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GENETIC STRUCTURE OF BLUE DUCK (*HYMENOLAIMUS MALACORHYNCHOS*) POPULATIONS REVEALED BY DNA FINGERPRINTING

SUSAN J. TRIGGS,[1] MURRAY J. WILLIAMS,[1]
STEPHEN J. MARSHALL,[2] AND GEOFFREY K. CHAMBERS[2]

[1]*Science and Research Division, Department of Conservation, P.O. Box 10420, Wellington, New Zealand; and*
[2]*School of Biological Sciences, Victoria University, P.O. Box 600, Wellington, New Zealand*

ABSTRACT.—DNA-fingerprinting analysis of Blue Ducks (*Hymenolaimus malacorhynchos*) with two minisatellite probes indicated a decrease in genetic similarity (proportion of DNA bands shared) as geographic separation between samples increased. The genetic similarity between individuals from different regions (0.17–0.24) is within the range of the genetic similarities found within populations of other avian species. We found a significantly higher genetic similarity (0.36–0.51) within populations of Blue Ducks. The high degree of genetic relatedness and inbreeding within populations leads us to suggest that dispersal is very limited and inbreeding is common. These appear to be natural characteristics of the Blue Duck social system, but may be exaggerated in populations in more modified habitats. Low allozyme variation ($H = 0.002$) precluded electrophoretic analysis of population structure. *Received 6 April 1990, Accepted 9 June 1991.*

DNA FINGERPRINTING is a powerful molecular-genetic technique that uses human probes for hypervariable minisatellite DNA to identify individuals and to determine parentage with a high degree of accuracy (Jeffreys et al. 1985a). Moreover, human probes can be used for a wide variety of other species, including plants (Rogstad et al. 1988), birds (Burke and Bruford 1987, Wetton et al. 1987, Burke et al. 1989, Kuhnlein et al. 1989), and mammals (Jeffreys and Morton 1987, Jeffreys et al. 1987). As yet, DNA fingerprinting has only rarely been used to determine genetic relationships within or among populations (Flint et al. 1989, Kuhnlein et al. 1989).

The Blue Duck (*Hymenolaimus malacorhynchos*), is a riverine anatid endemic to New Zealand. It is classified as a threatened species (Bell 1986), and its habitat has been affected extensively by riverine and agricultural development. Although once widespread throughout catchments in both North and South Islands of New Zealand, Blue Ducks are now dispersed as small populations in widely-separated high-country river headwaters (Bull et al. 1985). These remnant populations appear to be effectively isolated from each other, because there is little evidence of overland dispersal between headwaters (Williams 1988, 1991).

An example of this situation is the Wanganui River system (Fig. 1). Triggs et al. (1991) found that the population of Blue Ducks on the Manganuiateao River, a tributary of the Wanganui River, consisted of highly interrelated individuals. Genetic similarity (the percentage of DNA-fingerprint bands shared between individuals) averaged 43%, twice that of most species studied so far (Burke and Bruford 1987, Wetton et al. 1987). These findings are consistent with evidence of inbreeding and limited dispersal obtained from field studies of ecology and behavior of the same population of Blue Ducks (Williams 1991). However, it was not known whether the high degree of genetic relatedness within this population reflected the normal social structure of Blue Ducks, or whether it was a result of isolation.

In this study, we compared the genetic similarity of Blue Ducks on a larger geographic scale: within and between rivers, catchments, and regions. We also compared the genetic structure of a population found on an isolated river within a modified catchment (Manganuiateao) with that of a population in an extensive and relatively unmodifed catchment (Takaputahi).

The general question of how much gene flow occurs among populations of Blue Duck, and the particular question of whether the genetic structure of natural populations is disrupted by isolation, are of pressing concern for the con-

