

Genetic differentiation, taxonomy and conservation of Australasian teals *Anas* spp.

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Summary

Australasian teal consist of five taxa (*Anas gracilis*, *A. castanea*, *A. chlorotis*, *A. aucklandica* and *A. nesiotis*) whose taxonomic identities and relationships have been uncertain. Analysis of variation at 14 allozyme loci indicates limited but clear divergence of New Zealand taxa (*A. chlorotis*, *A. aucklandica*, *A. nesiotis*), in agreement with previous studies of morphological variation. The New Zealand taxa are “terminal and evolutionarily independent units” that clearly meet the criteria for specific recognition in line with the phylogenetic species concept (PSC). Because each is also geographically restricted and has small world population size, specific recognition supports increased conservation status for each. The three New Zealand species do not form a sister group with *A. castanea*, as previously hypothesized; instead, *A. castanea* and *A. gracilis* are sister taxa.

Introduction

The Australasian region is the native range of five small teals *Anas* spp (Figure 1). The most widespread is the grey-plumaged Grey Teal *A. gracilis* which presently breeds throughout continental Australia, Tasmania and New Zealand and is a regular vagrant to Indonesia, New Guinea, New Caledonia, Lord Howe Island and Macquarie Island (Marchant and Higgins 1990). Grey Teal are absent from late Quaternary fossil deposits in New Zealand indicating its colonization of New Zealand's two main islands is a most recent event (T.H.Worthy pers. comm. 1997). The other four teal are all brown-plumaged, show moderate levels of morphological differentiation (Livezey 1990, Williams *et al.* 1991, Williams and Robertson 1996), and have ranges that do not overlap. The Chestnut Teal *A. castanea* occurs in the Australian south-east and south-west and on Tasmania (Marchant and Higgins 1990), where it is sympatric with Grey Teal. New Zealand's Brown Teal *A. aucklandica chlorotis* (taxonomy of Turbott 1990) is now rare but formerly occurred throughout the three main islands of the archipelago, on some small nearshore islands and on Chatham Island 700 km to the east (Turbott 1990). Two small island groups in the New Zealand subantarctic—Auckland Islands and Campbell Island—each have morphologically distinctive endemic flightless teals presently recognized as *A. a. aucklandica* and *A. a. nesiotis*, respectively (Kinsky 1970, Turbott 1990).

The first thorough taxonomic review of these teals, by Delacour and Mayr (1945), has served as the basis for most subsequent treatises (e.g., Delacour 1956, Johnsgard 1978, Madge and Burn 1988). Delacour and Mayr (1945) recognized Grey Teal and Chestnut Teal as separate species, overturning Ripley's (1942)

