The Auk 117(1):154–163, 2000

PHYLOGENY, BIOGEOGRAPHY, AND TAXONOMY OF AUSTRALASIAN TEALS

MARTYN KENNEDY[1] AND HAMISH G. SPENCER
Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

ABSTRACT.—The taxonomy of the Australasian teals has been particularly unstable. Australasian Grey Teal (*Anas gracilis*) and Chestnut Teal (*A. castanea*) are widely viewed as specifically distinct, but the taxonomy of the New Zealand teals remains unsettled. Because conservation status is affected by taxonomic rank, it is important to resolve the status of the rare subantarctic teals. To estimate phylogenetic relationships of teals, we sequenced three mitochondrial DNA genes (12S, and ATPase 6 and 8). The resultant phylogeny unequivocally groups the Chestnut Teal with the Grey Teal, rather than with the New Zealand teals as has traditionally been held (Fleming 1953). A greater level of sequence divergence occurred within the New Zealand teals than between the Grey and Chestnut teals. This diversity, together with morphological and behavioral differences, implies that the New Zealand teals should be accorded specific status as *A. aucklandica, A. nesiotis,* and *A. chlorotis.* Although it is most likely that the teal that colonized the Auckland Islands and Campbell Islands originated in New Zealand, our data do not allow us to determine whether the ancestors of the Campbell Island Teal came from mainland New Zealand or the Auckland Islands. This uncertainty arises because, as our data show, the colonization events were separated by a short period of time. *Received 25 November 1998, accepted 16 June 1999.*

FIVE EXTANT TEALS inhabit the Australasian region and provide an interesting example of speciation in insular Southern Hemisphere waterfowl (see Livezey 1990). Grey Teal (*Anas gracilis*), which are small and drab, are widespread throughout Australia. Last century the species was rare and localized within New Zealand, but it is now widely distributed (Marchant and Higgins 1990). Grey Teal are broadly sympatric with the Chestnut Teal (*A. castanea*) in southeastern and southwestern Australia and with the Brown Teal (*A. chlorotis*) in mainland New Zealand (Marchant and Higgins 1990); vagrant Chestnut teal have been reported in New Zealand on several occasions (Guest 1992). Chestnut Teal are strongly sexually dichromatic; the male has a green head, chestnut breast, and dark upperparts, and the female closely resembles a Grey Teal. Brown Teal are less obviously dichromatic, with the female a more uniform brown than the male, which has a deep chestnut breast and a green iridescence on the crown and nape. Brown Teal were formerly widespread throughout North, South and Stewart Islands but are now rare and restricted in their distribution, with the main populations in the north of North Island and on Great Barrier Island (Marchant and Higgins 1990). The brown-plumaged teals (i.e. all teals except the Grey Teal) all exist in allopatry. The Auckland Island Teal (*A. aucklandica*) and Campbell Island Teal (*A. nesiotis*) occur only on their respective subantarctic island groups (see Fig. 1). They are smaller and darker than the Brown Teal, and unlike this species, they are flightless (Marchant and Higgins 1990).

The taxonomy of the Australasian teals has been the subject of much debate (e.g. Dumbell 1986, Williams and Robertson 1996). *Anas gracilis,* for example, was previously treated as a subspecies of *A. gibberifrons* of Indonesia (Livezey 1991). Although now universally accepted as separate species (e.g. Marchant and Higgins 1990, Turbott 1990, Livezey 1991, Christidis and Boles 1994), occasional debate has questioned whether Grey and Chestnut teals warrant separate specific status (Frith 1967) despite their widespread sympatry.

The taxonomic history of the brown-plumaged teals remains unresolved (see Dumbell 1986). Fleming (1953) considered the Brown, Auckland Island, and Campbell Island teals (the endemic New Zealand teals) to be subspecies of the Chestnut Teal, a position accepted by Frith (1967). More recently, however, the New Zealand teals have been accepted as specifically separate from the Chestnut Teal, although several different taxonomic arrangements have

[1] E-mail: martyn.kennedy@stonebow.otago.ac.nz

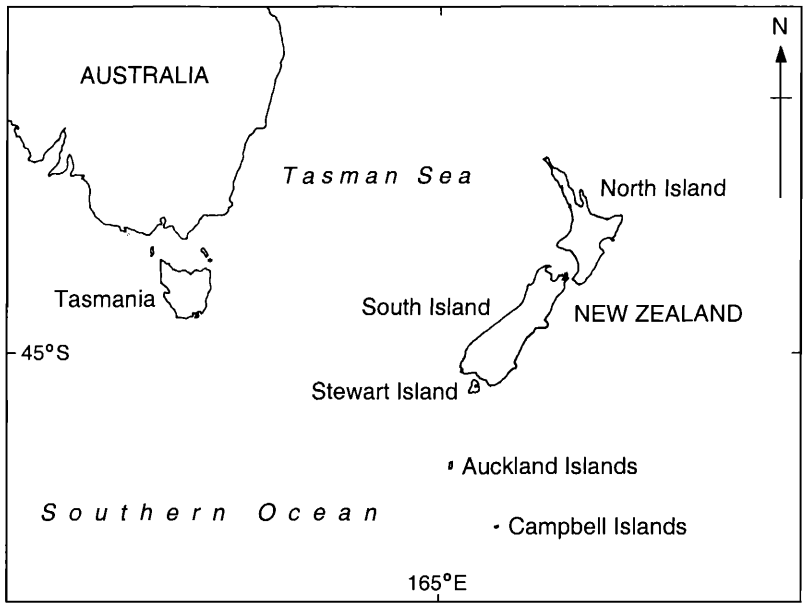

FIG. 1. The Australasian region.

been proposed. One arrangement considers them to be three allopatric subspecies (Kinsky 1970, Dumbell 1986, Turbott 1990), another accords all of them separate specific status (Marchant and Higgins 1990), and yet another accords specific status to the Brown Teal and Auckland Island Teal but places the Campbell Island Teal as a subspecies of *A. aucklandica* (Livezey 1990).