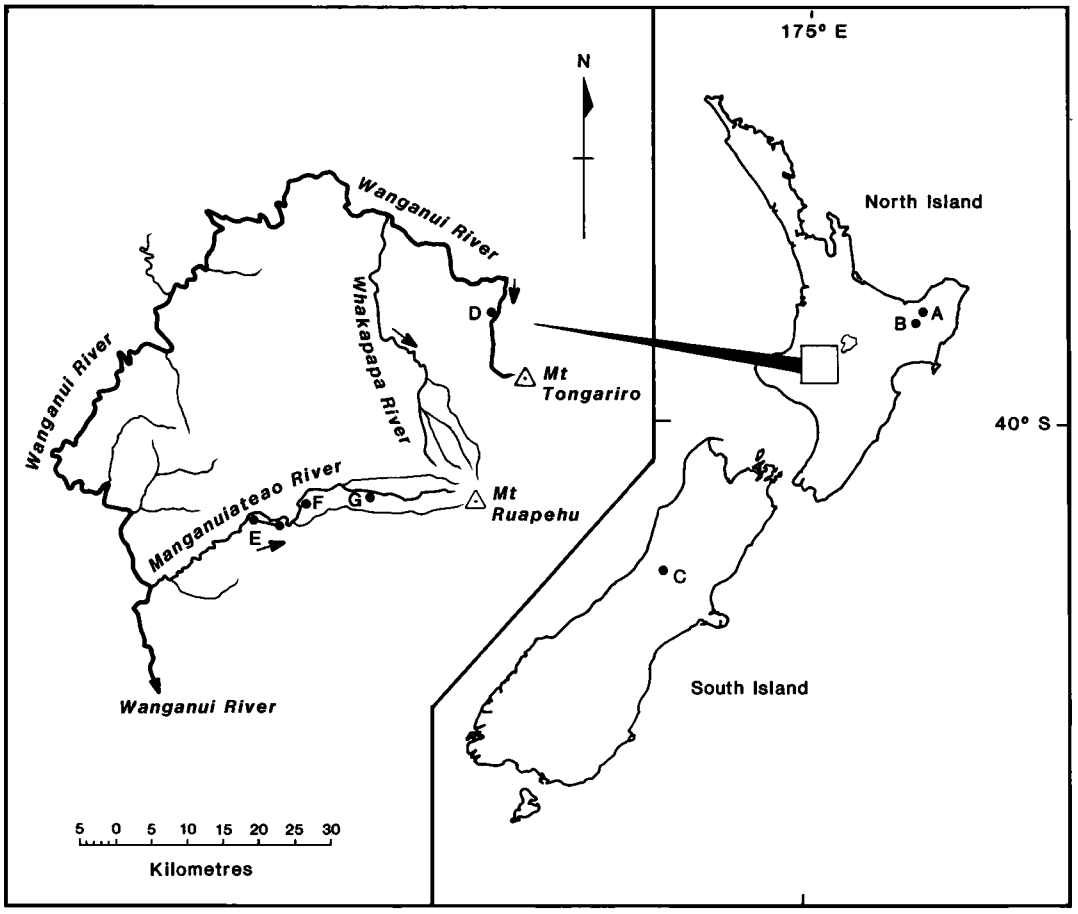

Fig. 1. Location of sampling sites (inset = Wanganui River system): (A) Takaputahi River, Motu Catchment, East Cape; (B) Moanui Stream, Waioeka Catchment, East Cape; (C) Otira River, Taramakau Catchment, West Coast; (D) upper Wanganui River, Wanganui Catchment, Wanganui; (E) lower section, Manganuiateao River, Wanganui Catchment; (F) middle section, Manganuiateao River; (G) upper section, Manganuiateao River. Arrows indicate presence of Blue Duck populations upstream.

servation of Blue Ducks. Small and isolated populations have a high risk of extinction and may suffer deleterious genetic effects (Soule 1987 and references therein).

Methods

Sample collection and study areas.—We took blood samples from 58 Blue Ducks (42 adults/independent juveniles and 17 ducklings) from five rivers in New Zealand (Fig. 1, Table 1). The main study area was the Manganuiateao River, which has a population of about 40 breeding pairs (Williams 1991). Three sections of this river were sampled (Fig. 1, Table 1). The "lower section" was at the downriver extremity of the birds' range and was 28–37 km from the river's confluence with the Wanganui River. In this section, the density of territorial pairs has increased slowly after a devastating volcanic lahar in 1975 which rendered this section uninhabitable for over 12 months. This 9-km stretch of river was the location of our earlier study of genetic relationships among adjacent territorial pairs (Triggs et al. 1991) and the longer ecological study (Williams 1991). The "middle" and "upper" sections each comprised 2-km stretches of the river separated by 7 km and 21 km, respectively, from the lower section.

Although the Manganuiateao River is a tributary of the Wanganui River, the study site is about 200 km via the river course from the nearest Blue Duck population in the Wanganui River catchment. However, the flight distance overland between populations in the headwaters of the Manganuiateao and those in

TABLE 1. Location and sample sizes from Blue Duck populations. n_t = total sample size; n_i = effective number of adults and independent juveniles.

Region	Catchment	River or stream	n_t	n_i
Wanganui, North Island	Wanganui	Manganuiateao		
		Lower	21	12
		Middle	7	5
		Upper	4	4
		Total	32	21
	Wanganui	Wanganui (upper)	3	2
East Cape, North Island	Motu	Takaputahi	12	12
	Waioeka	Moanui	6	2
West Coast, South Island	Taramakau	Otira (upper)	5	5
Total			58	42

the Whakapapa River (and other headwater tributaries of the Wanganui River) is only 7–10 km. Three individuals were sampled from the upper Wanganui (Fig. 1).