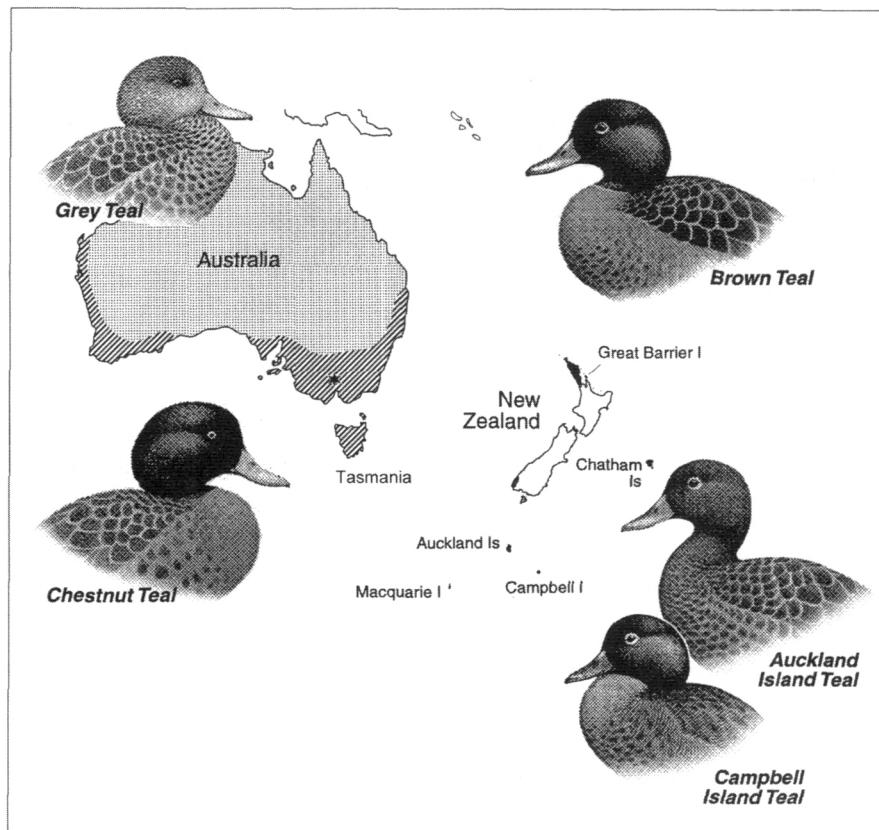


Figure 1. Distribution of Australasian teals and the localities from which samples for this study were obtained. Illustration based on Marchant and Higgins (1990).

view that they were only subspecifically divergent. They also recognized the three New Zealand forms as being island races of a single species and distinct from those in Australia. Delacour and Mayr (1945) and Condon (1975) considered Grey Teal comprised a single species *A. gibberifrons* with three distinctive geographical races: *gracilis* in Australia, *gibberifrons* in Indonesia and *albogularis* in Andaman Islands. More recent taxonomies have elevated all to full species (Marchant and Higgins 1990, Christidis and Boles 1994, Todd 1996). No taxonomic subdivision of Chestnut Teal has been advanced despite the apparent segregation of the two Australian mainland populations (Marchant and Higgins 1990).

In recent decades, taxonomy of the New Zealand teals has been labile (Dumbell 1986) but views have often been based more upon assertion than careful character analysis and new data. Falla (1953) asserted that “[*A.*] *chlorotis* is unquestionably a smaller, shorter-winged, more obscurely patterned derivative of *Anas castanea*”. Fleming (1953) accepted this view, making New Zealand teals synonymous with the Chestnut Teal, thus combining all the brown-plumaged teal at the species level. However, subsequent workers (Kinsky 1970, Madge and

Burn 1988, Turbott 1990) reverted to Delacour and Mayr's arrangement, ignoring the hypotheses of Falla (in Delacour 1956) and Westerskov (1960) that Campbell Island Teal are little more than recent wind-blown stragglers from the Auckland Islands. More recently, Marchant and Higgins (1990) have recognized each of the three New Zealand forms as full species, a decision which has received *post hoc* support from Livezey's (1990) morphological comparisons and also followed by Todd (1996).

In this study, we contribute to the taxonomic debate by examining allozyme variation in the five Australasian teals with reference to contemporary avian species concepts (McKittrick and Zink 1988, Zink and McKittrick 1995). In particular, we investigate whether any of these taxa deserve species recognition under the phylogenetic species concept (PSC, *sensu* Cracraft 1983). We then comment upon the conservation significance of our findings.

The evolutionary relationships of the brown-plumaged Australasian teals have also been the subject of conjecture. While an Australian source for the three New Zealand forms is unchallenged (e.g., Falla 1953, Livezey 1990), there are two competing hypotheses concerning their biogeographical history:

Hypothesis 1 The New Zealand taxa are derived from a single trans-Tasman colonization. In the *stepping stone* version (*hypothesis 1a*), implied by Oliver (1955) but proposed by Fleming (1982), who emphasized the rapid loss of flight relative to plumage change, the Auckland Islands were colonized from the New Zealand mainland, and Campbell Island subsequently colonized from Auckland Islands. In contrast, the *parallel colonization* model (*hypothesis 1b*) claims that the Auckland and Campbell Islands represent independent colonizations from a New Zealand source (Turbott 1968). This hypothesis is consistent with Livezey's (1990) view that "it is most probable that both populations arose from colonizations by dispersing birds from northern source populations". Under this model, the independent loss of flight on the two island archipelagos represents evolutionary parallelism in response to common subantarctic island ecological (selective) influences (Williams *et al.* 1991).

