

A reappraisal of the Orange-fronted Parakeet (*Cyanoramphus* sp.) - species or colour morph?

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ABSTRACT

Uncertainty still surrounds the status of the Orange-fronted Parakeet, *Cyanoramphus malherbi*. Doubts first raised in 1974 that it was merely a colour morph of the much more common Yellow-crowned Parakeet, *C. auriceps*, were supported by a morphometric study of museum specimens in 1981, and the results of cross-breeding experiments with wild-caught and aviary birds in 1986. Subsequently, the Orange-fronted Parakeet was deleted from the most recent Checklist of the Birds of New Zealand. However, some researchers and conservation managers remain unconvinced, because of doubts raised by electrophoresis of blood proteins, and claimed differences in the orange-fronted bird's size, behaviour and ecology. This paper reviews the topic, discusses the evidence and arguments in the species versus colour morph controversy, and supports the view that the 2 forms are colour morphs of a single species.

KEYWORDS: Orange-fronted Parakeet, Yellow-crowned Parakeet, *Cyanoramphus*, taxonomy, polymorphism, genetics.

INTRODUCTION AND METHODS

The Orange-fronted Parakeet (*Cyanoramphus malherbi*) was first described by Souance (1857) and redescribed by Buller (1869). At first, Finsch (1869) considered it to be the immature form of the Yellow-crowned Parakeet (*C. auriceps*), but later he was convinced of its specific status (Finsch 1875). Apart from colour differences, the Orange-fronted Parakeet has at various times been reported to be of a smaller size, have a weaker bill, inhabit more alpine habitats, and exhibit differing behaviour from Yellow-crowned Parakeets (Harrison 1970, Triggs & Daugherty 1996).

The first doubts this century that the Orange-fronted Parakeet was not a valid species were cast by Holyoak (1974) who after studying the literature and museum specimens, concluded that it was probably a colour morph of the Yellow-crowned Parakeet. He found that the often-quoted differences between the 2 forms in body size and bill structure were based on too few specimens, mostly of unknown sex. He also considered that the colour differences could be explained in terms of small changes in carotenoid pigmentation, probably under simple genetic control.

In an attempt to clarify whether any real differences in size and shape could be found between Orange-fronted and Yellow-crowned Parakeets, Nixon (1981) used multivariate statistical techniques to re-examine measurements of all museum specimens of both species available in New Zealand. He found no significant differences that would support the view that they were separate species.

During 1981 and 1982, the New Zealand Wildlife Service obtained 5 male and 2 female Orange-fronted Parakeets for breeding at Heatherbell's Aviaries at Hope, near Nelson. These birds were either captured in the wild, or hatched from eggs taken in the wild, from the Hope/Kiwi Rivers area in Lake Sumner Forest Park, Canterbury (Taylor *et al.* 1986). Breeding, and cross-breeding experiments with yellow-crowned birds, were conducted in captivity; and the resulting parent-offspring data were fully consistent with the combined findings of Holyoak (1974) and Nixon (1981) that the 2 forms are colour morphs of a single species (Taylor *et al.* 1986).

Taylor *et al.* (1986) recommended that: "*Cyanoramphus malherbi* (Souance 1857) should be deleted from the list of New Zealand birds and relegated to synonymy with *C. auriceps* (Kuhl 1820)". This finding was accepted by the Ornithological Society of New Zealand's Checklist Committee (Turbott 1990); and supported by Forshaw (1989).

However, some conservation managers and ornithologists in New Zealand are still uncertain of the status of the Orange-fronted Parakeet (Department of Conservation 1991, Elliott *et al.* 1996). This is mainly due to 10 years of doubt based on electrophoresis of blood proteins (Triggs & Daugherty 1996) suggesting marked genetic separation between the 2 colour forms. Triggs & Daugherty's genetical research has previously been the topic of 3 interim reports (Triggs & Daugherty 1987, 1988 a & b), their findings and recommendations have been quoted (as "in press") since 1991, and a summary of their results has now been published (Triggs & Daugherty 1996). Triggs & Daugherty (1996) found that "the available evidence leads to no firm resolution of the status of the Orange-fronted Parakeet". Apart from the genetic analysis, they built much of their case for "the precautionary reinstatement of the Orange-fronted Parakeet as a species" on claims regarding differences in the bird's morphology, behaviour and ecology.

This paper re-examines many of the historically claimed 'differences' between the 2 colour forms, contributes previously unpublished data, and addresses the evidence and conclusions of Triggs & Daugherty (1996). It seems timely to do this since the Department of Conservation has recently initiated new genetical and field research into the Orange-fronted Parakeet (Grant & Head 1996).

