

Genetic variation, systematics and management of kiwi (*Apteryx* spp.)

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ABSTRACT

Kiwi (*Apteryx*: Struthioniformes) are a family of ratite birds confined entirely to New Zealand. Since 1813, at least ten species have been described. Recent taxonomy has accepted three species: *A. owenii* (little spotted kiwi), *A. haastii* (great spotted kiwi) and *A. australis* (brown kiwi). *Apteryx australis* has three subspecies: *A. a. australis* (South Island); *A. a. mantelli* (North Island); and *A. a. lawryi* (Stewart Island).

We undertook a survey of genetic variation of all known types of kiwi. Between 1984 and 1992, blood samples were collected from populations of all presumed taxa of kiwi from 32 locations. The objectives of this survey were to: (a) describe patterns of geographic variation in blood proteins (allozymes); (b) assess competing taxonomic hypotheses for *Apteryx*; and (c) identify management units and populations of special conservation significance.

Cluster analysis of allozyme variation revealed four genetic groups differentiated at the species level: (a) northern brown kiwi from the North Island and Okarito on the West Coast of the South Island, corresponding to *A. mantelli*; (b) tokoeka or southern brown kiwi from Haast, Fiordland and Stewart Island, corresponding to *A. australis*; (c) little spotted kiwi; and (d) great spotted kiwi.

Within these major groups, three populations of special interest were revealed: (a) Okarito brown kiwi; (b) Haast tokoeka, which may be specifically distinct; and (c) Little Barrier Island brown kiwi.

Tokoeka from Fiordland and Stewart Island show high levels of genetic similarity. Populations of great spotted kiwi show moderate levels of genetic divergence with no apparent geographic pattern. The two populations of little spotted kiwi, on Kapiti and D'Urville Islands, are genetically very similar. Kapiti Island brown kiwi are of a hybrid *A. mantelli* × *A. australis* origin, and a single bird from Franz Josef was a hybrid *A. australis* × *A. owenii*. Other hypotheses regarding the latter bird are discussed.

Present theory recommends conservation of the entire range and geographic pattern of genetic variation. This study identified seven fundamental management units for kiwi, corresponding to genetically and geographically distinct populations or metapopulations. Management priority of these units should be determined by ecological factors such as rarity and immediate threats to survival. Translocations between management units should be prohibited. Research should be undertaken to resolve remaining taxonomic uncertainties.

1 . INTRODUCTION

The species of *Apteryx*, the only known genus of the Family Apterygidae, Order Struthioniformes (Sibley & Ahlquist 1990), are endemic to New Zealand and highly distinctive even by comparison to other presumed ancient and highly derived members of the New Zealand fauna. Flightless and with only vestiges of wings remaining, kiwi occupy a relatively secretive, nocturnal niche feeding on litter-dwelling invertebrates and perhaps some small vertebrates. Recent DNA analyses showing that kiwi are not the sister-group of the other New Zealand ratites, the moas, but represent an entirely separate group (Cooper et al. 1992) have strengthened the taxonomic distinctiveness of kiwi.

The distribution of the genus spans all three major islands of New Zealand. For at least a century kiwi numbers have been in decline. Large numbers of kiwi pelts were sent to European fashion markets in the late nineteenth century, and at the same time feral dogs (*Canis familiaris*) and other introduced mammals depleted numbers substantially. The effects of dogs may still be catastrophic for local populations (Taborsky 1988). More recently, the once widely distributed little spotted kiwi has been found to be virtually extinct on the mainland (Jolly 1985). All kiwi species are listed as 'category B' (second priority threatened species) by the New Zealand Department of Conservation (Molloy & Davis 1992).

In addition to their highly distinctive taxonomic status and conservation significance, kiwi occupy a special place in New Zealand culture. To Maori, kiwi are *taonga*, or natural treasures to be treated as sacred. Kiwi are the unofficial national emblem, by whose name all New Zealanders are known.

Few New Zealanders see or even hear kiwi in nature, because of the species' secretive habits, isolated habitats and low numbers. These factors also make study of kiwi difficult, and many aspects of kiwi biology have remained poorly known. In particular, geographic variation of kiwi has remained poorly described and its corollary, taxonomic classification, uncertain. At least ten species were described in the nineteenth century (Appendix 1), although recent workers have not accepted most of these. Conservation management of kiwi has been based on the taxonomy of Mathews (1931), who recognised three species of kiwi and three subspecies of brown kiwi. No recent classification has been tested by contemporary analytical techniques, although Mallophaga feather lice and DNA-DNA hybridisation analysis have cast doubt on Mathew's taxonomy for some time (Appendix 1).

Conservation planning requires knowledge of the entire range of variation and its geographic distribution within a taxon (IUCN, UNEP & WWF 1980; Frankel & Soulé 1981): in other words, a reliable taxonomy. Avise (1989) noted serious management mistakes can arise from reliance upon nineteenth-century taxonomies based upon outdated species concepts that have not been tested by genetic data and contemporary systematic methodologies. Although Avise (1989) directed his comments to taxonomy of North American vertebrates, his views are directly relevant to kiwi taxonomy.

Because of lingering questions regarding the taxonomic status of kiwi, the New Zealand Wildlife Service initiated collections of blood samples for genetic analysis in 1984, and these collections were continued by the Department of

Conservation and other interested groups. Using these blood samples, this study sought to:

- Examine geographic variation in allozymes (proteins showing Mendelian assortment) in all presently described species of kiwi, especially those populations of uncertain taxonomic status.
- Use these data to assess the existing taxonomy of kiwi.
- Identify populations or taxa of particular conservation significance.

We particularly wished to test the assumptions of Mathews' (1931) taxonomy against the geographic pattern of allozyme variation. The taxonomy of Oliver (1930)—four species in total, including two species of brown kiwi—offers a clear alternative hypothesis. We also wanted to assess the level of distinctiveness of little spotted kiwi: Do genetic data offer any support for separate generic identity?

2. METHODS

2.1 Samples and collection of blood

Approximately 1-2 ml of blood were collected from each of 245 individuals from 30 locations and 6 captive populations between 1984 and 1992. These samples represent all taxa recognised by recent taxonomies and as broad an array as possible of natural populations (Fig. 1, Appendix 2). Populations of particular interest included those where different species could occur sympatrically, those of uncertain origin on Kapiti Island and Little Barrier Island, and those already identified as being of special concern, especially Okarito brown kiwi. The origin of captive birds was determined whenever possible.

Sample sizes varied from one to 38 individuals per population. Small sample sizes are sufficient to assess specific status in most instances (Sarich 1977; Gorman & Renzi 1979): results are improved more by increasing the number of genetic loci examined than by increasing sample sizes.