Hypothesis 2 The New Zealand forms are derived from three *separate colonization* events each from an Australian source. This hypothesis was presented by Williams *et al.* (1991) when reporting an initial interpretation of the results of this study. This hypothesis predicts a closer genealogical relationship between Chestnut Teal and each of the New Zealand forms than among the New Zealand birds.

In this study we examine the pattern and extent of allozyme variation amongst the five teals to discriminate between these competing hypotheses.

Materials and methods

Collections and morphological identification

Blood samples were taken from the brachial vein of each of 79 individuals representing the five Australasian teals and from two Blue Ducks *Hymenolaimus malacorhynchos* as an outgroup (Table 1, Figure 1). The largest sample included 58 Brown Teal from three sites on Great Barrier Island; allozyme analysis showed that they were not genetically differentiable, and they were subsequently treated

Table 1. Species, localities of origin, and numbers of individuals used in this study

Species	Common Name	Locality	Number of Individuals
<i>Anas chlorotis</i>	Brown Teal	Awana, Great Barrier Island	23
		Saltwater, Great Barrier Island	14
		Whangapoua, Great Barrier Island	21
Total <i>Anas chlorotis</i>	Brown Teal	Great Barrier Island, NZ	58
<i>Anas aucklandica</i>	Auckland Island Teal	Ewing Island, Auckland Islands	7
<i>Anas nesiotis</i>	Campbell Island Teal	Dent Island near Campbell Island	3
<i>Anas gracilis</i>	Grey Teal	Victoria, Australia	3
<i>Anas castanea</i>	Chestnut Teal	Victoria, Australia	5
<i>Anas castanea</i>	Chestnut Teal	Held in captivity in New Zealand **	3
<i>Hymenolaimus malacorhynchos</i>	Blue Duck	Manganuateao River, North Island, NZ.	2

* Australian source of the captive stock thought to be southern New South Wales in 1965.

as a single population. While sample sizes of other taxa were small (2–7), large numbers of individuals are usually not necessary for species identification using allozyme data as most species show fixed rather than frequency differences at some loci (Sarich 1977, Gorman and Renzi 1979).

Blood samples were placed on ice immediately and centrifuged within several hours. Separated fractions (erythrocytes and plasma) were stored in liquid nitrogen in the field and then transferred to a freezer at –80°C for long-term storage.

Electrophoretic techniques

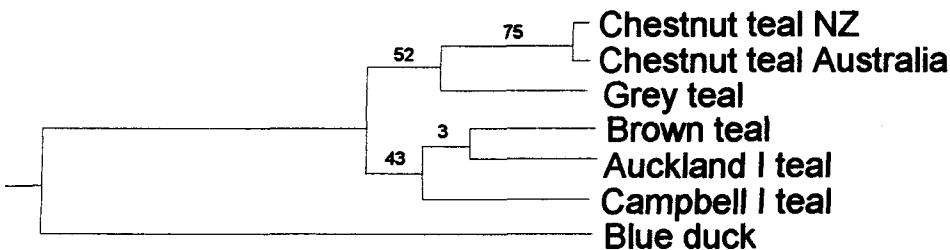
Tissues were subjected to starch gel electrophoresis according to the techniques of Allendorf *et al.* (1977). Erythrocytes were mixed with an equal volume of distilled water prior to electrophoresis, while plasma was used at full strength. A sample of the supernatant was transferred by a filter paper wick to a 12.5% horizontal starch gel (Sigma starch, catalogue no. S-4501). Direct current was applied to the gel for 3–4 hours.

All combinations of four gel/electrode buffer systems and 24 different protein (mainly enzyme) stains were examined for electrophoretic activity and resolution. Enzymes from different individuals that showed similar mobility were assumed to be encoded by the same Mendelian allele, whereas those showing different mobilities were assumed to represent different alleles. As not all amino acid substitutions alter the charge and therefore mobility of the resulting protein, allozyme analysis is generally recognized to be conservative, detecting no more than perhaps 30% of genetic variation at any structural locus (Lewontin 1974, King and Wilson 1975). Thus, estimates of genetic (allozyme) divergence are assumed to be substantial underestimates.

