C. ulietanus*)[1] NC	**Extinct†**
Black-fronted parakeet (*C. zelandicus*)[1] NC	**Extinct†**

HISTORICAL BACKGROUND

Souancé (1857) described this "nouvelle" parakeet while working at the Metz Museum in France. He provided no common name but dedicated the parakeet to M. de Malherbe (an early Museum benefactor), under the name *Cyanoramphus malherbi*. Salvadori (1891) reported that the type specimen was at the Museum in 1891 but cannot now be found (Monique Sary, Metz Museum, France, pers. comm.) The 1st recorded specimen with a habitat description is a bird supposedly collected from the Auckland Islands (Gray 1862). This is probably a yellow-crowned parakeet as Salvadori (1891) observed that the only known specimen from the Auckland Islands is "exactly like *C. auriceps*, only smaller." There is no mention in Salvadori's (1891) observations that this specimen was an orange-fronted parakeet and he doubts whether this "smaller form" should be given a new name. In his description of the orange-fronted parakeet he emphasises that the parakeet has an "orange frontal band connecting the eyes", clearly indicating that he knew the appearance of both species.

The Auckland Island specimen (Gray 1862), held in Paris and labelled as being from the "Astrolabe and Zelee Expedition Tasman Bay" and dated 1840, is the co-type and has recently been misplaced (Eric Pasquet, Muséum National d'Histoire Naturelle, Paris, pers. comm.). It is probable that this specimen was collected at Tasman Bay, South Island, on the earlier of the 2 *Astrolabe* and *Zelée* expeditions (1826-29), when they collected many "parroquets" (D'Urville 1907). The 2nd trip left Hobart (Tasmania) in Dec 1839

and did call at the Auckland Islands, but not at Tasman Bay, and collected no species peculiar to the area (McLaren 1948). Souancé must have seen the co-type for it to be described as such and therefore it must have been an orange-fronted parakeet. It is possible that the specimen is the other skin mentioned by Souancé (1857), held in Paris and described as a young bird, with a faint orange frontal band. It seems logical that this is the co-type.

The evidence from both Salvadori (1891) and Souancé (1857) suggests that the Auckland Island record of an orange-fronted parakeet is possibly an error, caused by confusion with records over time. We concur with Harrison (1970) and Taylor (1998) that the Auckland Island record is, at best, very doubtful.

Early taxonomy

During the latter half of the 19th century, debate over the species status of this parakeet was continuous (Gray 1862; Finsch 1868, 1869, 1874; Buller 1869a, 1869b, 1874, 1883; Morton 1872; Travers 1882) but no consensus was reached. Buller (1869b) had seemingly not recognised Souancé's earlier description as he named this parakeet *Platycercus alpinus*, the alpine parakeet. Mildly acrimonious academic discussion was not uncommon over the issue (Finsch 1869, 1874; Buller 1883; Travers 1882) and Buller's (1868) reply to Otto Finsch's review of his "Essays on New Zealand Ornithology" is a classic example, in which Buller states "I would, first of all, observe that the reviewer does not appear exactly to comprehend the object or purpose for which the essay was written."

During the last decade of the 19th century a more definite statement on the taxonomy came from Salvadori (1891). He recognised 14 full species of *Cyanoramphus*, although 2, *C. rowleyi* and *C. intermedius*, were queried. He was the first to make the connection between the *Platycercus alpinus* of Buller (1869b) and Souancé's (1857) *Cyanoramphus malherbi*. He stated that "Any one who examines Souancé's figure of his *C. malherbi* will agree that there is no difficulty in identifying *P. alpinus*, Bull., with it." By the end of the 19th century the scientific community seemed to have generally accepted *C. malherbi* as a full species.