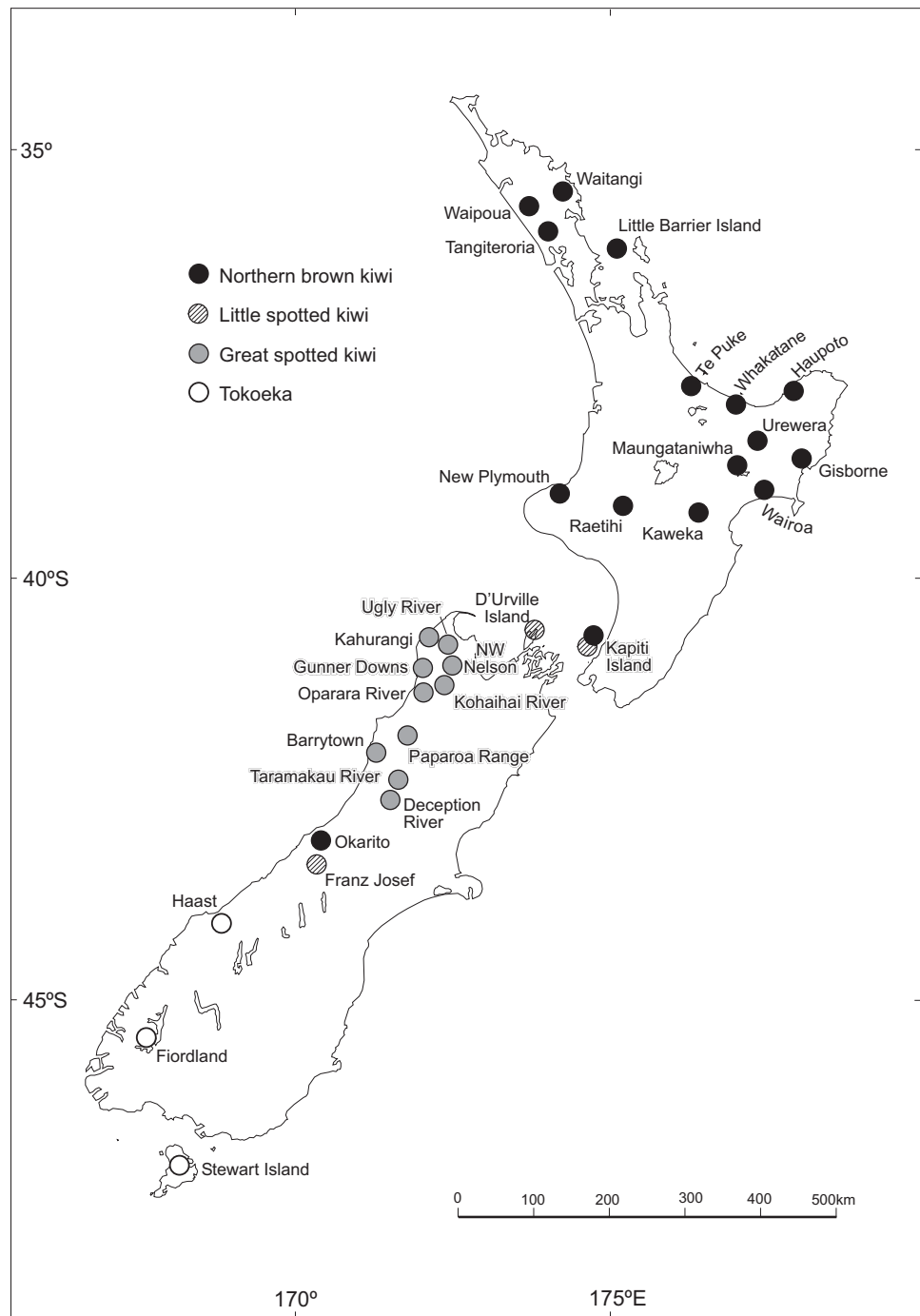
Blood was collected into heparinised needles from a vein running along the inside of the tarsometatarsus. Where feasible, whole blood was separated immediately into red cells and plasma by centrifugation. Red cell components were diluted 1:1 with distilled water in order to lyse the red cells. Blood fractions were snap frozen and stored at -80°C at the National Frozen Tissue Collection, National Museum, or at Victoria University, until subjected to allozyme analysis.

A complete set of allozyme loci could not be resolved from whole blood samples, so their use was discontinued.

2.2 Electrophoretic techniques

Red cells and plasma were subjected to starch gel electrophoresis according to the techniques of Allendorf et al. (1977) and Herbert et al. (1993). In order to maximise the number of loci examined, all combinations of four gel/electrode buffer systems and 40 different protein (mainly enzyme) stains were examined for electrophoretic activity and resolution. Proteins of individuals that showed

Figure 1. Locations and species of kiwi sampled. Captive birds of unknown origin are: brown kiwi (Auckland Zoo, Wellington Zoo, Mt Bruce, Mt Ngaroto) and great spotted kiwi (Mt Bruce, Otorohanga).



the same mobility on a gel stained for a particular enzyme were considered to be encoded by the same Mendelian allele, whereas those showing different mobilities were assumed to be encoded by different alleles. As not all amino acid substitutions alter the mobility of the resulting protein, allozyme electrophoresis is estimated to identify no more than 30% of variation at polymorphic loci (Lewontin 1974; King & Wilson 1975). Therefore, estimates of genetic (allozyme) divergence can be assumed to be substantial underestimates.

2.3 Allozyme nomenclature and analysis

The following nomenclature, based on the recommendations of Murphy and Crabtree (1985), has been used when labelling genetic loci and alleles:

1. Loci are indicated in italics.
2. Multiple loci are labelled sequentially beginning from the most cathodal locus.
3. Alleles are indicated by a lower case letter, not italicised, within parentheses. For example, *Ldb-1(c)* refers to the c allele at the most cathodal locus encoding the enzyme lactate dehydrogenase.

The BIOSYS-1 programme (Swofford & Selander 1981) was used to compute:

1. Gene and genotype frequencies for each population.
2. Unbiased estimates of genetic distance (*D*; Nei 1978) between pairwise combinations of populations.
3. A phenetic clustering algorithm (WPGMA; Sneath & Sokal 1973) over all populations.

3. RESULTS

3.1 Levels of allozyme variation

Genetic variation was detected at 12 of 30 blood loci examined. At four of these loci, rare alleles were identified in only one or a few populations. With one exception, the observed proportion of heterozygotes over all loci, \bar{H} varied from 0 to 0.03, levels that are normal for tetrapod vertebrates (Avice et al. 1980). The exception was a single bird captured at Franz Josef that was heterozygous at four loci ($\bar{H} = 0.14$). This unusually high variability was interpreted to indicate that the bird is an F_1 hybrid between little spotted and brown kiwi (see section 3.5.2).