Allozyme nomenclature and analysis

We followed the recommendations of Murphy and Crabtree (1985) in labelling enzymes, genetic loci, and alleles, e.g. *Ak-1(b)* refers to the b allele at the most cathodal locus encoding the enzyme adenylate kinase. The BIOSYS-1 program

(a)



(b)

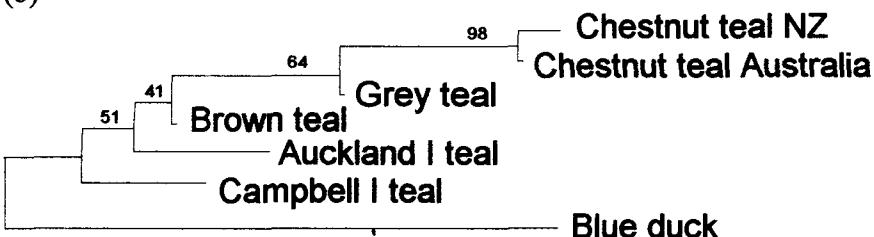


Figure 2. Topologies of (a) UPGMA tree (Sneath and Sokal 1973) and (b) neighbour-joining tree (Saitou and Nei 1987), both based on 14 allozyme loci, Nei's standard genetic distance, and 1000 bootstrap replications. The number on each internal branch signifies the percentage of bootstrap replicates that obtained that cluster of taxa when loci were resampled randomly with replacement.

(Swofford and Selander 1981) was used to calculate gene frequencies, genotype frequencies, and average unbiased heterozygosity per locus for each population, and unbiased estimates of normalized genetic identity (I) and distance (D) between each pairwise combination of populations (Nei 1978). The MEGA program (Kumar *et al.* 1993) was used to generate phenetic trees (UPGMA, Sneath and Sokal 1973) and neighbour-joining trees to estimate relationships among all populations (Saitou and Nei 1987, Saitou and Imanishi 1989, Nei 1991, Kim *et al.* 1993). The topology of the trees were tested by bootstrapping (with 1000 replicates) the allelic frequency data (see Table 3) using the program DISPAN (Ota 1993). The number on each internal branch (Fig. 2a,b) signifies the percentage of bootstrap replicates that obtained that cluster of taxa when loci were resampled randomly with replacement. Because Blue Duck may not be the proper sister group to the taxa examined, we also drew the trees with and without the inclusion of Blue Duck.

Table 2. Enzymes, loci, tissue distribution and electrophoretic conditions for allozymes used in this study

Enzyme	E.C. number	Locus	Tissue ^a	Buffer system ^b
Adenylate kinase	2.7.4.3	<i>Ak-1</i>	E	A
Esterase	—	<i>Est-1</i>	E	B
General protein	—	<i>Gp-2</i>	P	B
	—	<i>Gp-3</i>	P	B
	—	<i>Gp-5</i>	P	B
Glucose phosphate isomerase	5.3.1.9	<i>Gpi-1</i>	E	A
Haemoglobin	—	<i>Hb-1</i>	E	B
Lactate dehydrogenase	1.1.1.27	<i>Ldh-2</i>	E	A,C
Malate dehydrogenase	1.1.1.37	<i>Mdh-1</i>	E	A
	1.1.1.37	<i>Mdh-2</i>	E	A
Mannose phosphate isomerase	5.3.1.8	<i>Mpi-1</i>	E	C
Peptidase	3.4.1.1	<i>Pep-2</i>	E	B
Phosphogluconate dehydrogenase (decarboxylating)	1.1.1.44	<i>Pgd-1</i>	E	A,C
Superoxide dismutase	1.15.1.1	<i>Sod-1</i>	E	B

^aE, erythrocytes; P, plasma.^bA, Gel: 0.002 M citric acid, pH 6.0; electrode: 0.04 M citric acid, pH 6.1. Both buffers were pH adjusted with N-(3-aminopropyl)-morpholine (Clayton and Tretiak 1972).B, Gel: 0.076 M Tris, 0.005 M citric acid, pH 8.7; electrode: 0.3 M boric acid, 0.06 M NaOH, pH 8.2 (Selander *et al.* 1971).C, Gel: 0.069 M KH₂PO₄-NADP, pH 6.7; electrode: 0.138 M KH₂PO₄, pH 6.7 (Selander *et al.* 1971).