RESULTS AND DISCUSSION

Colour differences

The Orange-fronted Parakeet differs markedly in plumage colouration from the Yellow-crowned Parakeet. In the Orange-fronted Parakeet, the feathers of the frontal band above the bill and small coloured patches on either side of the rump are orange rather than red, the general body plumage is cold bluish green and the crown is pale lemon-yellow, in contrast to the yellowish green and golden yellow of the Yellow-crowned Parakeet (Holyoak 1974, Taylor *et al.* 1986).

Study of museum specimens shows that many minor variations between individuals exist within both Orange-fronted and Yellow-crowned Parakeets, in both the width and colour intensity of the frontal band, the length of the yellow crown,

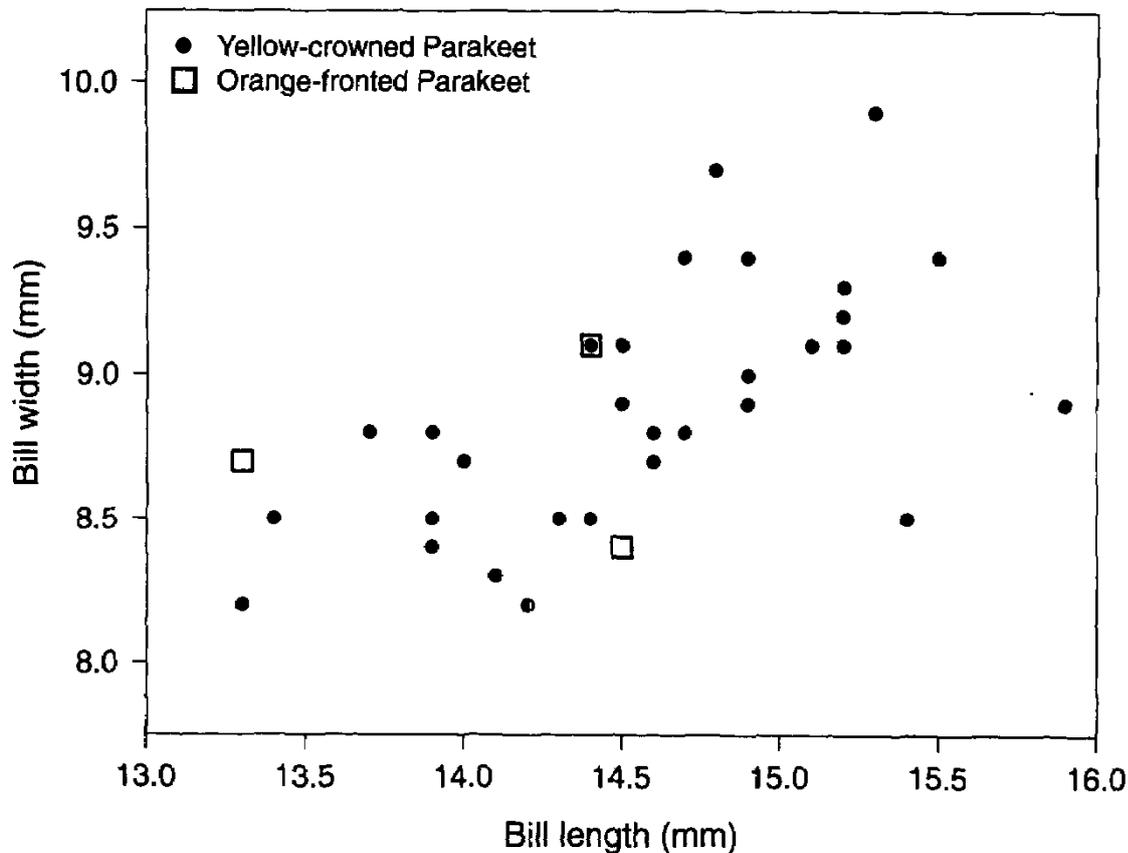


FIGURE 1 - Bill dimensions of 30 male Yellow-crowned Parakeets and 3 male Orange-fronted Parakeets from the Hope-Kiwi Region, Canterbury.

and particularly in the size of the rump patch (Holyoak 1974, R.H. Taylor unpubl.). There is no consistent difference in the colour of the bill, cere, legs, feet, or iris of the 2 parakeets (Holyoak 1974, Taylor *et al.* 1986, R.H. Taylor unpubl.).