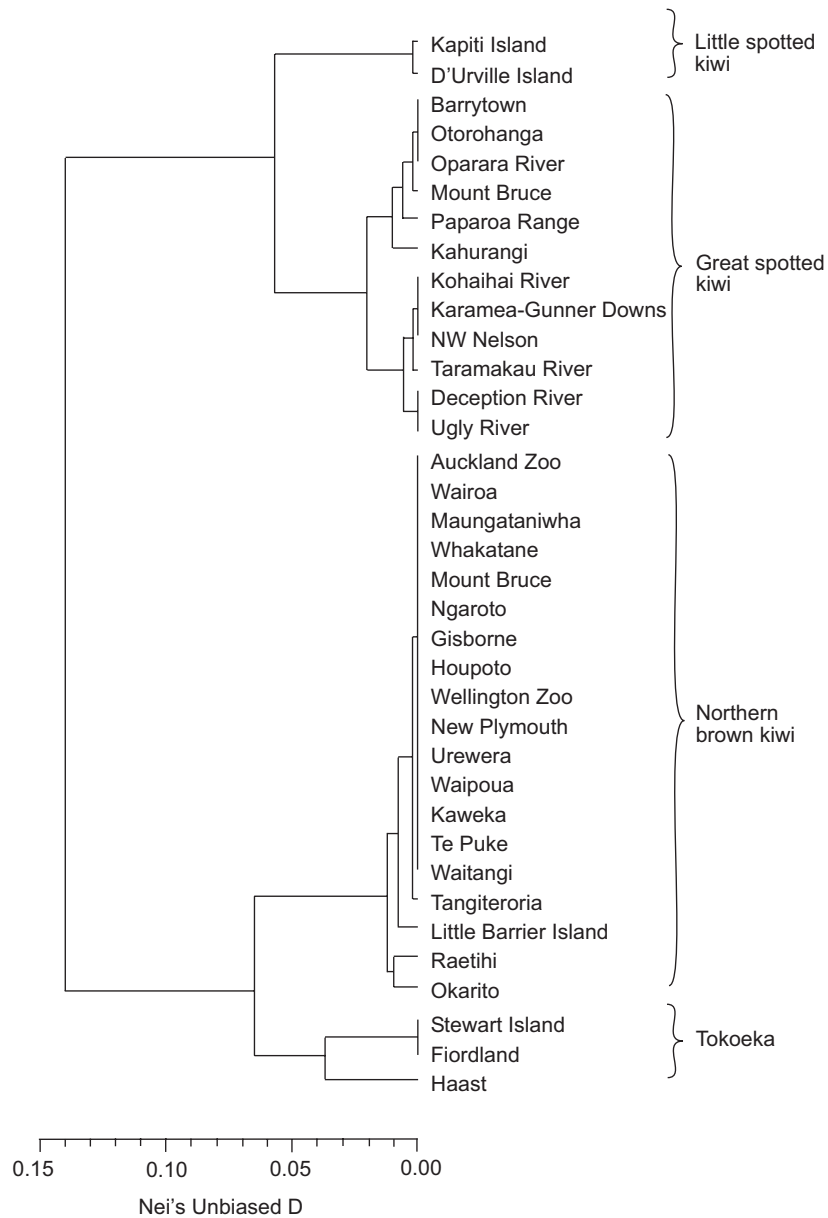
3.2 Geographic variation and species identification

Allozyme electrophoresis is a powerful tool for identification of specific differentiation when two divergent forms occur sympatrically (Allendorf et al. 1977; Daugherty et al. 1990). Fixation for alternate alleles at one or more loci, i.e. the absence of heterozygous individuals, confirms reproductive isolation, meeting the primary criterion of the biological species concept (Mayr 1969).

However, sympatric occurrence of kiwi species is rare, and thus we relied on an analysis of pattern and level of geographic differentiation to assess species status. Phenetic cluster analysis of allozyme variation in all populations clearly distinguished four main geographic groups of kiwi (Fig. 2):

- Little spotted kiwi, *A. owenii*, on Kapiti Island and D'Urville Island.
- Great spotted kiwi, *A. baastii*, all found in northwestern South Island.
- Northern brown kiwi, *A. mantelli*, including all North Island populations and that at Okarito on the West Coast of the South Island.
- Tokoeka, *A. australis*, including brown kiwi populations from Haast, Fiordland and Stewart Island.

Figure 2. Weighted pair group cluster analysis of allozyme variation among all species of kiwi. The Franz Josef hybrid individual and the Kapiti Island brown kiwi hybrid population are not included.



The effects of five variable loci (Table 1) define the four groups. Little spotted kiwi are distinguished from all other species by fixation (i.e. 100% occurrence) for the unique allele *Pep-3(b)*, and great spotted kiwi are fixed for the unique allele *Pep-3(c)* (Fig. 3A). Northern brown kiwi are fixed for the unique allele *Hb-2(a)* (Fig. 3B). Tokoeka are not distinguished by unique alleles, but are clearly differentiated from northern brown kiwi by possession of *Hb-2(b)* and from all other species by a unique combination of alleles at loci *Hb-2*, *Lap-1* and *Pep-3*.

The allopatric distribution of these four groups does not allow for a direct test of reproductive isolation under the biological species concept (Mayr 1969). However, fixation for alternate alleles at a number of loci strongly supports the view that gene flow among these groups is extremely limited.

Additionally, the data are consistent with recognition of at least four species under two other contemporary species concepts. The evolutionary species concept considers a species to be 'a single lineage of ancestral-descendant populations