Results

Allozyme variation

Fourteen presumed genetic (allozyme) loci were resolved consistently in all populations (Tables 2, 3). Eight of these (*Gp-2*, *Hb-1*, *Ldh-2*, *Mdh-1*, *Mdh-2*, *Pep-2*, *Pgd-1*, *Sod-1*) showed no variation. Only one of the six variable loci (*Gp-5*) represented a polymorphism in the Blue Duck outgroup but at which the teals were monomorphic. Variable loci possessed either two or three alleles, and unbiased estimates of average heterozygosity (H) varied from 0 to 0.04 (Table 3). No Brown Teal was heterozygous at any locus sampled, suggesting a history involving significant genetic bottlenecks and/or very low population sizes. This finding could possibly be due to small sample sizes in Auckland Island (*n* = 7) and Campbell Island (*n* = 3) teals, but was also true of Brown Teal, which had a large sample size (*n* = 58). Sample sizes were too small to allow calculation of Hardy-Weinberg proportions for populations with polymorphic loci, but patterns of variation gave no evidence of sympatric cryptic species: Grey Teal had a single heterozygous individual (ab) for *Mpi-1*, as did Australian Chestnut Teal for *Gpi-1* (ab), while the New Zealand-sourced Chestnut Teal had one of each of three possible genotypes represented by a single individual at *Gpi-1* (i.e. aa, ab, bb).

Population and species divergence

The lowest value of Nei's *D* (0.01) occurred between the Australian and New Zealand-sourced Chestnut Teal, reflecting a small frequency difference at a single locus (Tables 3 and 4). The highest values (*D* = 0.34–0.48), the result of fixed

Table 3. Allozyme frequencies, unbiased estimates of average heterozygosity, number of alleles per locus, and percentage of polymorphic loci (0.05 criterion) for variable loci in six populations of Australasian teals and Blue Duck

Locus	Allele	Brown Teal	Auckland Is. Teal	Campbell Is. Teal	Grey Teal	Chestnut Teal: NZ	Chestnut Teal: Aust	Blue Duck
<i>Ak-1</i>	a	1.00	1.00	1.00	—	—	—	1.00
	b	—	—	—	1.00	1.00	1.00	—
<i>Est-1</i>	a	1.00	1.00	—	1.00	1.00	1.00	—
	b	—	—	1.00	—	—	—	—
	c	—	—	—	—	—	—	1.00
<i>Gp-3</i>	a	1.00	1.00	1.00	1.00	—	—	—
	b	—	—	—	—	1.00	1.00	—
	c	—	—	—	—	—	—	1.00
<i>Gp-5</i>	a	1.00	1.00	1.00	1.00	1.00	1.00	—
	b	—	—	—	—	—	—	1.00
<i>Gpi-1</i>	a	1.00	1.00	1.00	1.00	0.50	0.92	1.00
	b	—	—	—	—	0.50	0.08	—
<i>Mpi-1</i>	a	1.00	—	1.00	0.83	1.00	1.00	—
	b	—	1.00	—	0.17	—	—	—
	c	—	—	—	—	—	—	1.00
H =	0	0	0	0.02	0.04	0.01	0	
A =	1.00	1.00	1.00	1.07	1.07	1.07	1.07	1.00
%P (0.05)=	0	0	0	7.1	7.1	7.1	7.1	0

(H, unbiased estimate of average heterozygosity (Nei, 1978); A, mean number of alleles per locus; %P(0.05), percentage of loci with the common allele occurring at a frequency > 0.95. Sample sizes as in Table 1.