Body mass

Very few body masses of wild Orange-fronted Parakeets have been recorded. Three males caught in the Hope-Kiwi area of Lake Sumner Forest Park in March 1981 (A. Cox unpubl.; R.H. Taylor unpubl.) and February 1988 (Triggs & Daugherty 1988 b) weighed 43, 44, and 49 g each (Appendix 1). Unfortunately, most birds caught by Wildlife Service Expeditions during the 1980s were not measured or weighed on capture, due to concerns of unduly stressing individuals being taken into captivity. Appendix 1 also gives the body masses of 30 male Yellow-crowned Parakeets caught on the same expeditions. Body masses of orange-fronted birds averaged 45.3 g, (S.D. = 3.2 g, range 43 - 49 g, N = 3); those of yellow-crowned averaged 48.2 g, (S.D. = 3.7 g, range 42 - 57 g, N = 30). These differences are not significantly different (Student's *t*-test, $t = 1.45$, d.f. = 2.6, $p = 0.26$).

Bill size

Despite thorough studies on numerous museum specimens showing no significant difference between the bills of the Orange-fronted and Yellow-crowned Parakeet (Holyoak 1974, Nixon 1981), the idea that the Orange-fronted Parakeet has a smaller bill, apparently still retains some credence. For instance, Triggs & Daugherty (1996) found that "Three wild-caught male Orange-fronted Parakeets, however, had a significantly shorter mean bill length (14.1 [S.D.] ± 0.67 mm) than seven sympatric wild male Yellow-crowned Parakeets (15.1 [S.D.] ± 0.26 mm) from the Lake Sumner area (*t*-test, $P < 0.05$). However, these data derive from an incomplete and potentially biased sample comprising 7 Yellow-crowned and 1 Orange-fronted Parakeet, caught in February 1988 (Triggs & Daugherty 1988 b), plus 2 orange-fronted birds caught in March 1981. In fact, 23 male Yellow-crowned Parakeets as well as the 2 male Orange-fronted Parakeets were caught and measured in the Lake Sumner Forest Park in March 1981 (A. Cox unpubl., R.H. Taylor, unpubl.). When the total combined samples from the 2 expeditions of 30 male Yellow-crowned ($\bar{x} = 14.6$ mm, S.D. = 0.63 , range 13.3-15.9 mm) and 3 male Orange-fronted Parakeets ($\bar{x} = 14.1$ mm, S.D. = 0.67 , range 13.3-14.5 mm) are compared, the bill lengths are not significantly different (Student's *t*-test, $t = 1.28$, d.f. = 2.4, $p = 0.31$; Figure 1, Appendix 1). No female parakeets were caught during March 1981 and only 1 in February 1988.

Body size and proportions

Nixon (1981) used multivariate statistical analysis to re-examine measurements of all museum specimens of Orange-fronted Parakeets (4 females, 7 males, and 8 unsexed) then available in New Zealand, and a much larger sample of Yellow-crowned Parakeets. He found no significant differences that would support the view that the 2 forms were different species.

Appendix 1 gives further measurements taken from live birds of both types in the Lake Sumner Forest Park. Student's *t*-tests showed that tail, wing and tarsus measurements were not significantly different ($p = > 0.05$) between the colour forms (tail, $t = 0.39$, d.f. = 2.2, $p = 0.73$; wing, $t = 0.37$, d.f. = 3.6, $p = 0.73$; tarsus, $t = 1.04$, d.f. = 2.1, $p = 0.40$).

Distribution

Although the vast majority of records of Orange-fronted Parakeets have been from the South Island (Harrison 1970), there are early references to Orange-fronted Parakeets in the North Island (Buller 1882), on Hen and Little Barrier Islands (Buller 1884, Reischek 1887, 1952), and on Stewart Island (Harrison 1970). There is also a very doubtful early record from the Auckland Islands (Harrison 1970). In the last 2 decades, South Island sightings have been confined to Canterbury and eastern Fiordland (Read & McClelland 1984, Taylor 1985, Taylor *et al.* 1986, O'Donnell & West 1992).

The North Island, Hen and Little Barrier records were discounted as unreliable by Harrison (1970), who proposed that orange-fronted birds were probably confined to the South Island. A strictly South Island distribution for Orange-fronted Parakeets would more conveniently fit with the theories of Pleistocene and post-glacial speciation of *Cyanoramphus* parakeets (Fleming 1974, 1979, 1980). Nixon (1981) and Taylor (1985) were not so dismissive of Reischek's and Buller's North Island reports, on the grounds that these early accounts gave particulars of birds observed and shot, that labelled museum specimens were in existence, and that the Hen and Little Barrier Island records could not be explained by escaped cage birds.