Parakeet population decline

At the end of the 19th century the orange-fronted parakeet was still "fairly represented" within the large flocks of parakeets that irrupted onto the Canterbury Plains (South Island, New Zealand), but "nowhere as common" as yellow-crowned or red-crowned (*C. novaezelandiae*) parakeets (Potts 1885). There are also a few records of orange-fronted parakeet from the North Island of New Zealand. In addition to the 4 records reported in Harrison (1970), we have located another, a specimen recorded as being collected from Drury, Auckland (for a world listing of museum specimens see Young & Kearvell 2001). The 2 records from Hen Island (Vienna Museum) have corroborative evidence from Reischek's diary.so we agree with Taylor (1998) and Nixon (1981) that orange-fronted parakeets occurred on the North Island.

Following extensive forest clearance (Wardle 1984) and numerous mammalian introductions (Wodzicki 1950), it was only a matter of time before declines in parakeet numbers were noted. Fulton (1907) was among the 1st to record the "passing" of parakeets and his observations as to the reasons are particularly perceptive, considering "weasels and rats" (*Mustela nivalis* and *Rattus* spp.) to be principal agents. Phillpotts (1919) voiced the 1st recorded warning about the decline of the orange-fronted parakeet in particular. "The three species of *Cyanoramphus* which were once so common in Otago are now seldom seen or heard in the small forests. *Cyanoramphus malherbi* Souancé, which was never so abundant as the other two, is in all probability extinct...."

Sightings of the orange-fronted parakeet became less frequent as the 20th century progressed and the last confirmed sighting, before being thought nationally extinct, was in the D'Urville Valley (Nelson Lakes) in 1965 (Butler 1985). This was only the 6th recorded location for the 20th century (Harrison 1970).

Taxonomic debate

In 1970, the Ornithological Society of New Zealand (OSNZ) checklist in 1970 (Kinsky 1970), included the orange-fronted parakeet as a full, but very rare, species. It was not until 1974 that the species status of the parakeet was questioned again, with the suggestion that it was "probably" a colour-morph of the yellow-crowned parakeet (Holyoak 1974).

The re-discovery of the 'extinct' orange-fronted parakeet in 1980, by A. Cox and M. McDougall in the Hope Valley, North Canterbury, sparked renewed interest in the taxon. Individuals and eggs were taken from the wild and subsequent cross- breeding experiments led Taylor *et al.* (1986) to conclude that "both [orange-fronted and yellow-crowned parakeets] are colour morphs of one species." The 3rd edition of the OSNZ checklist (Turbott 1990) concurred with these findings and relegated the orange-fronted parakeet to synonymy with the yellow-crowned parakeet.

However, Triggs & Daugherty's (1988) initial report to the Department of Conservation on the genetics of New Zealand parakeets stated that, "the available evidence leads to no firm resolution of the status of the orange-fronted parakeet. In view of the serious consequences of incorrect classification as a

colour-morph for the survival of orange-fronted parakeets, the specific status should be retained until evidence to the contrary is produced." They had based their statement on a study of 21 blood protein loci (Triggs & Daugherty 1996). An internal report of the Department of Conservation on the status and management of the parakeet concluded that the taxonomy was still uncertain and that priority should be given to collecting blood samples to resolve the issue (Butler 1990).

Meanwhile, Sibley & Ahlquist (1990) listed the orange-fronted parakeet as a colour morph, while Juniper & Parr (1998) stated that the genetic evidence "suggests" the parakeet should be reinstated as a separate species. Knox & Walters (1994) went further suggesting that "The taxonomic status of this species has been questioned, although its recent treatment as a colour morph of *C. auriceps* seems to be based on weak evidence".

The Department of Conservation responded to the evidence in Triggs & Daugherty (1988) by listing the species as Category B (Molloy & Davis 1992), but with a question mark over its taxonomy. Its status was raised to Category A in 1994 (Molloy & Davis 1994). Searches to find a suitable population and to obtain sufficient blood samples to allow a definitive mtDNA sequence study started in 1995.