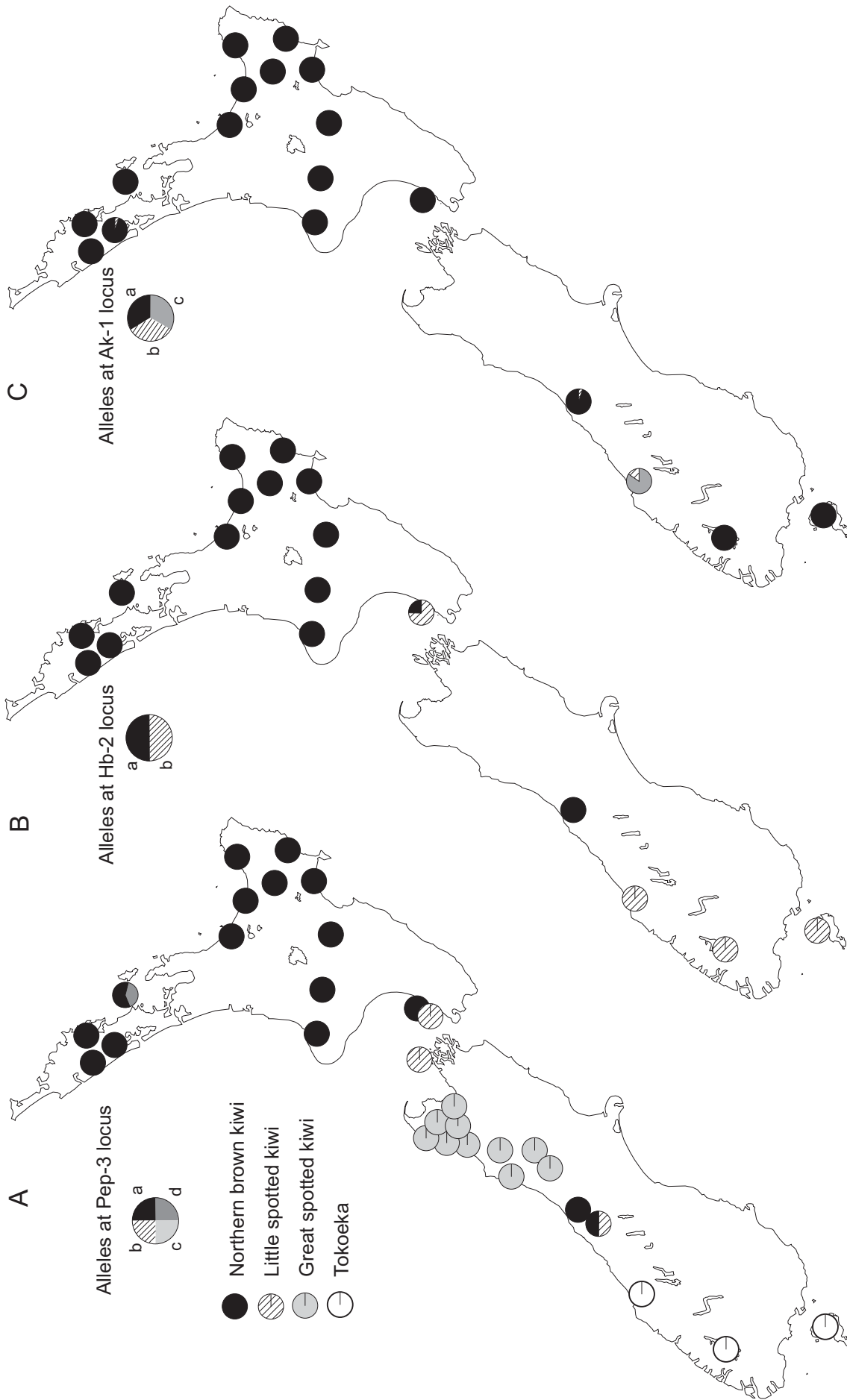


Figure 3. A. Variation at the *Pep-3* locus, discriminating northern brown kiwi, little spotted kiwi, great spotted kiwi, and tokoeka. Captive birds (Fig. 1): all captive northern brown kiwi have allele a, all captive great spotted kiwi have allele c. B. Variation at the *Hb-2* locus in brown kiwi, distinguishing northern brown kiwi from tokoeka. Note the hybrid population on Kapiti Island. All captive northern brown kiwi have allele a. C. Variation at the *Ak-1* locus in brown kiwi, distinguishing the Haast population of tokoeka from all others. All captive birds have allele a.

TABLE 1. ALLELIC DISTRIBUTION AT FIVE DIAGNOSTIC VARIABLE ALLOZYME LOCI THAT DISTINGUISH THE SPECIES OF KIWI AND THE TWO GROUPS OF TOKOEKA, AND SIGNIFICANT POPULATIONS AND HYBRIDS.

	LOCUS				
	<i>Ak-1</i>	<i>Gda-1</i>	<i>Hb-2</i>	<i>Lap-1</i>	<i>Pep-3</i>
Species (population)					
Little spotted kiwi	a ¹	a	b	b	b
Great spotted kiwi	a	a	b	b,c	c
Northern brown kiwi	a ¹	b ²	a	a	a
Tokoeka (Haast)	b,c	a,b	b	a	a
Tokoeka (Fiordland-Stewart Island)	a	b	b	a	a
Special populations/hybrids					
Little Barrier Island brown kiwi	a	b	a	a	a,d
Kapiti Island brown kiwi	a	b	a,b	a	³
Franz Josef hybrid kiwi	a	a,b	a,b	a?	a,b

¹ One or two rare heterozygotes for allele b present.

² Three heterozygotes for allele c present.

³ Could not be resolved.

which maintains its identity from other such lineages and has its own evolutionary tendencies and historical fate' (Wiley 1978). The phylogenetic species concept recognises a species as 'the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent' (Cracraft 1983). Both definitions would justify species status for tokoeka: the phylogenetic definition could be used to justify further taxonomic subdivision of tokoeka (see section 3.3.3).

Levels of differentiation among groups also support specific distinctiveness of each group. In general, birds show lower levels of allozyme divergence than other vertebrates: the mean level of Nei's *D* between congeneric pairs of bird species is approximately 0.05 (Avice et al. 1980; Baker et al. 1985). A Nei's *D* of approximately 0.06 separates the two species of brown kiwi from each other and the two species of spotted kiwi from each other. The two spotted kiwi differ from the two brown kiwi at a *D* of approximately 0.14, reflecting fixed differences at *Lap-1* and *Pep-3* and a nearly fixed difference at *Gda-1*.

Some previous taxonomies had proposed separate generic recognition for little spotted kiwi (Mathews 1931; Verheyen 1960). Allozyme data offer no support for this view, which would require that little spotted kiwi form a sister-group to all other species. Instead, the two spotted kiwi form one group, to which the brown kiwi are the sister-group (Fig. 2). The level of genetic differentiation (*D* = 0.14) is well within the range found within many congeneric species of birds (e.g. Baker & Strauch 1988).

3.3 Within-species divergence and populations of special significance

In general, levels of divergence among populations within the four species defined above were about an order of magnitude lower than that between groups (Fig. 2). For example, divergence between the two populations of little spotted kiwi

reflected only small frequency differences at two loci. However, a small number of populations of the other species exhibited distinctive patterns of allozyme variation that indicate they constitute separately evolving populations that require individual management or further research to confirm their status.

3.3.1 *Great spotted kiwi*

Allelic frequency differences at four allozyme loci (*Gp-2*, *Ldb-2*, *Lap-1*, *Pgi-1*) produced a pattern of variation that showed little correlation with geography. Some populations resembled distant populations more closely than they did geographically proximate populations. Values of *D* varied from 0 to 0.04. This level of divergence and the absence of geographic patterning could indicate that great spotted kiwi populations have limited gene flow with genetic drift as a primary evolutionary force.

Sample sizes for this taxon were too small to make firm conclusions. In the extreme case, the species may contain further taxonomic diversity that could be recognised by higher resolution studies with larger sample sizes. The population from Kahurangi Point differed notably from others due to a high frequency (0.5) of the unique allele *Ldb-1(d)*.

3.3.2 *Northern brown kiwi*

North Island populations of brown kiwi were quite uniform genetically. Of the three populations that appear distinct on the dendrogram (Fig. 2), that from Raetihi is only a single captive individual heterozygous for allele b at *Ldb-2*. Its significance could only be determined by further samples from that site.

The two other divergent populations are represented by larger sample sizes. The Little Barrier Island population (sample size, $N = 7$) has the only other heterozygote found for *Ldb-2(b)*. More significantly, this population is distinguished most strongly by the high frequency (0.43) of *Pep-3(d)*, an allele found only in Little Barrier kiwi. Remarkably, no heterozygotes were found at this locus: rather, only alternate homozygous types were found. This result could reflect: (a) technical difficulties in establishing genotypes at this locus; (b) sampling error; or (c) the existence of cryptic species of brown kiwi on this island. The latter possibility seems very remote, but cannot be excluded without further research.