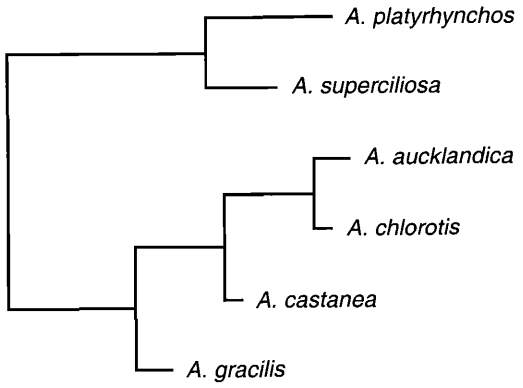

FIG. 2. Topology of morphological tree for the taxa used in this study (pruned from 59 taxa; Livezey 1991). Branch lengths are proportional to the number of changes along the branch. Livezey's (1990) tree has the same topology for the teals with the addition of *A. nesiotis* as sister taxon to *A. aucklandica* (*A. gracilis* is equivalent to *A. gibberifrons* of Livezey 1990).

Using morphological characters, Livezey (1991) generated a phylogeny for dabbling ducks that included most of the Australasian teals (Fig. 2). This phylogeny suggests a pattern of speciation in which the monochromatic Grey Teal separated from the common ancestor of the dichromatic brown-plumaged teals within Australia. Within the brown-plumaged teals, the Chestnut Teal later diverged from the progenitor of the New Zealand teals, the latter presumably invading New Zealand from Australia. The Auckland Island Teal then diverged from the Brown Teal after colonizing from the New Zealand mainland. In an earlier paper, Livezey (1990) presented a tree of the same topology that included only the teal and included the Campbell Island Teal as sister taxon to the Auckland Island Teal, consistent with the traditional hypothesis that the Campbell Islands were colonized from the Auckland Islands (Dumbell 1986). Alternatively, if the Auckland and Campbell Island teals are not sister taxa, the Auckland and Campbell Island colonizations represent separate events from the mainland, with Brown Teal stock giving rise to both species (Turbott 1968, Dumbell 1986). Livezey's (1990, 1991) phylogeny implies that the strong sexual dichromatism of the Chestnut Teal represents the ancestral state and is thus reduced in the insular forms, a pattern that tra-

ditionally has been interpreted as the loss of an isolating mechanism (i.e. dichromatism isolating the Grey and Chestnut teals).

The taxonomic status of the different teals has important conservation implications for taxa that are rare or endangered. The New Zealand Department of Conservation policy includes taxonomic distinctiveness as one of five factors assessed to determine conservation priorities (Molloy and Davis 1994). Within these five factors, taxonomic distinctiveness is only 1 of 17 criteria used to assess conservation priorities, but it is supposed to be a deciding factor when new conservation programs are planned (i.e. all else being equal, more distinct taxa will be given a higher priority; Molloy and Davis 1994).

In an attempt to resolve the taxonomic and systematic status of the Australasian teals, we sequenced mitochondrial DNA (mtDNA) from the members of this group. Sequence data can be used as a measure of the relative level of divergence among the teals and in the estimation of their phylogenetic relationships. A robust phylogeny for the group would allow us to evaluate the biogeographic origin of the different teals.

METHODS

Total genomic DNA was obtained for each of the samples using proteinase K followed by phenol/chloroform extraction (blood for all teals, muscle tissue for Mallard [*A. platyrhynchos*], and heart tissue for the Grey Duck [*A. superciliosa*]). Once extracted, the DNA was amplified for three mtDNA genes (12S ribosomal RNA and ATPase 6 and 8). We used the polymerase chain reaction (PCR) to amplify these regions with universal primers for 12S (Kocher et al. 1989) and primers for ATPase 6 and 8 (see Kennedy 1999). For ATPase 8 to be amplified, a new primer that is more suited to waterfowl, L9058 (5′-AGCCTTTTAAGCTACT-3′), was designed from the sequence of Ramirez et al. (1993). The prefix to the primer indicates that it is the light (L) strand and the number refers to the position of its 3′ end according to the chicken mtDNA sequence (Desjardins and Morais 1990). The primer pairs of L9265 and either H9922 or H9898 (required for the Brown Teal) were used to amplify ATPase 6 (see Kennedy 1999), whereas L9058 in combination with either of the heavy strand primers amplified ATPase 8 and ATPase 6.