P. Dilks, A. Grant, and J. Kearvell discovered a previously unknown and substantial population of orange-fronted parakeets in Sep 1995 in the South Branch of the Hurunui River. There they were sympatric with a substantial population of yellow-crowned parakeets. Until then only the Hawdon Valley was definitely known to hold a population of orange-fronted parakeets. From the 2 populations, a sufficient quantity of DNA material was obtained and preliminary ecological studies on the taxa began.

SUMMARY OF RECENT RESEARCH

Orange-fronted parakeet mtDNA

To clarify the level of genetic distinctiveness of orange-fronted parakeets, mtDNA samples from 17 individual *Cyanoramphus* parakeets were examined, representing 9 different populations and 6 taxa (Boon *et al.* 2000). Within this sample were 3 orange-fronted parakeets (from the South Branch of the Hurunui) and 7 yellow-crowned parakeets from 5 different sites as far apart as the Eglington Valley, Fiordland (southern South Island) and Little Barrier Island (northern North Island). Both the cytochrome *b* gene and the control region of the mtDNA were targeted initially but results indicated that the control region was a more appropriate locus for resolving the phylogenetic relationships of these taxa.

The research found significantly large, distinct, consistent and apparently fixed genetic differences between orange-fronted parakeets and sympatric yellow-crowned parakeets in the Hurunui Valley (Boon *et al.* 2000). The percentage of divergence between the 2 taxa placed them well beyond the level of interspecific genetic divergence observed between other interspecific comparisons of accepted *Cyanoramphus* species. The orange-fronted parakeet was therefore validated as a full species based on the Phylogenetic (Cracraft 1983), the Biological (Mayr 1970), Recognition (Paterson 1985), and Cohesion (Templeton 1989) species concepts (Boon *et al.* 2000).

The mtDNA analysis showed that the orange-fronted parakeet represents a diagnosable and monophyletic taxon (Phylogenetic Species Concept) while field observations showed strong assortative mating in the Hurunui Valley (Biological Species Concept). Assortative mating indicates separate mate recognition systems for both species (Recognition Species Concept) and separate mitochondrial gene pools indicate the existence of cohesion mechanisms (Cohesion Species Concept). Further, the various red-crowned parakeet subspecies were shown to be sister species to the orange-fronted parakeet instead of its conspecific, the yellow-crowned parakeet (Fig. 1). This phylogenetic pattern confirms that the orange-fronted parakeet is not conspecific with yellow-crowned parakeets and is, in fact, more closely related to the red-crowned parakeet.

Cyanoramphus mtDNA

An important aspect of studying the systematics of 2 closely related taxa is resolving their genetic relatedness relative to other members of the genus. Boon (2000) therefore produced evolutionary trees based on mtDNA sequences from up to 73 individuals representing 10 taxa, and including samples from 12 orange-fronted and 18 yellow-crowned parakeets. A summary of the results of Boon (2000) is presented in Fig. 1, where the orange-fronted parakeet formed a diagnosable monophyletic assemblage that was sister group to the red-crowned parakeet clade and not to the yellow-crowned parakeet clade. He also showed a high level of genetic divergence from both red- and yellow-crowned parakeets. This indicates they are able to maintain pre-zygotic reproductive isolation.

Boon (2000) showed that orange-fronted parakeets shared a most recent ancestor with red-crowned parakeets and that their sister taxon is the Macquarie Is parakeet (*C. erythrotis*) which includes Reischek's parakeet (*C. e. hochstetteri*) (Table 1; Fig. 1). It is worth noting that Salvadori (1891) pre-empted Boon's (2000) mtDNA work by suggesting *C. erythrotis* and *C. hochstetteri* might be allied! Boon *et al.* (2000) also showed that 2 of the Hope Valley orange-fronted parakeets had

haplotypes that resembled Eglington Valley yellow-crowned parakeets and interpreted this as the result of previous interspecific hybridisation in the Hope Valley. Hybridisation is likely to have taken place as a result of the orange-fronted parakeet populations in both the Eglinton and Hope valleys being so small that intraspecific mates were difficult to locate and orange-fronted parakeets resorted to seeking out yellow-crowned mates. It could be argued that this evidence suggests that the parakeets may be conspecific, however, this haplotype link is only evident in areas where the orange-fronted parakeet population is in final stages of decline. Further, when orange-fronted parakeets (from the Hope) were placed into aviaries with yellow-crowned parakeets, the birds took more than 1 yr to form pairs and breed successfully (Heatherbell, original log books). This form of hybridisation is well documented within *Cyanoramphus* (Triggs & Daugherty 1996; Taylor 1975, 1985).