The most significant northern brown kiwi population is that from Okarito ($N = 10$). It is clearly differentiated from other northern populations by a high frequency (0.6) of *Ldb-2(c)*, an allele found only in low frequency at Waitangi (0.06) and moderate frequency (0.16) at Tangiteroria. This is the only South Island population of the northern type, isolated by several hundred kilometres from the nearest conspecific population. The genetic distinctiveness and geographic isolation of this population fully support the protection accorded this population as the result of the work of C. Roderick and B.E. Reid (Peat 1990, New Zealand Wildlife Service File 25/4/21), and argue strongly for its continued high conservation priority.

3.3.3 *Tokoeka*

The Stewart Island population ($N = 35$) of tokoeka possesses rare alleles, at four loci (*Ak-2*, *Gp-2*, *Pep-2*, *6pg-1*), that are not found in the Fiordland sample ($N = 5$): otherwise, they show no differences in allozyme frequencies. This suggests that Foveaux Strait has posed little obstacle to gene exchange in recent

evolutionary time even for a flightless bird, a view supported by very limited allozyme divergence found also in kakapo with a similar distribution (Triggs et al. 1989).

The Haast tokoeka population ($N = 3$) shows marked genetic divergence associated with its geographic isolation. This results from a high-level frequency difference at *Gda-1* and a fixed difference at *Ak-1* (Table 1, Fig. 3C). The level of genetic difference ($D = 0.04$) between Haast versus other tokoeka populations approaches the average ($D = 0.05$) for congeneric populations of birds (Avice et al. 1980; Baker et al. 1985). In fact, Haast tokoeka meet the phylogenetic species criteria of Cracraft (1983): 'the smallest diagnosable cluster ...' A decision on their species status requires further evidence, but a high conservation priority based on genetic distinctiveness and geographic isolation is clearly warranted.

3.4 Origin of island populations

At least three populations of kiwi on islands are believed to have originated from transfers from mainland populations in European times: brown kiwi on Little Barrier Island, and brown kiwi and little spotted kiwi on Kapiti Island (Peat 1990).

3.4.1 *Kapiti Island little spotted kiwi*

Genetic data reveal little new information for Kapiti Island little spotted kiwi: they closely resemble the D'Urville Island birds. Allozyme data are consistent with a South Island origin, but cannot exclude a North Island origin or confirm that the birds are indigenous rather than introduced.¹

3.4.2 *Kapiti Island brown kiwi*

Allozyme data are more informative in the case of the Kapiti Island brown kiwi. These possess both alleles a and b at the diagnostic *Hb-2* locus. The a allele is found only in northern brown kiwi: the data cannot determine whether the northern brown kiwi ancestors were resident on Kapiti Island or were introduced from the mainland. The *Hb-2*(b) allele could only have come from hybridisation with either a tokoeka or, less likely, a little spotted kiwi. Hybridisation with a little spotted kiwi might be detected if the Kapiti Island brown kiwi possessed the diagnostic *Pep-3*(b) allele, but we could not resolve the genotype at that locus.

Two other loci offer further information. Kapiti Island brown kiwi are fixed for *Ak-1*(a), an allele found in northern brown kiwi and southern tokoeka, but not Haast tokoeka. This would seem to exclude the birds from having a Haast ancestry. Kapiti Island brown kiwi also are fixed for *Gda-1*(b), found in all brown kiwi populations.

The present data on *Hb-2* confirm that the Kapiti Island brown kiwi population has both southern tokoeka and northern brown kiwi ancestry. Further studies may be able to resolve the parentage of the Kapiti Island brown kiwi population more precisely.

¹ Jolly and Daugherty (this volume) suggest that the absence of archival evidence for the introduction of little spotted kiwi supports a natural origin for this species on Kapiti Island.

3.4.3 *Little Barrier Island brown kiwi*

This population possesses a unique allele, *Pep-3(d)*, in high frequency (0.43) and only in the homozygous condition (section 3.3.2). If this allele has been introduced to the island, its source mainland population is not represented among our sample sites. It is possible that this allele achieved high frequency via genetic drift in its isolated site. It is also possible that *Pep-3(d)* was the only allele at this locus in the island populations when birds from mainland populations were introduced, giving rise to present intermediate frequencies. The failure to find heterozygotes at this locus may be entirely due to technical difficulties in determining genotype at this locus, but the possibility of it reflecting reproductive isolation among two types on Little Barrier Island strongly supports further research on these birds.

3.5 Hybridisation

The primary criterion of the biological species concept (Mayr 1969) is reproductive isolation. Nonetheless, many pairs of congeneric species, including bird species, are fully interfertile (Mayr 1963), although hybridisation occurs only rarely due to behavioural isolating mechanisms. Such occasional hybridisation is often due to human-related factors such as habitat alteration or captivity, and is usually considered not to challenge seriously the separate specific recognition of the two species.

Shared rare alleles can provide circumstantial evidence of hybridisation. For example, one Kapiti Island little spotted kiwi was heterozygous for the allele *Ak-1(b)*, which is otherwise known only from brown kiwi from Tangiteroria, Okarito and Haast. The Kapiti Island heterozygote could thus reflect an ancient hybridisation of a little spotted kiwi with a Kapiti Island brown kiwi, which themselves are hybrids (sections 3.4.2 and 3.5.1). While other hypotheses could explain this event, allozyme data confirm at least two instances of hybridisation between kiwi species.

3.5.1 *Kapiti Island brown kiwi*

Kapiti Island brown kiwi are most likely the result of hybridisation of northern brown kiwi and southern tokoeka ancestral types (section 3.4.2). No management implications arise from this finding: healthy populations of both parental types exist, and no obvious gain would arise from any management action affecting this population. However, Kapiti Island brown kiwi should not be used as a source population for transfers to a new location.

3.5.2 *Franz Josef kiwi*

A single bird caught near Franz Josef township and identified morphologically as a small great spotted kiwi proved to be heterozygous at four loci (*Gda-1*, *Hb-2*, *Pep-3*, *Pgi-1*). At all four loci, one of the alleles proved to be of a type found in northern brown kiwi: alleles at the diagnostic loci *Hb-2* and *Pep-3* confirmed that one of the parents of this bird was a brown kiwi of a genetic type similar to the nearby Okarito population. DNA analyses also identified a mitochondrial type similar to that at Okarito, indicating that the mother had been a brown kiwi (A.J. Baker, pers. comm.). The other allele at each locus was a type found only in spotted kiwi: at *Pep-3*, the bird was heterozygous for the diagnostic allele b, indicating that one parent had been a little spotted rather than a great spotted kiwi.

This finding has several significant consequences. First, genetic data identified a parentage entirely unexpected by morphological appearance. Had the bird been a great spotted kiwi, and thus the sole known survivor of that species in South Westland (Jolly 1992), one management option was to move it to the nearest extant population. Such an action would have been entirely inappropriate, and was not undertaken when the true identity was established.

Second, hybridisation is confirmed to occur even among the most divergent types of kiwi under at least some conditions in nature. However, it may result from the greatly depleted state of little spotted kiwi in the region. One of the last little spotted kiwi known to occur on mainland South Island was seen at Okarito in 1938.