A typical 25-μL double-stranded PCR amplification contained extracted genomic DNA, 0.5 μM of each primer, one unit of *Taq* polymerase (Promega), 2.5 μL of 10× *Taq* buffer (Promega), 1 mM $MgCl_2$ (Promega), and 200 μM of each dNTP. Negative controls were included with each PCR reaction, and all mixtures were covered with mineral oil. The reaction began with denaturation (94°C for 3 min) followed by 40 cycles of annealing (1 min) at 55 to 57°C (for 12S) or 42 to 45°C (for ATPase), template extension at 72°C (1 min), and denaturation at 94°C (1 min). Final annealing (1 min) and extension (4 min) steps completed the reactions. The PCR product was purified using Gelase (Epicentre Technologies) and then sequenced by an automated sequencer using either the PCR primers or internal primers (Kennedy 1999). Wherever possible, both strands of DNA were sequenced for samples of two or more individuals of a species to verify the accuracy of the sequencing and control for DNA contamination (i.e. three individuals for Grey Teal, one Mallard, and two for the other taxa). The Grey Teal samples originated in New Zealand. Ambiguity codes were used when it was not possible to discriminate between alternative bases at a site, and these sites were treated as uncertain. These sites typically were bases that had little signal supporting either of two alternative bases rather than being strong double peaks. The ATPase sequence from Ramirez et al. (1993) for the Mallard was obtained from GenBank. Unlike the ATPase sequence, the segment of 12S sequenced by Ramirez et al. (1993) differed from that used here, so we sequenced 12S for a Mallard.

Sequences were aligned by eye. The 12S sequence was aligned with reference to the seabird data of Paterson et al. (1995) and using the secondary-structure model and conserved-motifs approach of Hickson et al. (1995). The sequences have been submitted to GenBank (accession numbers AF173480 to AF173494). Analyses were conducted using test version 4.0d64 of PAUP*, written by David L. Swofford. Phylogenetic trees were constructed with maximum parsimony (using exhaustive searches) and maximum likelihood (using branch and bound searches).

To investigate the support for our trees and the phylogenetic signal in our sequence data, we used bootstrapping (Felsenstein 1985), decay indices (Bremer 1988), Kishino-Hasegawa tests (Kishino and Hasegawa 1989), and spectral analysis (Hendy and Penny 1993). The bootstrap estimates statistical support for the branches of a tree, whereas the Kishino-Hasegawa test estimates the significance of the observed difference (in likelihood or tree length) between any trees being compared. For the bootstrap analyses, 1,000 replicates were performed for parsimony (using a heuristic search) and 100 for maximum likelihood (using a fast-heuristic search). The decay index is the difference between the length of the parsimony tree(s) and the shortest tree(s) lacking that node. The program Spectrum 2.0 (Charleston 1998), which implements spectral analysis (Hendy and Penny 1993), was used to further investigate the

phylogenetic signal in the data. Support for a split (a split is any bipartition of the set of sequences and thus is equivalent to a branch) is a function of the number of changes in character state that correspond to that split, and the conflict for a split is the sum of the support for the splits that conflict with it. For discussions of spectral analysis and its use, see Lento et al. (1995) and Page et al. (1998). The spectrum can be computed from two-state sequence data, but because of difficulties handling missing data (Page et al. 1998), we computed the spectrum from distance matrices. We used the Tamura-Nei model to correct for superimposed changes (this model allows for unequal base frequencies and a transition/transversion bias with two transition classes; Tamura and Nei 1993).

Results

Our alignment gave a 394-bp fragment of 12S, and the overlapping ATPase 6 and 8 coding genes gave a 778-bp fragment. A partition-homogeneity test (Farris et al. 1995) showed that there was no significant difference in phylogenetic signal between the ATPase and 12S sequence, so we analyzed them as a single data set (100 replicates, $P = 1.0$). Of the 115 variable sites, 73 of the characters were parsimony informative. Both the significantly skewed tree-length distribution ($g_1 = -1.198$ from 10,000 random trees, $P < 0.001$; Hillis and Huelsenbeck 1992) and a PTP test (1,000 replicates, $P = 0.001$; Faith 1991, Faith and Cranston 1991) showed that the data contained significant signal. With the Mallard and Grey Duck defined as outgroups and all sites weighted equally, the resulting parsimony tree had a length of 107 steps (Fig. 3). We found the same topology for parsimony when transversions were given greater weight than transitions, and in the maximum-likelihood analysis (consequently, we present only the equally weighted parsimony tree).

High decay index values and 100% bootstrap values were found for three of the four internal branches, i.e. separating the Grey Duck and Mallard from the teals, the sister-taxa grouping of the Grey and Chestnut teals, and grouping the New Zealand teals (Fig. 3). The short internal branch grouping the Brown and Campbell Island teals had high bootstrap support (91%) but a low decay index. Similar bootstrap values were found for both the weighted-parsimony and maximum-likelihood analyses. The spectral analysis also showed high levels of support, and low or nonexistent levels of conflict, for the split that groups the Mallard and Grey Duck separately from the teals, for grouping the Grey and Chestnut teals, and for grouping the New Zealand teals together (Fig. 4). The spectrum, like the decay index, showed that the level of support for grouping the Brown and Campbell Island teals is relatively low. There was, however, no conflict in our data against grouping the Brown and Campbell Island teals together, with virtually no support and some conflict for the alternative arrangements grouping either the Brown and Auckland Island teals or the Auckland Island and Campbell Island teals (Fig. 4).