Boon *et al.* (2000a) re-classified the genus, recognising 10 species and several subspecies (Table 1). They proposed that the ancestor of *Cyanoramphus* dispersed from New Caledonia to New Zealand in the past 500,000 years and may have arisen from the Australian *Platycercus* via proto-*Eunymphicus* in New Caledonia. The most ancient lineage of *Cyanoramphus* so far analysed appears to be the New Caledonian endemic *C. saisseti*, which is the probable source of the radiation of species in New Zealand and its offshore islands, including Norfolk and Macquarie Is.

Assortative pairing

As a direct test for interbreeding between orange-fronted and yellow-crowned parakeets, field observations were undertaken to detect mixed species pairs of parakeets in the South Branch of the Hurunui River between 1996 and 1999 (Boon *et al.* 2000). Each pair was assigned a map co-ordinate and no new pair was recorded unless it was outside a 100 m radius from the nearest pair contact, thus avoiding multiple counting of the same pair.

Boon *et al.* (2000) observed that sympatric orange-fronted and yellow-crowned parakeets, in the Hurunui Valley, appeared to pair, court, mate and nest strictly assortatively. There was a total of 32 pairs where both members were orange-fronted parakeets and 26 pairs where both members were yellow-crowned parakeets. No mixed pairs were encountered. A further 220 observations of pairs performing feeding and maintenance behaviour were recorded. Although these were not designated as breeding pairs, there were no mixed pairs recorded within this category either. The assortative pairing data confirms the existence of separate gene pools for orange-fronted and yellow-crowned parakeets as maintained by effective mate recognition systems (Paterson 1984).

Bill morphology

The bill of the orange-fronted parakeet has featured prominently in the debate over its taxonomic status. Buller (1882), Oliver (1955), and Falla *et al.* (1970) stated that it was weaker and smaller than the yellow-crowned bill whereas Holyoak (1974), Nixon (1981), and Taylor (1998) found no significant differences between the forms in bill size.

After exhaustive searches for museum specimens worldwide, Young & Kearvell (2001) sampled 87% of the 77 known museum specimens of orange-fronted parakeet and 85% of the 222 known museum specimens of yellow-crowned parakeet. All museums were sent specific measurement protocols and asked to record the average of 3 measurements for each parameter, to minimise error. Birds known or suspected to have been captive were excluded from the analysis because Nixon (1981) had shown captive birds to have larger bills than wild individuals. Eventually, only individuals known to be from the South Island were analysed, because (at that time) some yellow-crowned parakeet populations were indicated to be genetically distinct, and hence possibly morphologically different (Triggs & Daugherty 1996). This reduced the data set to 108 (62 orange-fronted; 46 yellow-crowned). Although Young & Kearvell (2001) had access to many measurements from live-caught birds of both species these were excluded. The birds were suspected of being a 'self-selected' biased sample because the capture methodology used male birds as decoys.

Analysis showed that the bills of male orange-fronted parakeets were significantly shorter than bills of male yellow-crowned parakeets, with the difference between sample means being 0.7 to 0.8 mm. Bill width measurements were similar for the 2 taxa. However, Young & Kearvell (2001) state that this does not, on its own, support the orange-fronted parakeet as a distinct species. Using power analysis, Young & Kearvell (2001) also showed that other researchers probably failed to detect a difference because of small sample sizes.