For instance, on 24 October 1880, Reischek (1952) climbed to the top of Taranga (Hen) Island. He records: "to my surprise I found between the rocks little Alparrakeets, which I had formerly seen in the Southern Alps but had not found anywhere in the North Island. Even in the literature of the subject, the occurrence here had never been noted before". It is clear he encountered Orange-fronted Parakeets (then called the Alpine Parakeet) on Hen Island, for by that date he had travelled extensively on collecting trips (Reischek 1952, Westerskov 1980) in the Thames, Auckland and Northland districts – including a visit to Little Barrier Island – where he would have seen many yellow-crowned birds.

I have examined and measured 2 orange-fronted birds labelled 'Taranga Island' and dated '1880' (Nos. 50382 and 50383) in the Reischek collection in the Vienna Museum, Austria. These 2 specimens are typical Orange-fronted Parakeets, visually similar in colour pattern and shade to 6 other orange-fronted birds, all from the South Island, in the same collection. Notes and measurements on the Taranga Island specimens are given in Appendix 2. As previously stated (Taylor 1985), I fully accept Reischek's records of orange-fronted birds from these northern offshore islands.

Interestingly, a single bird tentatively identified as an Orange-fronted Parakeet was seen on 2 occasions on Taranga Island in 1985 (Mark Bellingham, pers. comm.).

Habitat

Although recorded in the past from near sea level up to subalpine scrublands, recent sightings of Orange-fronted Parakeets have been mainly near the edges of *Nothofagus* forest below 900 m a.s.l. (Harrison 1970, Read & McClelland 1984, Taylor 1985). In the Hope/Kiwi area, Lake Sumner Forest Park, South Island, nesting birds have only been found in forest dominated by tall red beech (*Nothofagus fusca*) between 600 and 900 m a.s.l., where they seem to prefer areas bordering on mountain beech (*N. solandri*) forest (D. Crouchley unpubl.). They share this habitat with Yellow-crowned Parakeets. The early idea that Orange-fronted Parakeets occupied an alpine niche was corrected by Harrison (1970), and there are no reports, or even suspicions, of them occurring outside of the range, or habitat, of yellow-crowned birds.

Feeding

Food items eaten by Orange-fronted Parakeets in the wild include flower and leaf buds of silver (*N. menziesii*), red, and mountain beech; flowers and young seeds of red and mountain beech; old seed of mountain toatoa (*Phyllocladus alpinus*), berries, scale insects on beech branches, and small grubs and other invertebrates from dead wood, under beech bark, and on *Polystichum* fronds (Oliver 1955, Harrison 1970, A. Cox unpubl.; D. Crouchley unpubl.; Forshaw 1989, R.H. Taylor unpubl.). It has been claimed that “Orange-fronted Parakeets seem to have different food preferences to Red and Yellow-crowned Parakeets, and scale insects, grubs, flower and leaf buds, flowers, young leaves and seeds are commonly eaten” (Anon. 1991). However, years of personal field observations indicate that these food items are also amongst the preferred foods of Yellow-crowned Parakeets in South Island beech forests (Taylor 1985, & R.H. Taylor unpubl.). These items also feature in the diet of Yellow-crowned Parakeets from eastern Fiordland (Elliott *et al.* 1996). Wherever they occur together, both birds form mixed feeding flocks. There appears to be no documented difference in feeding ecology between the 2 forms.

Behaviour differences

Triggs & Daugherty (1996), citing verbal communications from D. Crouchley, A. Cox and D. Mudge, report that “some differences in behaviour [of Orange-fronted] from Yellow-crowned Parakeets have been observed”. Unfortunately, they publish no further details.

Reporting on live-capture operations, A. Cox (unpubl.) recorded that “in the holding crate the orange-fronted ... were very confiding and less flighty than the yellow-crowns”, and that “all orange-fronted observed in the wild were also confiding. Although the occasional yellow-crowned was as tame”. He noted no feeding preferences between the birds, in the wild or in the holding crate. D. Crouchley (unpubl.) similarly considered “Orange-fronted Parakeets to be more confiding and less flighty than the Yellow-crowned Parakeet” both in the field and in captivity.

As regards the species versus colour-morph quandary, Cox concluded: “All the data and personal impressions that we gained on this trip [12-27 March 1981] fail to point us in any direction. All the differences in behaviour that we noticed could perhaps be attributed to an individual rather than a species difference”. On the other hand, after his 2-22 October 1982 trip, Crouchley (unpubl.) concluded that “although the sample size is still very small what data we did collect seems to point towards the orange-fronted parakeet being a species rather than a colour morph”. As well as the more confiding behaviour already noted, he mentioned perceived differences in calls and egg size (see below). During a later trip from 16-22 February 1988 (Triggs & Daugherty 1988 b), 1 Orange-fronted Parakeet and 23 Yellow-crowned Parakeets were identified; no observations on perceived behavioural differences were reported.