We chose the second study area, the Takaputahi River (Fig. 1), because it contains part of a large continuous population that occupies relatively unmodified habitat in the Motu River catchment and, presumably, represents the natural population structure of Blue Ducks. The Takaputahi sample of 12 adults was obtained along a 16-km continuous stretch of Takaputahi River and two tributaries, Whitikau and Ngaupokotangata Streams. The Takaputahi River, the mainstem Motu River, and at least six other major tributaries of the Motu contain Blue Ducks (D. M. Cunningham, pers. comm.); the total number probably exceeds 180, thereby comprising North Island's largest continuous population of Blue Ducks. Adjacent catchments, such as the Waioeka, also contain Blue Ducks. One adult and its five ducklings (hence, an effective sample of two adults) were sampled from Moanui Stream, Waioeka catchment. The distance between the Moanui and Takaputahi sampling sites is approximately 140 km by river and, at their closest point, the headwaters are 40 km apart overland. We sampled five adults from the Otira River headwaters in Arthurs Pass National Park in South Island (Fig. 1).

Blue Ducks were captured by gently herding an individual, a pair, or family downstream into a mist net erected across the river. Individuals were sexed, and weighed. A blood sample of up to 1 ml was taken by venipuncture using a sterile, heparinized syringe. Blood samples were separated into serum and red cell fractions with a field centrifuge (2,000 rpm for 5 min), kept on ice, and frozen in liquid nitrogen as soon as possible (0–4 h). Samples were stored at −70°C for the duration of the study.

Genetic analysis.—Initially, we intended to use both electrophoresis and DNA fingerprinting to analyze population structure. However, the electrophoretic analysis detected virtually no allozyme variability in Blue Ducks (see Appendix), rendering the technique unsuitable.

DNA fingerprints were produced using two minisatellite DNA probes, 3'HVR (Fowler et al. 1988) and 33.15 (Jeffreys 1985a). Two probes were used to give independent estimates of genetic similarity values and because variability within species (and, hence, discriminatory power) may depend on probe type (Chambers, unpubl. data). Red-cell fractions (50 μl) were digested overnight at 37°C in a solution containing proteinase K (BRL, Bethesda Research Laboratories) and sodium dodecyl sulphate (BRL) according to the method of Maniatis et al. (1982). Red-blood-cell debris was removed by solvent extraction with phenol and chloroform/isoamyl alcohol (Maniatis et al. 1982). DNA was precipitated with ethanol, air-dried, and redissolved in TE buffer (10 mM Tris. Cl, 1 mM EDTA, pH 8.0). DNA yields were estimated by gel electrophoresis and comparison with bacteriophage lambda DNA quantitative standards. Samples of DNA (2 μg) were digested with the restriction endonuclease *Hae*III (BRL) as per the supplier's instructions, then electrophoresed under standard conditions (Maniatis et al. 1982) on 1% agarose gels in TBE buffer (0.089 M Tris, 0.089 M Boric acid, 0.002 M EDTA). The separated DNA fragments in the gels were depurinated and transferred by Southern blotting onto Amersham Hybond N nylon membranes (Southern 1975) in 20× SSC (3 M NaCl, 0.3 M sodium citrate, pH 7.0). Blots were baked for 2 h at 80°C under vacuum to bind DNA to the membrane, then hybridized overnight at 55°C with ^{32}P-labelled 33.15 or 3'HVR probe, washed under conditions appropriate for the analysis of human DNA (Fowler et al. 1988, Jeffreys et al. 1985), and autoradiographed at −70°C.

We calculated the degree of genetic similarity (D) from DNA fingerprints as the proportion of bands (DNA fragments) shared between each pair of individuals, that is