Vocalisation

The "chatter" call of the parakeet is the most frequent vocalisation given by either species (Pickard 1990) and is therefore most likely to be useful in differentiating the 2 species in the field. To investigate further, calls were recorded opportunistically in the South Branch Hurunui, where yellow-crowned and orange-crowned parakeets are sympatric (Kearvell & Briskie in press).

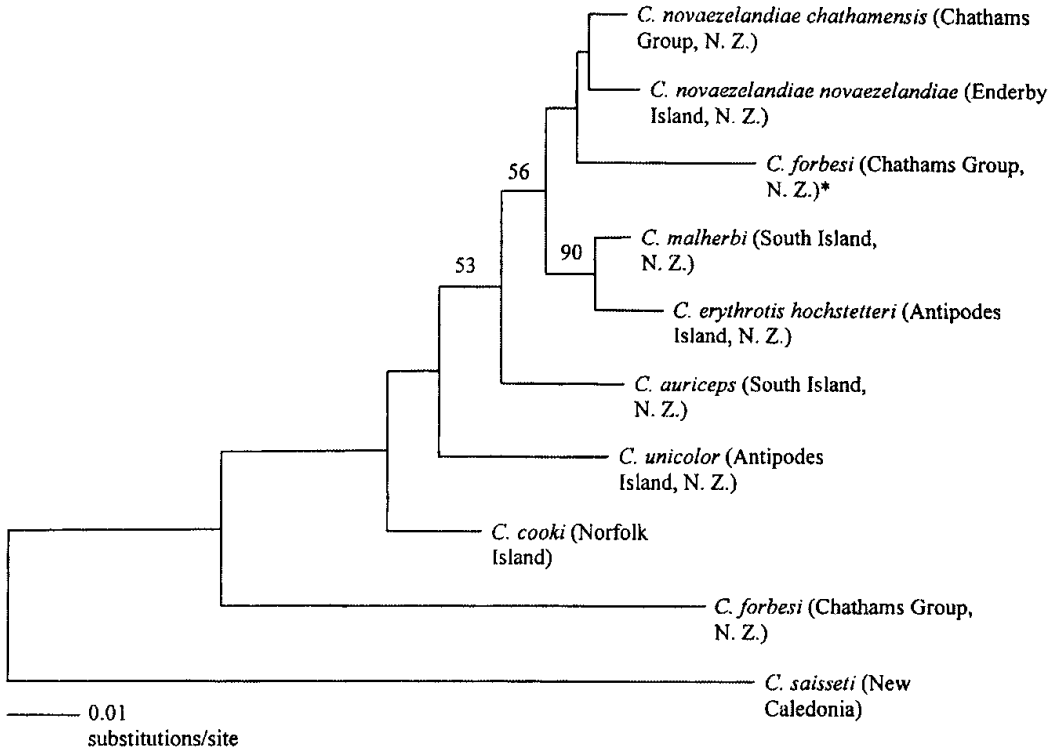

Fig. 1 Maximum likelihood phylogeny (*-ln*=3938.43) obtained using 1613 nucleotides of mitochondrial control region sequence. The Hasegawa-Kishino model of nucleotide substitution (Hasegawa *et al.* 1985) was used with gamma approximation of variable sites (α = 0.13). Bootstrap values above 50% are indicated at respective nodes. The taxon labelled with an asterisk* represents a possible hybrid between a haplotype of *C. novaezelandiae* with *C. forbesi* (see Boon *et al.* 2001).

The "chatter" calls of orange-fronted parakeets (*n*=62) did not differ significantly from those of yellow-crowned parakeets (*n*=42) for 4 variables: total duration (s); number of syllables; duration of each syllable (ms); and frequency at peak amplitude (kHz). However, there were significant differences between the species in the number of syllables per unit time (Kearvell & Briskie *in press*). They suggested that the over all similarity possibly results from recent common ancestry or that both species may use these calls in interspecific interactions. Mixed species flocks are common and the calls may be used to maintain flock structure and cohesion. Such use would select for either the retention or convergence of call structure to ensure unambiguous communication between individuals (Kearvell & Briskie *in press*). The similarity of calls makes it difficult to distinguish the 2 species on vocalisations alone, although it has been noted that biologists in the field are able to detect slight differences with practice (Grant & Kearvell, pers. obs.).