I was a member of the March 1981 expedition, and was also in the field for part of the follow-up trip in September-October 1981, and returned to the area again in October-November 1983. My notes on a group of 4 Yellow-crowned and 1 Orange-fronted Parakeets that approached a taped call were that the "orange-fronted was smaller and less-active. Sat a bit lower and apart from others, but interacted with them" as they moved about in the foliage. This could have been a sex or age difference, for on several other occasions when the 2 types were flocking and feeding together, no behavioural differences were noted. In contrast to others' comments (above), my notes describe the 2 orange-fronted males captured in March as being "more flighty (e.g., harder to catch)" when in the holding crate than the yellow-crowned males. I am in sympathy with Cox who, reporting on 15 September-14 October 1981 trip, states "the small sample size must be borne in mind. I draw no conclusions".

During several years of aviary observations on wild-caught birds of both colour types, I was unable to detect any consistent behavioural differences or food preferences. In my opinion, little weight can be given to any of the anecdotal and often conflicting reports of such differences.

Calls

My field notes from 3 expeditions to the Lake Sumner Forest Park during 1981-1983 record that the calls of free-living and captured wild birds of both colour forms were not noticeably distinct – an observation reinforced later by several years of aviary experience with both types. However, Crouchley (unpubl.) states that when the 2 types were calling in the same location "on a couple of occasions" he noted "a very slight difference in their calls". Age and sex differences, which are known to exist in Yellow-crowned Parakeets (Pickard 1990), may have been involved.

Compared with major differences found between the calls of other *Cyanoramphus* taxa, no significant difference was found between the calls of the orange-fronted and yellow-crowned birds, in the limited samples so far studied by sonograph analysis (Pickard 1990).

Flocking

It has been suggested that the very occasional occurrence of single-species flocks of Orange-fronted Parakeets support the view that they are separate species (Fleming 1980, Triggs & Daugherty 1996). However, the few flocks of Orange-fronted Parakeets recorded have all been small and could simply represent family groups with 2 orange-fronted parents. Many more mixed-species flocks, both large and small, have been seen (Potts 1885, Oliver 1955, Harrison 1970, Nixon 1981, Gray 1982, R.H. Taylor, unpubl.).

Breeding in the wild

Time of breeding

There has never been any suggestion that the breeding season of Orange-fronted Parakeets differs from that of Yellow-crowned Parakeets. Certainly there is no difference in the Lake Sumner area, where both forms have been found nesting at the same time of year. During October 1982, "parakeets at all stages of breeding were observed; several yellow-crowned pairs were seen prospecting for nest sites, one orange-fronted pair were found incubating, one yellow-crowned pair was found with a nest with young chicks, and two juvenile Yellow-crowned Parakeets shortly out of the nest were seen" (D. Crouchley unpubl.).

Nest sites

The nest site of the pair of Orange-fronted Parakeets found breeding in the Lake Sumner area in October 1982 was in a cavity behind a knot-hole (8 cm in diameter) about 10 m up in a living red beech tree. Nesting sites of Yellow-crowned Parakeets in the same area were in very similar sites in either living or dead trees (D. Crouchley unpubl., A. Cox unpubl., R.H. Taylor unpubl.).

Would random mating between colour-morphs be expected?

Triggs and Daugherty (1996) report that "two Orange-fronted x Orange-fronted Parakeet nesting pairs have been recorded from Lake Sumner Forest Park, compared to a single Orange-fronted x Yellow-crowned Parakeet pair"; and reason that, "as only about 7% of observed parakeets in this area are Orange-fronted, the probability of these pairings occurring by chance if Orange-fronted and Yellow-crowned Parakeet are mating randomly (i.e., the same species) is only 0.013".

These statements contain errors of fact and incorrect assumptions. Observations of Orange-fronted Parakeets seen in pairs during the 1981 and 1982 expeditions have been confused with 'nesting pairs'. Only 1 nesting pair of Orange-fronted Parakeets was found, not 2 (D. Crouchley unpubl., Taylor *et al.* 1986). During field trips, nests were not found randomly. Nearly all searching was concentrated in areas where Orange-fronted Parakeets had previously been found. As the object was to obtain Orange-fronted Parakeets (or their eggs) for captive breeding, direction of the search depended on sightings of orange-fronted birds.