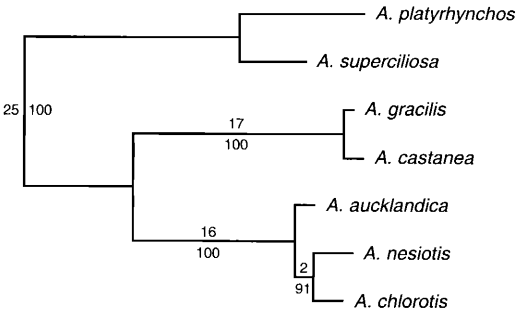

FIG. 3. Equal weights maximum-parsimony phylogram (tree length = 107, CI = 0.944, RI = 0.935). Branch lengths represent the number of substitutions along each branch. The percentage of bootstrap replicates (out of 1,000) that supported each node (≥50%) are shown below the branches, and the decay indices are shown above the branches. Both weighted parsimony analyses (i.e. with transversions given greater weight than transitions) and maximum-likelihood analyses (with transition to transversion ratio, the proportion of invariable sites, and the gamma shape parameter all estimated) found the same topology. The bootstrap values were almost identical for weighted parsimony and were similar for maximum likelihood.

Our equally weighted parsimony analysis produced one most-parsimonious tree of length 107 and two trees of length 109. No other trees had a length of less than 123. The two trees with a length of 109 grouped either the Brown and Auckland Island teals or the Auckland Island and Campbell Island teals. A Kishino-Hasegawa test comparing all three trees of length 109 and smaller showed that we cannot reject these alternate topologies ($P > 0.05$). Livezey's topology (Fig. 2) has a length of 125 and can be rejected by the Kishino-Hasegawa

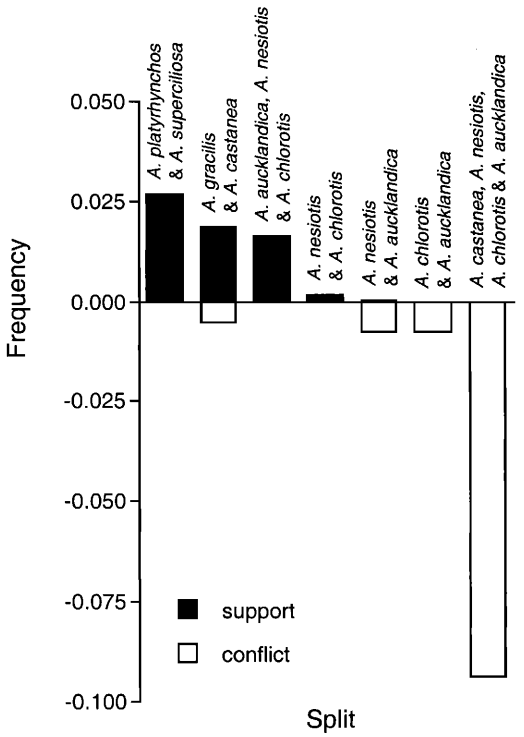

FIG. 4. The support/conflict spectrum. The splits are labeled by the taxa they group and are ordered left to right by their (positive) support values (i.e. expected number of substitutions per site), with the (negative) conflict values normalized following Lento et al. (1995).

test ($P < 0.0001$; i.e. no significant support for it in our data). Similarly, the spectrum showed no support and extremely high conflict for the split grouping the Chestnut, Brown, Auckland Island, and Campbell Island teals (Fig. 4).

Our phylogeny (Fig. 3) shows that the Grey and Chestnut teals are sister taxa and the New Zealand teals are monophyletic. Branch lengths, which are proportional to the number of substitutions, indicate that the New Zealand teals are as divergent from one another as the Grey and Chestnut teals. Pairwise comparisons (Table 1) show that Grey and Chestnut teals differ by 0.29%, and the divergences between the New Zealand teals vary from 0.63 to 0.70% (Table 1).

We also combined our mtDNA data set with all other available mtDNA sequence data (more than 1,000 bases each of two mtDNA genes, cytochrome *b* and ND2, obtained from GenBank; Johnson and Sorenson 1998) to construct a phylogeny for the group. A partition-homogeneity test showed that there was no significant difference in phylogenetic signal between Johnson and Sorenson's (1998) cytochrome-*b* and ND2 sequence and our ATPase and 12S sequence; thus, we analyzed it as a single data set of more than 3,200 bases (100 replicates, $P = 0.27$). With this combined data set, we found a single equally weighted parsimony tree that grouped the Grey and Chestnut teals as sister taxa (bootstrap value of 100% and high decay index, Fig. 5). The New Zealand teals form a monophyletic group with a bootstrap value of 100% and a high decay index, and the combined data set placed the Auckland Island and Campbell Island teals as sister taxa. Although the bootstrap support for grouping the Auckland Island and Campbell Island teals was reasonable (76% vs. 23% that supported grouping the Brown and Campbell Island teals, which was the next most-parsimonious tree), the decay index of only 2 showed that the strength of the signal was weak. A Kishino-Hasegawa test did not reject either of the alternative hypotheses, i.e. that the Brown and Campbell Island teals or the Brown and Auckland Island teals are sister taxa ($P > 0.05$). As before, a Kishino-Hasegawa test

TABLE 1. Percent sequence divergence between different taxa based on the model of Tamura and Nei (1993). Values below the diagonal are for our data alone, and values above the diagonal are for our data combined with those of Johnson and Sorenson (1998).