Comparative ecology

During the spring and summer of 1998/9 (a mast season for the *Nothofagus* spp. beeches), the comparative ecology of sympatric yellow-crowned and orange-fronted parakeets was studied in the South Branch of the Hurunui river. The parakeets were observed over a total of 48 days and each observation included an extensive series of variables designed to describe the behaviour of the individual at that time (Kearvell *et al.* 2002).

Observations of the feeding birds indicated that the diet of the 2 parakeet species was similar, although some differences were observed. Both species were often seen feeding on invertebrates in spring, but orange-fronted parakeets were more frequently seen feeding on invertebrates than yellow-crowned parakeets. The latter fed on flowers more often than orange-fronted parakeets. When beech (*Nothofagus* spp.) seeds became available in summer, both species changed to a similar seed-dominated diet, although yellow-crowned parakeets were observed feeding on mountain toatoa (*Phyllocladus alpinus*) more often. Behaviourally, the parakeets were quite similar. Yellow-crowned parakeets vocalised more often than orange-fronted parakeets. Orange-fronted parakeets were observed on the ground and low vegetation more often. Because breeding behaviour was not studied, the observed vocalisation differences should be treated with caution (Kearvell *et al.* 2002) as they may indicate different stages in the individual species' breeding strategies.

Kearvell *et al.* (2002) considered that several factors may have contributed to the decline of both parakeet species. The 1st is the greater competition

between the 2 species in a substantially modified habitat and competition with introduced species, such as cardueline finches. Competition with wasps (*Vespula* spp.) for invertebrates and their vulnerability to introduced predators may have affected orange-fronted parakeets in particular, because they appear to feed more on invertebrates and make greater use of the ground and low-growing plants. Such differences in feeding sites might not be expected if the orange-fronted parakeet was simply a colour morph of the yellow-crowned parakeet.

Distribution

As orange-fronted parakeets are, so far as is known, presently confined to just 2 beech forested valleys in North Canterbury, efforts are being made to discover new populations. There have been unsubstantiated reports of orange-fronted parakeets from the Maruia Valley, Westland (1997), the North Branch Hurunui Valley (2001), Ada Pass (1996) and Jollie Brook, North Canterbury (1996), and the Bordman and Wairaurahiri Valleys, Southland (1999). Searches in the North Branch Hurunui Valley, Hope Valley, Bordman Valley (Southland), Andrews Valley, Nina Valley, Poulter Valley and Maruia (1999 and 2000) complex have so far all failed to locate any individuals. Surveys conducted in the Hawdon and South Branch Hurunui valleys have shown that orange-fronted parakeets are present throughout the entire length of both valleys. Thus, at present, the orange-fronted parakeet has a very restricted distribution.

DISCUSSION

Conservationists managing biodiversity today require that populations with an independent evolutionary history (Moritz 1994) are identified and these can be genetic 'species', 'subspecies', or 'populations'. The discussions over 'species' concepts in the literature have been both controversial and endless, with taxonomic boundaries in birds being no exception (Krajewski 1994). Unfortunately in many countries conservation legislation depends totally on categorisation of fauna and flora to the what is sometimes taken to be the arbitrary level of 'species'. As a consequence, molecular methods are being used increasingly to investigate evolutionary distinctiveness of taxa, especially when limited management resources are available. The orange-fronted parakeet is a prime example, with molecular genetic techniques used to assess its taxonomic status and thus its qualification for a share of finite management resources.

In New Zealand avian systematics, no debate has been as long-standing or as polarised as the issue of the specific status of the orange-fronted parakeet. The inconclusive taxonomic results in the past have seriously hindered any effort to protect the remaining populations, because full species status could not be confirmed. This contributed to a steady decline in the species to its present endangered state (McClellan & Stattersfield 2000). Boon (2000) and Boon *et al.* (2001) have now studied the systematics of nearly the entire genus, providing conservation managers with invaluable and in some cases entirely novel, information.