Rothschild (1893, 1899) described the West Coast little spotted kiwi, which he named *A. occidentalis*. He described it as larger in size than *A. owenii*, with more regular, wide pale bars, and more developed feathers with a lighter tip. Buller (1905) noted that the plumage of a West Coast spotted kiwi which he called *A. occidentalis* was similar 'to *A. baastii* [sic], but paler'. He also noted that this bird had dark coloured legs, in which respect it agreed with the colouration of *A. baastii*. It is not surprising, therefore, that the Franz Josef bird was originally identified as a great spotted kiwi.

The occurrence of this hybrid in the same region where *A. occidentalis* was originally described suggests several hypotheses. First, *A. occidentalis* may be a name applied to a recurring interspecific hybrid at sites where brown and little spotted kiwi occur in sympatry: in other words, *A. occidentalis* was never a distinct species. Second, *A. occidentalis* may have been a distinct species that is now extinct, but whose genes have survived in the bird we analysed via hybridisation. Third, *A. occidentalis* may have been a distinct species but has no relationship to the bird we analysed and is now extinct.

If the parent of this hybrid bird was a little spotted kiwi, it would represent one of the most recent instances of that species surviving on the mainland.

4. DISCUSSION

The primary working goal of this research was to test existing taxonomies of kiwi, but the larger issue was providing information to assist their management. As Avise (1989) eloquently observed, taxonomies are not irrelevant abstractions but the essential foundations of conservation practice. Taxonomy may be destiny for endangered plants and animals (May 1990). The first criterion for ranking for protection by the New Zealand Department of Conservation is 'taxonomic distinctiveness' (Molloy & Davis 1992).

Historically, conservation activities were directed at the species level, but more recent authors have argued that populations and metapopulations—conspecific groups of interacting populations—are the proper focus for conservation (IUCN, UNEP & WWF 1980; Avise 1989; Crozier 1992). A focus on the species level may fail to protect the full range of diversity because (a) different species concepts can produce differing formal taxonomies, and (b) most species exhibit geographic genetic variation, sometimes considerable in extent, over their entire range (Rojas 1992). A preferable method for dealing with these

problems is to use genetic data to identify key populations or groups of populations that, collectively, conserve the full range of variation within taxa (Avice 1989; Crozier 1992). This view has been acknowledged in the 1992 Convention on Biological Diversity (UNEP 1992) and is accepted in our management recommendations below.

Within New Zealand, genetic data have revealed significant cryptic diversity, particularly among terrestrial reptiles (Daugherty et al. 1990a, 1990b, 1993; Patterson & Daugherty 1990). Subsequent taxonomic revisions have provided a firmer foundation for management, but the pattern of geographic variation should serve as the primary criterion for determining conservation priorities (Daugherty et al. 1990).

Genetic data have been used to assess geographic variation of an array of New Zealand birds (Triggs & Daugherty 1990; Baker 1991; Daugherty & Triggs 1991). Patterns of allozyme variation have challenged the taxonomic classification of Blue Penguins, *Eudyptula minor* (Meredith & Sin 1988; Turbott 1990), for example, but unexpected diversity has been found less commonly than in reptiles (e.g. Triggs et al. 1989; Herbert et al. 1993).

Allozyme variation in kiwi reveals an uncommon pattern for birds, in that congeneric species are well differentiated genetically, as are some local populations. In many ways, the outcome of the study presented here markedly resembles that of a similar survey of genetic variation in tuatara, *Sphenodon* sp. (Daugherty et al. 1990), in that:

- Both kiwi and tuatara represent ancient New Zealand lineages of the highest international conservation significance.
- The pattern of genetic variation supports a taxonomy for each genus that had been described by an earlier author, but was rejected without adequate, comprehensive studies of geographic variation using contemporary methodologies.
- In each case, recent taxonomies underestimated the number of species within the genus and thus the number of high priority management units.

Allozyme data for kiwi, in identifying four species, agree most closely with the taxonomy of Oliver (1930). Our findings differ from that taxonomy in showing that the northern brown kiwi, *A. mantelli*, extends as far south as Okarito on the West Coast of the South Island. Our findings differ from all previous taxonomies in identifying the Haast tokoeka as significantly divergent from other populations of tokoeka, *A. australis*, possibly warranting recognition as a distinct fifth species.

The reservations of Serventy (1950) regarding the taxonomic methods and views of Mathews seem prescient in light of genetic data. Mathews apparently worked entirely from surveys of the historical taxonomic literature, rather than from collection and assessment of new data. Serventy (1950) said of Mathews that 'he gave every indication that he felt the name to be more important than the bird'. Mathews' (1931) taxonomy of kiwi followed that of Oliver (1930) by only a year, but it resulted in systematic misunderstanding of kiwi variation for over 60 years. In turn, it provided an inadequate foundation for kiwi conservation.

5 . S U M M A R Y

1. Extant populations of kiwi comprise at least four species:
 - Little spotted kiwi, *A. owenii*
 - Great spotted kiwi, *A. baastii*
 - Northern brown kiwi, *A. mantelli*, including the population at Okarito
 - Tokoeka, or southern brown kiwi, *A. australis*.

This taxonomy agrees most closely with that of Oliver (1930).

2. The northernmost population of tokoeka at Haast is highly genetically distinct. By some species criteria, it would warrant recognition as a fifth species. In contrast, tokoeka from Fiordland and Stewart Island show high levels of genetic similarity.
3. The geographically disjunct northern brown kiwi population at Okarito is genetically distinctive.
4. The northern brown kiwi population on Little Barrier Island is genetically distinct. The pattern of variation may indicate unresolved cryptic variation.
5. Populations of great spotted kiwi show moderate levels of genetic divergence with no apparent geographic pattern. This is likely to be the result of genetic drift operating on geographically isolated populations. The possibility of unresolved taxonomic differentiation cannot be excluded.
6. The two populations of little spotted kiwi (on Kapiti and D'Urville Islands) are genetically very similar.
7. Kapiti Island brown kiwi have a hybrid origin, with both northern brown and tokoeka ancestry. The tokoeka stock were probably from Fiordland rather than Haast.
8. A single bird from Franz Josef township, which was identified morphologically as a great spotted kiwi, instead has a hybrid origin. One parent is a northern brown kiwi of the nearby Okarito type. The other parent is probably a little spotted kiwi. Alternatively, we cannot exclude the possibility that the other parent was a type representing *A. occidentalis*, or that *A. occidentalis* was a name given to recurring hybrids between brown kiwi and little spotted kiwi.

6 . R E C O M M E N D A T I O N S

1. The following populations and metapopulations, identified on the basis of their genetic distinctiveness and geographical isolation, should be used as the fundamental management units of kiwi:
 - Little spotted kiwi: The D'Urville population represents an important second location, but it is not significantly genetically distinct.
 - Great spotted kiwi: Present genetic knowledge is insufficient to subdivide management units of this group further, but apparent levels of variation warrant further study.
 - Northern brown kiwi, North Island: Mainland populations exhibit little differentiation in allozymes, but the possibility of significant divergence cannot be excluded without higher resolution studies using DNA or further

allozyme studies with larger sample sizes. Each of the major geographically disjunct populations in the North Island (i.e. Urewera, Taranaki, Northland, Coromandel Peninsula, Western Bay of Plenty) deserves separate management.