Taxon	1	2	3	4	5	6	7
1 Mallard	—	0.94	5.63	5.45	6.40	6.54	6.09
2 Grey Duck	1.75	—	5.74	5.55	6.40	6.48	5.98
3 Grey Teal	6.09	5.64	—	0.09	5.37	5.22	5.05
4 Chestnut Teal	5.58	5.06	0.29	—	5.36	5.32	5.02
5 Auckland Island Teal	5.77	4.96	3.98	3.95	—	0.92	0.84
6 Campbell Island Teal	6.39	5.50	3.87	4.14	0.70	—	0.77
7 Brown Teal	6.09	5.23	4.06	3.96	0.63	0.63	—

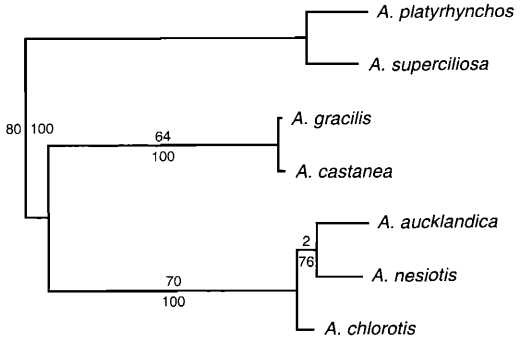

FIG. 5. The equal weights maximum-parsimony phylogram for the combined data set (i.e. our sequence plus that of Johnson and Sorenson 1998). Tree length = 324, CI = 0.951, and RI = 0.951. Branch lengths represent the number of substitutions along each branch. The percentage of bootstrap replicates (out of 1,000) that supported each node (≥50%) are shown below the branches, and the decay indices are shown above the branches.

rejected the hypothesis ($P < 0.0001$) that places the Chestnut Teal as a sister taxon to the New Zealand teals (i.e. Fig. 2)

In addition to the taxa already discussed, we obtained blood samples of two South Island Brown Teals (*A. chlorotis peculiaris*) from the remnant population in Fiordland National Park. Mathews (1937) proposed subspecific status for South Island Brown Teal based on smaller wing measurements than their North Island counterparts. We sequenced the same genes for the South Island Brown Teal to assess its taxonomic status and phylogenetic position. Sequencing these individuals proved difficult, and we were unable to sequence 120 bases of 12S because one of the primers would not provide any readable sequence. The South Island Brown Teal sequence was added to our data set and analyzed using both parsimony and maximum likelihood to find the best estimate of the phylogeny. Surprisingly, rather than grouping the South Island Brown Teal with the North Island Brown Teal or one of the subantarctic teals, the South Island Brown Teal grouped with the Mallard and Grey Duck. This grouping was supported by high bootstrap values (100% for grouping with the Mallard and Grey Duck and 96% for being a sister taxon to the Mallard from 1,000 parsimony bootstrap replicates) and by low levels of divergence between the South Island Brown Teal and Grey Duck (1.09%) and Mallard (1.17%). The levels of divergence between the South Island Brown Teal and the other teals exceeded 5%.

Initially, we considered that a contamination event occurred, but new subsamples of the originals showed that this was not the case. The difficulties obtaining sequence for these individuals and the level of genetic divergence between the Grey Duck and Mallard versus the South Island Brown Teal may be explained if these sequences were of nuclear origin. Another possible explanation is that because mtDNA is inherited maternally, there was a hybridization event (as noted in Brown Teal; Dumbell 1986) between a female Mallard or Grey Duck and a male South Island Brown Teal, and that both of the individuals we sequenced were descendants of such a mating. From our sequence, we cannot tell if such a hybridization event would have been with a Mallard or Grey Duck, which hybridize extensively in the wild.

DISCUSSION

Our phylogeny shows that the hypothesis that the Grey Teal and the brown-plumaged teals (Chestnut and New Zealand teals) diverged before the latter colonized New Zealand (see Fig. 2) and further diversified is not correct. All of our results show that the Grey Teal and Chestnut Teal are sister taxa, and we can reject the hypothesis that places the Chestnut Teal and New Zealand teals as sister taxa. Our phylogeny thus implies that the common ancestor of all the Australasian teals diverged in two lineages, one in Australia and the other in New Zealand. Following the traditional perspective, we assume that teal from Australia colonized New Zealand (Falla 1953, Livezey 1990), but our phylogeny contains no evidence that the colonization must have been in this direction. Within Australia, the teal diverged into the Grey and Chestnut teals, and given the divergence between the two (Table 1), the split probably occurred at approximately the same time as (or perhaps after) the New Zealand teals diverged from one another.

We were unable to resolve the topology within the New Zealand teals. Although we obtained good bootstrap support for grouping the Brown and Campbell Island teals, there was a low decay index and low support from spectral analysis for that relationship. The spectrum (Fig. 4) showed that the high bootstrap support

that grouped the Brown and Campbell Island teals resulted from a lack of signal in the data for any alternative groupings.

Monophyly of the Grey and Chestnut teals.—The finding that the Grey and Chestnut teals are sister taxa is extremely well supported by both bootstrapping and decay indices (Fig. 3) and by the spectral analysis (Fig. 4). Other molecular evidence, including DNA (Sraml et al. 1996, Young et al. 1997, Johnson and Sorenson 1998) and allozymes (Daugherty et al. 1999), indicates that the Grey Teal and Chestnut Teal are sister taxa (although the UPGMA and neighbor-joining trees constructed from the allozyme data differ somewhat and have poor bootstrap support for this grouping). Moreover, the morphological similarity of the female, juvenile, and eclipse male Chestnut Teal and Grey Teal and behavioral information (Marchant and Higgins 1990) support grouping these species. Display bouts, for example, distinguish Grey Teal from any other species apart from Chestnut Teal (Marchant and Higgins 1990). The similarity of the male breeding plumages of the brown-plumaged teals has had a major influence on their taxonomy, overwhelming other evidence that supports grouping the Chestnut Teal and Grey Teal (Daugherty et al. 1999).