Further, it is quite wrong to expect that pairing within all species of parakeet would be by chance. There is abundant evidence that non-random mating occurs within bird species (Huxley 1955, Findlay 1987, Partridge & Halliday 1984). The act of mating non-randomly does not imply that birds are of different species, as claimed by Triggs & Daugherty (1996). Both assortative and disassortative mating based on plumage colouration occurs in a number of polymorphic bird species (Buckley 1987). Experimental interference of colour patterns in various breeds of domestic fowls showed the hens prefer mates of similar colour to themselves (McFarland 1987). The Lesser Snow Goose (*Anser caerulescens*) is dimorphic for

plumage colour, with blue and white forms. About 90% of birds pair with a partner the same colour as themselves, as a result of imprinting on parental and sibling phenotypes developed in early life (Cooke 1978, Cooke *et al.* 1991).

To sum up, there is no evidence that assortative mating occurs within the Yellow-crowned/Orange-fronted Parakeet complex; but even if it does, this is not evidence that the 2 colour forms are different species.

Egg size

Few data are available on the eggs of either Orange-fronted or Yellow-crowned Parakeets, but there is evidently an overlap in size range. The only egg measurements published for Orange-fronted Parakeets are for 2 from Mount Peel, Canterbury (21.2 mm x 18 mm and 21.8 mm x 18 mm; Oliver 1955). It is not clear how they were identified (Harrison 1970). For Yellow-crowned Parakeets, Oliver (1955) gives data on 2 eggs from Codfish Island of 24 mm x 20 mm and 24 mm x 18.5 mm; and Forshaw (1989) gives 22.9 mm (range 21.6 - 24.2) x 18.9 mm (range 17.8 - 20.0) for 7 eggs of unspecified provenance. The 3 Orange-fronted Parakeet eggs taken from the wild for captive incubation in 1982 were not measured, as handling was kept to a minimum to increase their chance of successful hatching. However, Crouchley (unpubl.) reported that they "were much smaller... about 2 mm smaller on both axis" when visually compared with eggs laid by the fostering Yellow-crowned Parakeet. This comparison tells us very little, since the larger foster bird was of aviary stock.

Breeding in captivity

Captive cross-breeding experiments have shown that a polymorphism exists between yellow-crowned and orange-fronted birds that follows the simple Mendelian theory of dominant/recessive inheritance at a single locus (Taylor *et al.* 1986). The results suggest that the orange factor is recessive.

Taylor *et al.* (1986) found that yellow-crowned birds that are homozygous for yellow will breed true and their offspring will be yellow-crowned. If 2 orange-fronted birds are mated they will also breed true. If an orange-fronted bird is crossed with a homozygous yellow-crowned, the first generation offspring (F1) will all be yellow-crowned in appearance, but be heterozygous and inherit the allele for orange colouration. When 2 of these heterozygous F1 birds are crossed, both yellow-crowned and orange-fronted birds are produced in approximate proportions of 3 yellow-crowned to 1 orange-fronted – the Mendelian 3:1 ratio. If birds from the F1 generation are back-crossed to their parental homozygous yellow-crowned stock, the offspring will all appear yellow-crowned but half will be heterozygous. If the F1 birds are back-crossed to orange-fronted birds they will have yellow-crowned and orange-fronted young in about equal numbers. Taylor *et al.* (1986) considered that these findings were in complete agreement with the suggestion that the 2 forms were colour morphs of a single species – e.g., in the same way that there are black and pied forms of the South Island Fantail (*Rhipidura fuliginosa fuliginosa*) (Caughley 1969; Craig 1972).

Polymorphism or hybridisation

Polymorphism is the co-existence in a single interbreeding population of 2 (dimorphism), or more (polymorphism), readily distinguishable and genetically determined forms – called ‘morphs’ (Huxley 1964). Hybrids are offspring of a cross between 2 closely related species, though normally behavioural and ecological isolating mechanisms would keep them apart (Taylor 1975). In natural habitats, hybrids are usually eliminated from a population because they are less well adapted to the environment than either of the parental forms (Ford 1964).

Triggs & Daugherty (1996) claim that the orange-fronted birds produced in aviary experiments are hybrids and that the breeding studies of Taylor *et al.* (1986) “relate to no presently accepted definition of a species”. When dealing with sympatric populations, I accept “species” as groups of naturally interbreeding individuals that are reproductively isolated from other such groups, and occupy a specific niche in nature (Mayr 1982); i.e., a definition fitting within both the biological species and the phylogenetic species concepts (McKittrick & Zink 1988). Reproductive isolation means lack of gene flow, due to ecological or fertility barriers. I know of no evidence indicating how yellow-crowned birds could be reproductively isolated from orange-fronted birds in the wild.