- Northern brown kiwi, Little Barrier Island: Further investigation of genetic structuring within this population is warranted.
 - Okarito northern brown kiwi: The surprising discovery that this population is the most southerly in its species, and its genetic distinctiveness, strongly support continuation of the high conservation priority it has been accorded.
 - Haast tokoeka: This is the most genetically distinctive population of all kiwi species. Its rarity and geographic isolation warrant a high priority comparable with that of the Okarito population.
 - Southern tokoeka: The two major geographic groups of this type, in Fiordland and on Stewart Island, warrant separate management.
2. Management priority among the populations and metapopulations defined in 1 above should be based on ecological factors such as rarity and threats to survival. Some of these populations (e.g. Haast tokoeka) may warrant listing in 'category A' (highest priority threatened species) of Molloy & Davis (1992), because of their taxonomic distinctiveness and rarity.²
 3. Translocations should not occur between the fundamental management units. For example, kiwi should not be transferred from the mainland to Little Barrier Island or vice versa. Additionally, kiwi should not be transferred between Fiordland and Stewart Island, or between the geographic regions of the North Island.
 4. The Kapiti Island hybrid brown kiwi population should not be used as the source population for any future transfer.
 5. Further research is warranted to confirm or determine the taxonomic status of the following:
 - Relationships among great spotted kiwi populations
 - Little Barrier Island brown kiwi
 - Haast tokoeka.

More fine-grained genetic studies of all populations offer the opportunity for discovery of further genetic/taxonomic structuring. Such structuring is likely in at least some instances where populations have not been examined in detail. Opportunities for such studies should be exploited where possible.

6. Future evidence of spotted or unusual kiwi in the Franz Josef area, or in other regions not known to have kiwi, should be promptly investigated. Genetic or other analyses of such birds could lead to discovery of little spotted kiwi on the South Island, or even confirmation of the existence of *A. occidentalis*.

² The Haast tokoeka, North Island brown kiwi and the Okarito brown kiwi were all listed as Category A in the second edition of the Department of Conservation's *Setting priorities for the conservation of New Zealand's threatened plants and animals* (Molloy & Davis 1994).

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APPENDIX 1. HISTORY OF KIWI TAXONOMY

A1.1 Brown kiwi

The first kiwi specimen brought to the attention of European scientists was a brown kiwi from Dusky Sound, named *Apteryx australis* by Shaw and Nodder (1813). Bartlett (1850) concluded that *A. australis* consisted of two distinct species, a northern type that he called *A. mantelli*, and a southern one that kept the name *A. australis*. The specific distinctiveness of *A. mantelli*, however, was much debated. Buller (1868) initially accepted Bartlett's views, noting that *A. australis* was restricted to the extreme south of the South Island. Subsequently, he contended that *A. mantelli* and *A. australis* were conspecific (Buller 1870), and he then reverted to acceptance of *A. mantelli* as the North Island species (Buller 1873, 1882).

Buller disagreed with most of the diagnostic characters used by Bartlett (1850), but he accepted that the feathers of each species had a difference in texture that he considered to be a constant specific character. Others considered such differences to be of insufficient importance to differentiate species (e.g. Finsch, in Buller 1876). Rothschild (1899) considered *A. mantelli* to be a subspecies of *A. australis* because, in his view, the differences between the two were slight. Bartlett (1900), however, maintained that *A. mantelli* was a separate species.

Potts (1872) proposed two further species: *A. mollis*, a type showing a high frequency of albinism, and *A. fusca*, a form that he described as 'altogether like the kiwi, only darker'. Newton and Gadow (1896) noted that *A. mollis* and *A. fusca* were not proven species.

Yet more species of brown kiwi were to be identified. Sharpe (1888) recognised a North Island type of brown kiwi, but concluded that *A. mantelli* was a 'pure synonym' for *A. australis*. He proposed that the North Island brown kiwi be named *A. bulleri*. Buller (1888, 1891) immediately accepted this view, noting Finsch's remark that '... all characters given by [Bartlett] are without value ... The North Island bird, if it is in reality a distinct species, must have a new name' (Buller 1888). Other workers (Brandon 1890; Rothschild 1899) criticised this name change and it was generally not accepted. Buller (1896) concluded that there was 'no doubt' of the existence of two species of North Island brown kiwi. He assigned the name *A. bulleri* to a series of blackish kiwi from the east coast of the North Island and retained the name *A. mantelli* for the rest (Buller 1896, 1905).

Buller (1891) assigned the name *A. maxima* to some large kiwi collected from Stewart Island. Rothschild (1893) believed that *A. maxima* was 'only an overgrown *A. baasti*' [sic], and therefore renamed the kiwi from Stewart Island as *A. lawryi*. Rothschild (1899) was unable to find consistent differences between *A. lawryi* and *A. australis* and synonymised the Stewart Island kiwi with *A. australis*. Buller (1905) concluded that Rothschild's synonymy was incorrect, perhaps due to faulty labelling by the collectors of some of his series, and reinstated *A. lawryi*.

A1.2 Grey kiwi

Gould (1847) described and named the little spotted kiwi, *A. owenii*. Potts (1871) described *A. baastii*, the great spotted kiwi. Rothschild (1893) recognised a third spotted kiwi species, *A. occidentalis*, which he described as larger and more distinct in its markings than *A. owenii*. Rothschild (1899) considered *A. occidentalis* to be a subspecies of *A. owenii*, as did Oliver (1930). Hutton and Drummond (1904) listed *A. occidentalis* as ‘a doubtful species’.

A1.3 Modern views

At least ten species of kiwi had been described by the end of the nineteenth century (Table A1), but most authors in the twentieth century have accepted only three or four. Modern avian taxonomy in New Zealand dates from the work of Oliver (1930), who listed four species: *A. mantelli* (North Island kiwi), *A. australis* (South and Stewart Island kiwi), *A. baastii* (large grey kiwi) and *A. owenii* (little grey kiwi). Oliver’s (1930) criteria for acceptance of two forms as separate species were that they ‘differ from one another distinctly in characters that do not overlap, and breed separately’.

Mathews (1931) reduced this list to only three species. He placed all brown kiwi in a single species with three subspecies: *A. australis australis* from the South Island; *A. a. mantelli* from the North Island; and *A. a. lawryi* from Stewart Island. He retained *A. baastii*, but assigned the little spotted kiwi to a new genus, *Stictapteryx*. He split *Stictapteryx* into two subspecies, *S. owenii owenii* and *S. owenii occidentalis*, and later added a third subspecies, *S. owenii iredalei*, from the North Island (Mathews 1935).