Livezey's (1991) phylogeny (Fig. 2) has four characters that group the Chestnut Teal with the New Zealand teals. Given the weight of evidence grouping the Grey and Chestnut teals, these characters need to be reevaluated, and possibly either recoded or considered as convergent traits. The first of Livezey's (1991) characters (26) is the presence or absence of a chestnut wash on the sides, belly, and breast. This character is linked with dichromatism in the group, with only the males having the chestnut wash (Marchant and Higgins 1990). Dichromatism may have been lost repeatedly within the dabbling ducks (Omland 1997), and thus it is possible that monochromatism is the derived state in Grey Teal (vs. dichromatism in the other taxa). The second of the characters (30) is the presence or absence of a generalized, poorly differentiated greenish postorbital iridescence. This character may have been miscoded. Rather than being shared by all of the brown-plumaged teals, this character appears to be shared by only the New Zealand teals, because male Chestnut Teals (like Mallards) have a fully green head (Marchant and Higgins 1990). The third of the characters (42) is the cranial border of the speculum, formed by the tips of the caudal-most row of greater secondary coverts. This character has four states (not contrastingly colored, black, white, and buff or rufous) and also may have been miscoded because the brown-plumaged teals are supposed to share the buff or rufous state, but this state appears to be shared by only the New Zealand teals (Marchant and Higgins 1990). The Chestnut Teal shares the white state with the Grey Teal (Marchant and Higgins 1990). The last of the characters (82) is the presence or absence of a subrectangular whitish patch surrounded by dark areas on the flanks of males in alternate plumage. This character is related to dichromatism and either may be convergent or needs to be reassessed in terms of the possible subsequent loss of dichromatism in Grey Teal (see Omland 1997).

Other morphological characters that are not related to male breeding plumage are more consistent with the Grey Teal and Chestnut Teal being sister taxa. Both species have red eyes, whereas New Zealand teals have brown eyes with a white eye ring (character 104 of Livezey 1991; Daugherty et al. 1999). Similarly, head shape and underwing patterns are very similar in the Grey Teal and Chestnut Teal and distinguish them from New Zealand teals (Marchant and Higgins 1990).

Phylogenetic and biogeographic implications.—We could not resolve the pattern of divergence within the New Zealand teals with confidence. Because of prevailing winds and the relative position and sizes of the different islands (Fig. 1), it is implausible that the teals colonized mainland New Zealand from Australia via the subantarctic islands. If we assume that the teals are monophyletic and that mainland New Zealand was colonized from Australia, our phylogeny suggests that teal from the mainland first reached the Auckland Islands and then shortly afterward via a second colonization reached the Campbell Islands (thus, the Brown Teal and Campbell Island teal are sister taxa). The level of bootstrap support for this grouping is high (91%), but this reflects a lack of conflicting signal in our data for either of the other possible bifurcating patterns within these three taxa. We could not reject the alternative hypotheses that either the Campbell Island and Auckland Is-

land teals or the Brown and Auckland Island teals are sister taxa.

The analyses of Johnson and Sorenson (1998) and Young et al. (1997) place the Campbell Island and Auckland Island teals as sister taxa, thus supporting the traditional colonization hypothesis. The combined data set grouped the Auckland Island and Campbell Island teals as sister taxa (Fig. 5), but the amount of change along the internal branch of the tree was insufficient to allow us to reject either of the alternative topologies.

Three possible biogeographic scenarios are apparent for the colonization of the subantarctic islands by teal. First, our sequence data suggests two colonizations, with flighted mainland teal first colonizing the Auckland Islands and then later colonizing the Campbell Islands (Turbott 1968). Second, the combined data set favors the traditional hypothesis of a mainland taxon colonizing the Auckland Islands, which in turn colonized the Campbell Islands before becoming flightless in both the Auckland Islands and Campbell Islands (Dumbell 1986). Third, the allozyme data of Daugherty et al. (1999) provide a low level of support for an affinity between the Brown Teal and Auckland Island Teal, which suggests two colonizations of the subantarctic islands, the first reaching the Campbell Islands and the second the Auckland Islands (Turbott 1968). We cannot distinguish between these three options with our sequence data or with the combined sequence data. The short internal branches grouping the Brown and Campbell Island teals (i.e. with the decay index of 2; Fig. 3) and the Auckland Island and Campbell Island teals (i.e. with the decay index of 2; Fig. 5) suggest that however the teals reached the subantarctic islands, the colonization events were separated by only a short period of time (i.e. hundreds or thousands vs. hundreds of thousands of years). An additional hypothesis, that the three New Zealand teals represent separate colonizations by Chestnut Teal (Williams et al. 1991), can be rejected because it receives no support from the phylogenetic relationships of the taxa (i.e. the Chestnut Teal is not a sister taxon to any of the New Zealand teals).