Can stable dimorphism occur as a result of interspecific hybridization?

Triggs & Daugherty (1996) state, “colour variation may often be encoded by one or a few genes (Holyoak 1974, Nixon 1982), even between species (e.g., Tauber & Tauber 1977). The breeding studies showing apparent single-locus control of orange/yellow colouration (Taylor *et al.* 1986) are therefore not a test of the specific status of the Orange-fronted Parakeet”. That polymorphism within a species can be encoded by 1 or a few genes is widely known and accepted (e.g., Holyoak 1974, Taylor *et al.* 1986). However, the idea that stable dimorphism can occur as a result of hybridization between 2 species of birds, or other animals, finds no support in the literature.

Tauber & Tauber (1977) – quoted by Triggs & Daugherty (1996) in support of their claim (above) – studied 2 species of green lacewings (Insecta; Neuroptera) and proposed a genetic model for sympatric speciation. Even in this case, 50-100% of the hybrids obtained by laboratory breeding were of various colours ‘intermediate’ between that of the 2 parent species – as previously noted in all hybrids between different *Cyanoramphus* and other closely related parrot species (Cain 1955, Taylor 1975, Taylor *et al.* 1986). Huxley (1964) emphasises that “it is important to distinguish true polymorphism from polymorphic variability due to recombination after hybridization. The latter is not genetically stabilised or selectively balanced; it will tend to settle down into a unimodal type if extensive hybridization has occurred”. If Huxley is correct, the offspring from the *Cyanoramphus* cross-breeding experiments (Taylor *et al.* 1986) cannot be hybrids.

Tauber & Tauber’s (1977) genetic model for sympatric speciation involves individuals being genetically adapted by assortative mating, and then (most

importantly) reproductively isolated to different habitats and reproductive seasons. Once reproductive isolation is attained in such “sibling species”, “other genetic differences are likely to occur rapidly” (Bickham 1983). Orange-fronted and Yellow-crowned Parakeets do not differ in either habitat or timing of breeding; nor is there any evidence of other potential isolating characters. Tauber & Tauber’s (1977) ideas, and other sympatric speciation theories, have been severely criticised on both theoretical and empirical grounds by Fautuyma & Mayer (1980).

Genetic analysis

The current opinion in official conservation circles in New Zealand is that genetic studies support the contention that the Orange-fronted Parakeet is a separate species. For example, the Orange-fronted Parakeet is still ranked as a “Highest Priority Threatened Species” by the Department of Conservation (Molloy & Davis 1994). The Department has further stated in a 1994 submission to IUCN (unpubl.) that “A more comprehensive genetic study would confirm this conclusively but, currently, there is no reason to question the status of *C. malberbi* as a separate species”. This opinion is based on claims such as: “Reduction of the taxonomic status of Orange-fronted Parakeets is premature” (Daugherty & Triggs 1991).

Triggs & Daugherty (1996) found no significant difference in the genetic distance between Orange-fronted and Yellow-crowned Parakeets, but concluded that “the results of genetic analysis... suggest that Orange-fronted Parakeets are separated from both sympatric and geographically distant South Island Yellow-crowned Parakeets by as much as the genetic distance between subspecies of Red-crowned Parakeets”. They present no genetic data, except in a dendrogram.

The genetic difference between groups can be measured by D , the standard genetic distance (Nei 1978). A low value of D between 2 groups means they are closely related. Between species of birds within a genus D averages 0.044, between subspecies of the same bird species D averages 0.005, and between populations D averages 0.002 (Triggs & Daugherty 1988 a). Three reports by Triggs & Daugherty (1987, 1988 a, 1988 b) give mean values for D . However, allelic frequencies, heterozygosity, standard errors, statistical significance, etc., have never been reported; these are needed before any weight can be given to their results – especially since various conflicting D values have previously been reported for the same samples by the same authors. For example, in 2 reports by Triggs & Daugherty (1987, 1988 a) the level of genetic differentiation between 7 birds (cross-bred from wild-caught orange-fronted and captive yellow-crowned aviary stock) and 25 Chetwode and Little Barrier Island wild-caught Yellow-crowned Parakeets is given in the text as $D = 0.015$. However, a value of $D = 0.008$ is indicated in dendrograms accompanying both reports.

Similarly, blood samples collected from 4 Orange-fronted and 8 Yellow-crowned Parakeets, all wild-caught from the Lake Sumner area were analysed in 1988 by Triggs and Daugherty (1988 b) for genetic variation by “electrophoresis for 22 protein loci”. They concluded that “the four OFP show a high overall similarity to the YCP

from the same area... ($D = 0.002$). However, Triggs & Daugherty (1996) indicate in their dendrogram a genetic difference based on the same 12 birds of $D = 0.008$. They used the same technique ("protein electrophoresis... at 21 allozyme loci"). No explanation is given for the 4-fold increase in genetic distance between the 1988 and 1996 reports.