Table 4. Standard genetic distances (*D*) among six populations of Australasian teals and Blue Duck

	Brown Teal	Auckland Is. Teal	Campbell Is. Teal	Grey Teal	Chestnut Teal: NZ	Chestnut Teal: Aust	Blue Duck
Brown Teal	—						
Auckland Is. Teal	0.07	—					
Campbell Is. Teal	0.07	0.15	—				
Grey Teal	0.08	0.13	0.16	—			
Chestnut Teal: NZ	0.17	0.27	0.27	0.09	—		
Chestnut Teal: Aus	0.16	0.24	0.24	0.08	0.01	—	
Blue Duck	0.34	0.34	0.34	0.43	0.48	0.45	—

differences at four or five loci, separated Blue Ducks from all other species. Brown Teal differed by a single fixed difference ($D = 0.07$) from both Auckland Island Teal (*Mpi-1*) and Campbell Island Teal (*Est-1*), with both loci differentiating these last two taxa. The allele *Est-1(b)* occurred only in Campbell Island Teal, and *Mpi-1(b)* was found only in all Auckland Island Teal and a single heterozygous Grey Teal.

Phenetic analysis (Figure 2a) indicates that Australasian teal fall into two groups (Chestnut/Grey Teal vs Brown/Auckland Island/Campbell Island Teal). Neighbour-joining analysis (Figure 2b) of these taxa supports a similar grouping, with the three New Zealand teal distinct from Chestnut and Grey Teal. Genetic differentiation among Brown/Auckland Island/Campbell Island Teal ($D = 0.07$ –

0.15), whose species status with respect to one another has been uncertain, is only slightly less than the levels of differentiation from them to Grey Teal ($D = 0.08\text{--}0.16$) or between Grey and Chestnut Teals ($D = 0.08\text{--}0.09$). The genetic distances between the New Zealand teals and Chestnut Teal ($D = 0.16\text{--}0.27$) are considerably larger (Table 4).

When Blue Duck is not included as an outgroup, the topology of both trees is unchanged, supporting the dichotomy between Australian and New Zealand teals.

Discussion

Species identification

The most significant finding presented here is the limited but clear genetic divergence among teal from the New Zealand mainland, Campbell Island and Auckland Islands. Each taxon is distinguished by one or two fixed genetic differences from the others. The genetic distinctiveness of each taxon parallels previously described differences in morphology (body size, wing size, sexual dichromatism: Livezey 1990, Williams and Robertson 1996) and life history (egg size, clutch size: Williams *et al.* 1991).

Levels of allozyme differentiation among New Zealand's three brown-plumaged teal are equivalent to or greater than the level between them and Grey Teal, whose specific distinctiveness is not questioned (Marchant and Higgins 1990, Christidis and Boles 1994) and also equivalent to the genetic distance ($D = 0.08$) between Grey and Chestnut Teal. Genetic distances do not in themselves form sufficient criteria for species recognition, but taxonomic and genetic differentiation have been shown to be correlated over a wide array of taxa (Thorpe 1983, Frost and Hillis 1990, Highton 1990).

Birds generally show less divergence in allozymes at particular taxonomic levels than other animals (Avise and Aquadro 1982). Levels of genetic differentiation among the three New Zealand brown-plumaged teals exceed that commonly found among conspecific populations of birds. For example, smaller values of D (0.06) than those between Brown and either Auckland Island or Campbell Island Teal (0.07) have been used to support specific differentiation in some shorebirds and passerines (Avise and Zink 1988). Some avian taxa whose species status has been confirmed by reproductive isolation have had no detectable allozyme differentiation (Tegelstrom *et al.* 1980, Ryttman and Tegelstrom 1981).

Appropriate criteria for species determination have been debated at length in recent decades, especially among avian biologists (e.g. McKittrick and Zink 1988, Collar 1996, Hazevoet 1996). The Biological Species Concept (Mayr 1970), while occupying a central place in twentieth century biological thinking, is generally accepted to have limited applicability to allopatric populations, especially those separated by major geographical barriers (e.g. Cracraft 1983, McKittrick and Zink 1988, Zink and McKittrick 1995). Increasingly, systematists have accepted the Phylogenetic Species Concept (PSC, Cracraft 1983) as offering more objective criteria for defining a species as the "observable result of evolutionary history" (Hazevoet 1996). Under the PSC, a species is a uniquely diagnosable and independent evolutionary lineage.