With the substantial combined data set we were unable to resolve relationships among the New Zealand teals with certainty. Thus, the relationship appears to be close to a trichotomy (i.e. a single event colonizing both subantarctic island groups) and may prove very difficult to resolve with confidence. Future lines of evidence that may help infer relationships among New Zealand teals include additional sequence data and comparisons with other similarly distributed taxa. If these comparisons showed a consistent pattern of colonization, support for a particular hypothesis may be inferred. Parasites would be an additional source of information if they have cospeciated with teals (e.g. Paterson et al. 1993, Page et al. 1998). For example, lice have been shown to have an increased rate of mtDNA evolution compared with their hosts (Page et al. 1998), so it may be possible to confidently resolve the parasite phylogeny and thus infer teal phylogeny.

Irrespective of the pattern of colonization, flightlessness probably evolved separately in the subantarctic teals (contra Livezey 1990). Because many of the changes in morphology of these species probably are related to loss of flight (Livezey 1990), morphological similarity of the Campbell Island Teal and the Auckland Island Teal is to be expected and thus might be the result of convergence.

Taxonomic status.—Our sequence data show that the three New Zealand teals are more genetically divergent from one another (0.63 to 0.70%) than the Grey Teal and Chestnut Teal are from each other (0.29%), a result that agrees with allozyme data (Daugherty et al. 1999). For the combined data set (i.e. including Johnson and Sorenson 1998), we found that the level of divergence between the Grey and Chestnut teals was 0.09%, whereas divergences between the New Zealand teals varied from 0.77 to 0.92% (Table 1).

Levels of divergence in the sequence data (albeit low; Table 1) suggest that the Brown Teal, Auckland Island Teal, and Campbell Island Teal should be accorded the same taxonomic status as the Grey Teal and Chestnut Teal. In addition to the divergence data, several other lines of evidence support the species status of these taxa. Diagnostic allozyme characters allow these taxa to be separated under the phylogenetic species concept (see Daugherty et al. 1999). Some behavioral characters differ between the mainland and subantarctic teals (e.g. territoriality, voice, precopulatory behavior; Marchant and Higgins 1990), and substantial morphological differences occur between the

taxa (Livezey 1990, Marchant and Higgins 1990). Only superficial plumage similarities argue against the species status of the New Zealand teals.

Conservation implications.—Along with several recent workers (e.g. Daugherty et al. 1999) we suggest that the Brown Teal, Auckland Island Teal, and Campbell Island Teal be accorded specific status, which warrants separate conservation strategies. We cannot comment on the taxonomic status of the remnant South Island Brown Teal because our sequence data do not allow us to determine the level of divergence between it and North Island Brown Teal. Apparent morphological differences (J. Fraser and I. Southey pers. comm.) between the North Island Brown Teal and South Island Brown Teal suggest some divergence, and it is clear that the South Island Brown Teal warrants further investigation. As we have argued above, traditional taxonomy has subsumed important genetic and morphological differences in the New Zealand teals (as it has in the tuatara [*Sphenodon*]; Daugherty et al. 1990), and it is possible that morphological differences in the South Island Brown Teal are correlated with important genetic differences.

ACKNOWLEDGMENTS

We thank M. Williams (New Zealand Department of Conservation) and B. Evans for providing samples; J. Fraser, R. Gray, I. Southey, and M. Williams for helpful discussions; and C. Daugherty, M. Williams, J. Hay, K. Johnson and M. Sorenson for advance copies of their work. The manuscript benefited from the comments of three anonymous reviewers, A. Baker, A. Paterson, M. Roy, I. Southey, and H. Suter. Genetic work was carried out in the Evolutionary Genetics Laboratory of G. Wallis, with the assistance and advice of T. King and L. Wallis. The initial ATPase primers were designed by A. Baker and O. Haddrath of the Royal Ontario Museum. The programs used for the analyses were written by D. L. Swofford (PAUP*), M. A. Charleston (Spectrum 2.0), and T. Eriksson and N. Wikström (AutoDecay 3). This work was supported by grants from the University of Otago to HGS. MK was supported by a University of Otago Postgraduate Scholarship.

LITERATURE CITED

BREMER, K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42:795–803.

CHARLESTON, M. A. 1998. Spectrum: Spectral analysis of phylogenetic data. Bioinformatics 14:98–99.

CHRISTIDIS, L., AND W. E. BOLES. 1994. The taxonomy and species of birds of Australia and its territories. Royal Australasian Ornithologists' Union, Melbourne.

DAUGHERTY, C. H., A. CREE, J. H. HAY, AND M. B. THOMPSON. 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). Nature 347:177–179.

DAUGHERTY, C. H., M. WILLIAMS, AND J. M. HAY. 1999. Genetic differentiation, taxonomy and conservation of Australasian teals *Anas* spp. Bird Conservation International 9:29–42.

DESJARDINS, P., AND R. MORAIS. 1990. Sequence and gene organization of the chicken mitochondrial genome. A novel gene order in higher vertebrates. Journal of Molecular Biology 212:599–634.

DUMBELL, G. S. 1986. The New Zealand Brown Teal: 1845–1985. Wildfowl 37:71–87.

FAITH, D. P. 1991. Cladistic tests for monophyly and nonmonophyly. Systematic Zoology 40:366–375.

FAITH, D. P., AND P. S. CRANSTON. 1991. Could a cladogram this short have arisen by chance alone? On permutation tests for cladistic structure. Cladistics 7:1–28.