Based on the standard genetic distance ($D = 0.002$) reported in 1988, there is no basis for the claim that "Orange-fronted Parakeets are separated from both sympatric and geographically distant South Island Yellow-crowned Parakeets by as much as the genetic distance between subspecies of Red-crowned Parakeets" (Triggs & Daugherty 1996).

CONCLUSION

There are no published field or aviary observations of any substance that indicate the 2 forms have differing morphology, behaviour, or ecology, that would act as isolating mechanisms in the wild. The 2 colour forms are known to interbreed in the wild and in captivity, where the parent-offspring data are fully consistent with the theory that the 2 forms are colour morphs of a single species (Taylor *et al.* 1986). The evidence and arguments in this review support this conclusion.

It is now 10 years since genetic studies of New Zealand parakeets commenced (Triggs & Daugherty 1988). These studies have detected obvious differences between Antipodes Island (*C. unicolor*), Forbes (*C. auriceps forbesi*), Red-crowned, and Yellow-crowned Parakeets; and between some island sub-species of Red-crowned Parakeets, and between some geographically distinct populations of Yellow-crowned Parakeets (Triggs & Daugherty 1990, 1996, Daugherty & Triggs 1991). However, as regards the status of Orange-fronted Parakeets they have produced confusion, and have revealed no significant differences between sympatric orange-fronted and yellow-crowned birds from Lake Sumner Forest Park.

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APPENDIX 1 - Measurements of Yellow-crowned Parakeets and Orange-fronted Parakeets from the Hope/Kiwi region, Canterbury.

No.	Body mass (g)	Bill length from cere (mm)	Bill width (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)
Yellow-crowned Parakeets						
1	46	13.9	8.4	106	116	19.0
2	47	14.3	8.5	114	128	18.2
3	51	15.9	8.9	116	130	19.9
4	48	13.9	8.5	108	119	19.9
5	44	14.1	8.3	105	118	19.0
6	47	13.7	8.8	107	114	19.8
7	47	14.0	8.7	104	112	19.3
8	47	14.9	9.0	107	118	19.3
9	49	15.2	9.2	113	124	19.6
10	52	14.7	8.8	110	119	18.8

No.	Body mass (g)	Bill length from cere (mm)	Bill width (mm)	Wing length (mm)	Tail length (mm)	Tarsus length (mm)
11	48	13.9	8.8	108	119	18.7
12	57	15.5	9.4	-	-	-
13	43	14.6	8.8	109	116	19.5
15	51	14.5	8.9	110	128	19.5
16	54	15.2	9.3	114	120	20.3
17	54	14.5	9.1	103	113	20.1
18	44	14.2	8.2	106	-	18.1
20	42	13.3	8.2	107	109	18.3
21	47	14.9	8.9	109	118	19.0
22	53	14.4	9.1	108	118	20.0
23	45	14.6	8.7	103	119	20.2
24	47	14.4	8.5	106	119	20.3
25	42	13.4	8.5	105	115	17.6
186	51	15.3	9.9	100	109	20.0
187	52	15.1	9.1	101	101	22.6
188	46	15.4	8.5	100	98	21.5
190	49	14.9	9.4	107	107	19.8
192	50	14.8	9.7	108	115	19.5
194	46	15.2	9.1	102	94	16.8
195	47	14.7	9.4	100	99	20.1
Mean	48.2	14.6	8.9	106.8	114.8	19.5
S.D.	3.71	0.63	0.43	4.24	8.86	1.12
Orange-fronted Parakeets						
14	43	14.5	8.4	106	117	19.8
19	44	13.3	8.7	106	122	19.3
185	49	14.4	9.1	110	96	22.8
Mean	45.3	14.1	8.7	107.3	111.7	20.6
S.D.	3.21	0.67	0.35	2.31	13.80	1.89

Nos. 1 - 25 from Taylor (unpublished)

Nos. 185 - 195 from Triggs & Daugherty (1988b)

APPENDIX 2 - Measurements of two Orange-fronted Parakeets collected in 1880 from Taranga (Hen) Island, in the Reischek Collection, Vienna Museum of Natural History, Austria.

Collection Number	Sex	Bill length from cere (mm)	Bill width (mm)	Wing length (mm)	Tail length (mm)
50382	Male	13.5	8.3	101	102 (worn)
50383	Female	11.3	6.8	98	117