New Zealand's brown-plumaged teals meet all the requirements for designation as separate species under the PSC. They are diagnosable on objective genetic criteria, and genetic differentiation is mirrored in morphological and ecological distinctiveness that indicates each is an evolutionarily independent lineage. These findings support the recent taxonomic trend (Livezey 1990, Marchant and Higgins 1990, McClelland 1993) of giving each specific recognition as *A. chlorotis* (Brown Teal), *A. aucklandica* (Auckland Island Teal) and *A. nesiotis* (Campbell Island Teal).

Systematic relationships

Our results demonstrate a clear divergence of the three New Zealand taxa (*chlorotis/aucklandica/nesiota*) from the two Australian taxa (*gracilis/castanea*), a finding identical to that of Young *et al.* (1997) from an analysis of mitochondrial ND2 sequences. Our results further indicate that the New Zealand taxa are not sister taxa of Chestnut Teal in contrast to previous hypotheses (Falla 1953, Livezey 1990) and, thus, negate both of the hypotheses erected as the basis of this study. In fact, the New Zealand taxa are genetically closer to Grey Teal than to Chestnut Teal (Table 4).

Whereas a common ancestor for the Australasian teals is likely, our results

- (i) indicate that the "radiation" within the New Zealand region occurred subsequent to the separation of the New Zealand lineage from the Australian taxa;
- (ii) support the parallel colonization hypothesis (hypothesis 1b) whereby teal on the two subantarctic islands originated from a New Zealand source independently; and
- (iii) suggest that colonization and differentiation on Auckland Islands was a more recent event than on Campbell Island, although we acknowledge that the level of resolution of the Brown–Auckland Island–Campbell Island Teal trichotomy is very low.

We have identified Grey and Chestnut Teals as sister taxa but we note that the genetic distance between them is of a similar magnitude to that between Grey and Brown Teals on the one hand and between Brown Teal and each of Auckland Island and Campbell Island Teal on the other (Table 4). From this we infer the separation of the two Australian taxa to have been roughly contemporaneous with the differentiation of the subantarctic teals from the Brown Teal.

The finding that the genetic distances between Chestnut Teal and any of the New Zealand teals are greater than those between Chestnut and Grey Teal, so as to imply no direct relationship between Chestnut Teal and the New Zealand teals, is a challenge to existing wisdom. Chestnut Teal and the three New Zealand teals are commonly viewed as "brown-plumaged teals" wherein the males, especially in breeding plumage, have similar colouring and patterning including a glossy green head and a conspicuous white patch at the base of the tail. This similarity of male breeding plumage, seemingly, has had a major influence in the interpretation of relatedness (e.g. Falla 1953, Fleming 1953, Livezey 1990), sufficient to overlook obvious and possibly significant differences. For example:

- (i) both Grey and Chestnut Teals have red eyes in contrast to brown eyes and a surrounding white eye ring in all New Zealand teals;
- (ii) female plumages in the Australian teals are more greyish and more similar to each other than to the dark brown of all New Zealand teals;
- (iii) Chestnut Teal females, males in eclipse, and juveniles are very similar to and often confused with Grey Teal in the field on account of similar colouring, identical head shape and similar upper- and underwing patterns (Marchant and Higgins 1990), all of which contrast with the New Zealand teals;
- (iv) body proportions, especially within elements of legs and wings, sort the poorly flighted to flightless and more cursorial New Zealand teals into one group and the strongly flighted Australian teals into another (Livezey 1990); and
- (v) Williams *et al.* (1991) identified that "the display repertoire (of Brown Teal) differs strikingly from that of *castanea*", noting, in particular, the absence of conspicuous courtship displays and long display sequences and the greater use of more subtle displays derived from comfort movements in the New Zealand teals. Johnsgard (1965), Prawiradilaga (1985) and Marchant and Higgins (1990) have highlighted the very close similarity of the courtship displays of Chestnut and Grey Teals.