FALLA, R. A. 1953. The Australian element in the avifauna of New Zealand. Emu 53:36–46.

FARRIS, J. S., M. KÄLLERSJÖ, A. G. KLUGE, AND C. BULT. 1995. Constructing a significance test for incongruence. Systematic Biology 44:570–572.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783–791.

FLEMING, C. A. 1953. Checklist of New Zealand Birds. A. H. and A. W. Reed, Wellington, New Zealand.

FRITH, H. J. 1967. Waterfowl in Australia. Angus and Robertson, Sydney.

GUEST, R. 1992. Rare bird reports in 1991. Notornis 39:319–321.

HENDY, M. D., AND D. PENNY. 1993. Spectral analysis of phylogenetic data. Journal of Classification 10: 5–24.

HICKSON, R. E., C. SIMON, A. COOPER, G. S. SPICER, J. SULLIVAN, AND D. PENNY. 1995. Conserved sequence motifs, alignment, and secondary structure for the third domain of animal 12S rRNA. Molecular Biology and Evolution 13:150–169.

HILLIS, D. M., AND J. P. HUELSENBECK. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. Journal of Heredity 83:189–195.

JOHNSON, K. P., AND M. D. SORENSON. 1998. Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome *b* and ND2) in the dabbling ducks (tribe: Anatini). Molecular Phylogenetics and Evolution 10:82–94.

KENNEDY, M. 1999. The behaviour and phylogeny of

the Pelecaniformes. Ph.D. thesis, University of Otago, Dunedin, New Zealand.

KINSKY, F. C. 1970. Annotated checklist of the birds of New Zealand. A. H. and A. W. Reed, Wellington, New Zealand.

KISHINO, H., AND M. HASEGAWA. 1989. Evaluation of the maximum likelihood estimate of the evolutionary tree topologies from DNA sequence data, and the branching order in Hominoidea. Journal of Molecular Evolution 29:170–179.

KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, F. X. VILLABLANCA, AND A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA 86: 6196–6200.

LENTO, G. M., R. E. HICKSON, G. K. CHAMBERS, AND D. PENNY. 1995. Use of spectral analysis to test hypotheses on the origin of pinnipeds. Molecular Biology and Evolution 12:28–52.

LIVEZEY, B. C. 1990. Evolutionary morphology of flightlessness in the Auckland Islands Teal. Condor 92:639–673.

LIVEZEY, B. C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. Auk 108:471–507.

MARCHANT, S., AND P. J. HIGGINS. 1990. Handbook of Australian, New Zealand and Antarctic birds, vol. 1: Ratites to ducks. Oxford University Press, Oxford.

MATHEWS, G. M. 1937. Notes on New Zealand ducks. Emu 37:31–32.

MOLLOY, J., AND A. DAVIS. 1994. Setting priorities for the conservation of New Zealand's threatened plants and animals. Department of Conservation, Wellington, New Zealand.

OMLAND, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: Repeated loss of dichromatism in dabbling ducks (Anatini). Evolution 51:1636–1646.

PAGE, R. D. M., P. L. M. LEE, S. A. BECHER, R. GRIFFITHS, AND D. H. CLAYTON. 1998. A different tempo of mitochondrial DNA evolution in birds and their parasitic lice. Molecular Phylogenetics and Evolution 9:276–293.

PATERSON, A. M., R. D. GRAY, AND G. P. WALLIS. 1993. Parasites, petrels and penguins: Does louse phylogeny reflect seabird phylogeny? International Journal of Parasitology 23:515–526.

PATERSON, A. M., G. P. WALLIS, AND R. D. GRAY. 1995. Penguins, petrels and parsimony: Does cladistic analysis of behavior reflect seabird phylogeny? Evolution 49:974–989.

RAMIREZ, V., P. SAVOIE, AND R. MORAIS. 1993. Molecular characterization and evolution of a duck mitochondrial genome. Journal of Molecular Evolution 37:296–310.

SRAML, M., L. CHRISTIDIS, S. EASTEAL, P. HORN, AND C. COLLET. 1996. Molecular relationships within Australasian waterfowl (Anseriformes). Australian Journal of Zoology 44:47–58.

TAMURA, K., AND M. NEI. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Molecular Biology and Evolution 10:512–526.

TURBOTT, E. G. 1968. Buller's birds of New Zealand. Whitcombe and Tombs, Wellington, New Zealand.

TURBOTT, E. G. (Ed.). 1990. Checklist of the Birds of New Zealand and the Ross Dependency, Antarctica. Random Century, Auckland, New Zealand.

WILLIAMS, M., F. MCKINNEY, AND F. I. NORMAN. 1991. Ecological and behavioural responses of Austral teal to island life. Pages 876–884 *in* Acta XX Congressus Internationalis Ornithologici (B. D. Bell, Ed.). Christchurch, New Zealand, 1990. New Zealand Ornithological Congress Trust Board, Wellington.

WILLIAMS, M., AND C. J. R. ROBERTSON. 1996. The Campbell Island Teal *Anas aucklandica nesiotis*: History and review. Wildfowl 47:134–165.

YOUNG, H. G., M. D. SORENSON, AND K. P. JOHNSON. 1997. A description of the Madagascar Teal *Anas bernieri* and an examination of its relationships with the Grey Teal *A. gracilis*. Wildfowl 48:174–180.

Associate Editor: A. J. Baker