Most recent listings have followed Mathews (1931): for example, Fleming (1953), Oliver (1955), Kinsky (1970), Reid and Williams (1975), Reid (1985), Peat (1990) and Turbott (1990). Most authors, however, place all species in the genus *Apteryx*, omitting *Stictapteryx*, and place all subspecies of the little spotted kiwi in the single species *A. owenii*. Verheyen (1960) argued that the little spotted kiwi was sufficiently distinct to be placed in its own genus, which he designated *Kiwi*, but other workers have not followed this view.

The role of Mathews is not without controversy. Serventy (1950) argued that ‘Mathewsian’ taxonomy, which comprehensively addressed the entire Australasian avifauna, should be treated with caution. In particular, Mathews pioneered the use of trinomial nomenclature in Australasia, elevating many local races to subspecific status. Serventy (1950) claimed, although not with particular reference to kiwi, that Mathews was ‘over-zealous in manufacturing trinomials’, and that ‘many of Mathews’ races were described in a most uncritical way and were of no validity’.

Information from other sources has raised doubts about the taxonomic status of kiwi. Studies of host-specific Mallophaga feather lice (Clay 1972; Tandan 1972; Palma et al. 1989) and DNA-DNA hybridisation

TABLE A1. SPECIES OF KIWI DESCRIBED IN THE NINETEENTH CENTURY.

SPECIES	SOURCE
<i>Apteryx australis</i>	Shaw and Nodder 1813
<i>Apteryx owenii</i>	Gould 1847
<i>Apteryx mantelli</i>	Bartlett 1850
<i>Apteryx baastii</i>	Potts 1871
<i>Apteryx mollis</i>	Potts 1872
<i>Apteryx fusca</i>	Potts 1872
<i>Apteryx bulleri</i>	Sharpe 1888
<i>Apteryx maxima</i>	Buller 1891
<i>Apteryx lawryi</i>	Rothschild 1893
<i>Apteryx occidentalis</i>	Rothschild 1893

analysis (Sibley & Ahlquist, cited in Diamond 1983) have shown patterns of variation inconsistent with accepted taxonomies, especially for brown kiwi. Some local populations also appeared to be morphologically distinctive. In the late 1970s, New Zealand Wildlife Service personnel C. Roderick and B.E. Reid believed the Okarito brown kiwi to be sufficiently different from other populations that they recommended logging not proceed in the area, in order to save the very small population existing there (Peat 1990, New Zealand Wildlife Service File 25/4/21).

APPENDIX 2. POPULATION SITES, SPECIES ASSIGNMENT
 BASED ON ALLOZYME ANALYSIS, SAMPLE
 SIZE, AND INDIVIDUALS WHO COLLECTED
 SAMPLES INCLUDED IN THIS STUDY

LOCATION	TAXON	NUMBER	COLLECTOR
Arawhata R., Haast Range	<i>A. australis</i>	3	R. Colbourne
Auckland Zoo	<i>A. mantelli</i>	5	B. Reid, D. Folwell, M. Sibley
Barrytown	<i>A. baastii</i>	1	B. and L. Alexander, L. Williams, R. Simpson
Deception R.	<i>A. baastii</i>	2	J. McLennan
D'Urville Island	<i>A. owenii</i>	2	R. Colbourne, J. Jolly, S. Triggs
Fiordland (Deep Cove)	<i>A. australis</i>	4	R. Colbourne
Fiordland (Takahe Valley)	<i>A. australis</i>	1	S. Triggs, B. Lloyd, B. Reid, T. Reid, A. Tollan
Franz Josef	Hybrid: <i>A. owenii?</i> × <i>A. mantelli</i>	1	R. Colbourne
Gisborne	<i>A. mantelli</i>	1	B. Reid, A. Billing
Gunner Downs, Karamea	<i>A. baastii</i>	1	J. McLennan
Haupoto	<i>A. mantelli</i>	1	B. Reid, A. Billing
Kahurangi Point	<i>A. baastii</i>	4	J. McLennan
Kapiti Island	Hybrid: <i>A. mantelli</i> × <i>A. australis</i>	2	R. Colbourne
Kapiti Island	<i>A. owenii</i>	31	B. Reid, M. Finglan, R. Colbourne, J. Jolly
Kaweka	<i>A. mantelli</i>	1	J. McLennan
Kohaihai R, Karamea	<i>A. baastii</i>	3	J. McLennan
Little Barrier Island	<i>A. mantelli</i>	8	J. Hay, S. Keall
Maungataniwha	<i>A. mantelli</i>	1	B. Reid, A. Billing
Mount Bruce	<i>A. mantelli</i>	2	B. Reid, C. Daugherty
	<i>A. baastii</i>	3	
New Plymouth	<i>A. mantelli</i>	5	S. Triggs, S. Walker, B. Reid, M. Bell, I. Bryant, B. Williams, C. Thorn, C. Daugherty
Ngaroto	<i>A. mantelli</i>	2	B. Reid, A. Billing
NW Nelson (Boulder Lake)	<i>A. baastii</i>	1	J. McLennan
NW Nelson (Heaphy Track)	<i>A. baastii</i>	8	J. McLennan
Okarito	<i>A. mantelli</i>	10	B. and L. Alexander, L. Williams, R. Simpson, R. Colbourne
Oparara River, Karamea	<i>A. baastii</i>	1	J. McLennan
Otorohanga (National Kiwi Centre)	<i>A. baastii</i>	3	B. Reid, P. Walker, I. Bryant, M. Thompson, C. Daugherty
Paparua Range, Ohikanui River	<i>A. baastii</i>	3	J. McLennan
Raetihi	<i>A. mantelli</i>	1	B. Reid, A. Billing
Stewart Island	<i>A. australis</i>	38	R. Colbourne, S. Triggs, B. Lloyd, S. Triggs, B. Reid, T. Reid, P. Garland, I. Adams, A. Richardson

LOCATION	TAXON	NUMBER	COLLECTOR
Tangiteroria	<i>A. mantelli</i>	31	M. Potter
Taramakau R.	<i>A. baastii</i>	6	J. McLennan
Te Puke	<i>A. mantelli</i>	1	B. Reid, A Billing
Te Urewera National Park	<i>A. mantelli</i>	3	J. McLennan, C. Daugherty, R. Colbourne
Ugly River, Karamea	<i>A. baastii</i>	5	J. McLennan
Waipoua	<i>A. mantelli</i>	7	R. Colbourne
Wairoa	<i>A. mantelli</i>	3	S. Triggs, S. Walker, B. Reid, M. Bell, I. Bryant, C. Daugherty, B. Reid
Waitangi	<i>A. mantelli</i>	36	R. Colbourne, C. Thorn, P. Thorn, G. Rasch, J. McLennan, M. Taborsky
Wellington Zoo	<i>A. mantelli</i>	7	P. Watson, B. Reid, S. Walker, B. Hansen, R. Goodswaard, C. Daugherty, S. Triggs, B. Reid, T. Reid, C. Thorn, P. Garland, I. Adams, A. Richardson
Whakatane	<i>A. mantelli</i>	3	B. Reid, A. Billing, C. Daugherty