It appears that the New Zealand parakeets are still actively speciating (Boon *et al.* 2001). As a consequence, these parakeets may also be capable of successful interspecific hybridisation with any close congener, especially when mates are rare and notably where habitat is modified by human activity (Nixon 1982; Taylor 1985; Boon 2000). Records of hybridisation between red- and yellow-crowned parakeets on the South Island are not uncommon, for instance, and have been observed for some time (Butler 1986; Buller 1874). It is thus difficult to apply the biological species concept to these birds, as the *Cyanoramphus* taxa can hybridise in captivity (Boon *et al.* 2001; Pickard 1990; Taylor 1985). This is true even when there is no record of hybridisation in the wild between sympatric taxa (e.g., Antipodes green [*C. unicolor*] and Reischek's parakeet [*C. e. hochstetteri*] Pickard 1990). Although these 2 species are genetically very distinct (Boon 2000) extensive habitat damage on Antipodes Island could result in hybridisation, probably to the detriment of the Antipodes green parakeet.

The taxonomic complexities of the genus were not successfully resolved by the more traditional methods, such as morphology (Salvadori 1891). This is not surprising, because all 3 of the species that occur on the South Island, for example, show extensive overlap in morphological measurements (Nixon 1982). The parakeet mate recognition systems, as demonstrated by their distinctive gene pools and assortative pairing (Boon *et al.* 2000), possibly operate through a mixture of head colour recognition and behavioural cues. Genetic distances between bird species are usually small when compared to other vertebrates and this has led to the idea that few genetic changes are involved in speciation (Snell 1991). Some of the factors that are involved in premating isolation (interbreeding barrier), such as plumage colour, can be under single gene control (Grant & Grant 1997). That orange-fronted (and yellow-crowned) parakeet head colour is probably under single gene control (Taylor *et al.* 1986) strongly suggests that it has an important role in maintaining premating isolation between orange-fronted and yellow-crowned parakeets. Behavioural compatibility would also be vital to the maintenance of this reproductive barrier.

The cryptic nature of many bird species continues to cause problems for taxonomists and conservation managers alike. Molecular methods can accurately solve these problems but need to be used in conjunction with other tools to provide a definitive solution. As an example of the rise in the identification of cryptic species over the last decade, there has been a 31% increase, to 42, in the number of species within the Eurasian *Phylloscopus* (Old World leaf warblers) complex (King 1997). Three more species, using both mtDNA and vocalisation analysis, have recently been added (Irwin *et al.* 2001). Before the recent mtDNA work on New Zealand parakeets, Higgins (1999) recognised 8 subspecies of red-crowned parakeet while Salvadori (1891) recognised 8 full species, based on distribution and morphological data. Boon (2000) recognised 10 *Cyanoramphus* species, which includes 4 species of red-crowned parakeets (and 4 subspecies), and 6 other *Cyanoramphus* species. As with many other birds and *Cyanoramphus* parakeets in particular, the need to rely on morphological similarities between species has resulted in taxonomic problems.

Future of the orange-fronted parakeet

The primary evidence, from mtDNA sequence data and assortative pairing, is now considered by the Department of Conservation to strongly indicate that the orange-fronted parakeet is a separate species. The Department therefore accepted the full species status of the orange-fronted parakeet as recommended by Boon *et al.* (2000), classifying the parakeet as acutely threatened, with a Category 2 "nationally endangered" ranking (Molloy *et al.* 2001). We recommend that the orange-fronted parakeet (*Cyanoramphus malherbi* Souancé, 1857) be returned to full species status in future checklists, and that measures to ensure its conservation be taken before it is too late.

ACKNOWLEDGEMENTS

This project was supported by the Department of Conservation and the Institute for Molecular Systematics, Victoria University of Wellington, and also Canterbury and Lincoln Universities.

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