Some or all of these differences have been viewed as examples of ecological adaptation and differentiation of a single ancestral (proto-*castanea*?) form (e.g. Livezey 1990, Williams *et al.* 1991). Certainly, body proportions related to flight ability are likely to be an ecological adaptation. But it is hard to consider the others as such. Since male breeding plumage is, apparently, the only convincing characteristic of taxonomic similarity between Chestnut Teal and the New Zealand teals, perhaps a more parsimonious explanation is called for: that (1) Chestnut Teal are more closely related to Grey Teal than to the New Zealand teals, and (2) the New Zealand teals may be derived from the Grey Teal lineage rather than from a Chestnut Teal lineage.

Conservation significance

Taxonomies are the foundation for determination of conservation priority (Avise 1989, Daugherty *et al.* 1990a, Molloy and Davis 1992, Collar 1996, Hazewoet 1996), and the choice of species concept can thus have critical significance to conservation (Rojas 1992). Hazewoet (1996) argued that taxonomies should reflect "genealogical biodiversity" as the proper basis for conservation. He noted that failure to develop "lineage thinking" rather than "list thinking" will lead conservationists to incorrect determination of conservation priority for allopatric populations.

Collar (1996) and others have objected on the grounds of impracticality. Wide-scale application of the PSC might have the effect of creating so many new taxa as to make species lists so long that they would confound their use in, among other things, establishing conservation priority for threatened taxa.

In the past decade, allozyme and DNA studies have shown significant and sometimes unexpected levels of differentiation among geographically disjunct populations of many New Zealand avian taxa (Daugherty and Triggs 1991, Baker

et al. 1995, Triggs and Daugherty 1996, Foggo et al. 1997). Similar surprising discoveries have been made among disjunct populations of New Zealand frogs (Bell et al., 1998), lizards (Daugherty et al. 1990b), and tuatara *Sphenodon* (Daugherty et al. 1990a). These findings have often supported significant taxonomic revision giving full species status to geographical isolates using the PSC.

Just as in the Cape Verde Islands (Hazevoet 1996), use of inflexible ‘list’ thinking to describe biodiversity in New Zealand would result in the loss of many of the distinctive lineages for which New Zealand is biologically famous. This study, for example, arose from the need to resolve the “uniqueness” of Campbell Island Teal for conservation purposes. Presently only about 50 birds survive in the wild, restricted to a 23-ha islet adjacent to Campbell Island (Williams and Robertson 1996). Campbell Island, presumably on which this teal was formerly widespread and abundant, has supported a dense population of Norway rat *Rattus norvegicus* since its initial discovery in 1810 by sealers, and most small ground-nesting birds (passerines and petrels) no longer breed there (Westerskov 1960). Other workers (e.g. Fleming 1953, Westerskov 1960, Kinsky 1970) have consigned Campbell Island Teal to the status of an almost extinct isolate of a more widespread species (either *A. aucklandica* or *A. chlorotis*). This view exemplifies a “list thinking” approach to biological diversity, whereby the extreme morphological changes in Campbell Island Teal associated with flightlessness represent only geographical novelty of no real significance. The outcome of this view can ensure extinction through neglect or inadvertent transfer of rats to its present rat-free sanctuary. “Lineage thinking”, on the other hand, as recommended by Zink and McKittrick (1995) and Hazevoet (1996), views the morphological divergence of Campbell Island Teal, supported by allozyme evidence reported here, as evidence of a significant evolutionary outcome warranting full species status for the Campbell Island Teal. Recent acceptance of this view has fuelled the writing and implementation of a species recovery plan (McClelland 1993), a concerted captive breeding programme (Preddy 1995) and more detailed enquiry into its biological characteristics and ecological adaptations (Williams and Robertson 1996). And, not insignificantly, this taxonomic status and the bird’s parlous conservation status have served to promote and advance planning for the removal of rats from, and the ecological restoration of, the spectacular subantarctic Campbell Island.

Acknowledgements

We thank Grant Dumbell and Ian Norman for providing Brown Teal and Chestnut Teal blood samples, and Sue Keall for essential technical and laboratory assistance. Contributory funds were provided by the New Zealand Lottery Board. Additional financial and logistical support was provided to M.W. by the Department of Conservation and to C.H.D. and J.M.H. by the School of Biological Sciences, Victoria University of Wellington. M.W. gratefully acknowledges the stimulus to and interest in the study accorded by Frank McKinney.

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