$$D = 2n_{AB}/(n_A + n_B),$$

where n_A and n_B are the number of bands in the fin-

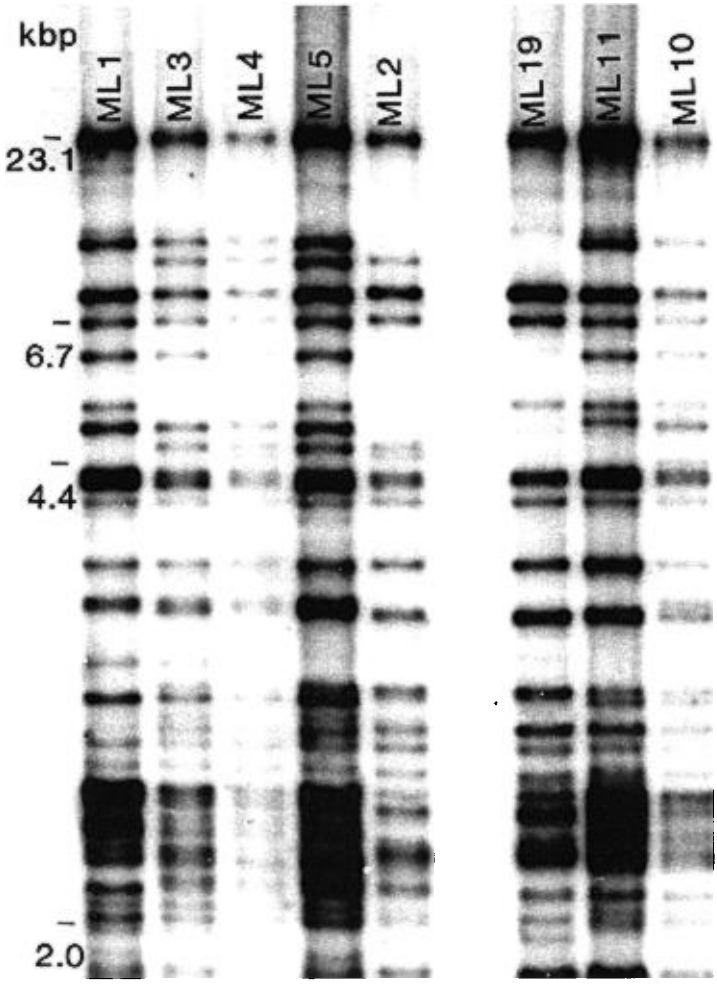

Fig. 2. Example of a DNA fingerprint of Blue Ducks using probe 33.15. Molecular markers shown in left lane. ML1 and ML2 are parents of ML3-5; ML10 is father of ML11; ML1, ML2, ML10, and ML19 are not known to be related. All individuals come from lower section of Manganuiateao River.

gerprints of individuals A and B, and n_{AB} is the number of bands shared by A and B (Wetton et al. 1987). D is equivalent to Jeffreys' (1985a) statistics x between unrelated individuals. All clear bands larger than 2 kilobase pairs (kbp) were scored. Poor resolution on some autoradiographs meant that a few individuals could only be scored for one probe ("no data" entries in Table 1). Comparisons between individuals on different gels were made by photocopying one autoradiograph to the exact size of the other. This was standardized by including control Blue Duck samples and a lambda-*Hin*dIII molecular-weight standard on each gel. Individual fingerprints were cut out of the photocopy to allow side-by-side comparison. These were viewed by three of us but scored by only one. Based on the extensive experience of one of us (GKC) with human forensic data, the error resulting from this procedure will be less than 5%. Genetic similarity among a group of birds was estimated by the mean of D-values between each pair of individuals in the group. All statistics (mean ± standard deviation) were calculated independently for each of the two probes.

Results

We scored $\bar{x} = 22.3$ (±4.3) bands greater than 2 kbp per individual for the 33.15 probe and 21.3 (±3.2) bands for 3'HVR. An example of a DNA fingerprint is shown in Fig. 2.

We compared genetic similarity between North and South Islands, between regions, between rivers within regions, between sections

TABLE 2. Genetic similarity given as mean $D \pm$ SD (n) within and between populations of Blue Duck.

Comparison	Probe	
	3'HVR	33.15
Between islands		
North vs South Island	0.24 ± 0.10 (53)	0.17 ± 0.10 (63)
Between regions		
Wanganui vs West Coast	0.24 ± 0.09 (26)	0.17 ± 0.09 (36)
East Cape vs West Coast	0.24 ± 0.11 (27)	0.18 ± 0.11 (27)
Wanganui vs East Cape	0.23 ± 0.09 (109)	0.21 ± 0.07 (74)
Between rivers within regions		
Manganuiateao vs Wanganui	0.26 ± 0.08 (29)	0.30 ± 0.08 (40)
Motu vs Waioeka	0.29 ± 0.06 (12)	0.25 ± 0.10 (17)
Between sections of the Manganuiateao		
Lower vs middle	0.36 ± 0.09 (29)	0.39 ± 0.19 (26)
Lower vs upper	0.34 ± 0.07 (29)	0.35 ± 0.11 (25)
Middle vs upper	0.38 ± 0.10 (20)	0.35 ± 0.05 (3)
Within rivers		
All Manganuiateao	0.39 ± 0.13 (110)	0.46 ± 0.18 (102)
Lower Manganuiateao	0.45 ± 0.17 (31)	0.51 ± 0.19 (55)
Lower + middle Manganuiateao	0.41 ± 0.13 (70)	0.47 ± 0.19 (82)
Middle + upper Manganuiateao	0.38 ± 0.09 (36)	0.42 ± 0.11 (7)
Takaputahi	0.37 ± 0.11 (40)	0.36 ± 0.13 (41)

of rivers, and within rivers or sections of rivers. We interpret the results (Tables 2 and 3) to indicate a hierarchical genetic structure that corresponds with geographic structure. Genetic similarity increased with decreasing geographic separation between samples. Thus, individuals from the different islands and regions were the most dissimilar, whereas Blue Ducks from within the same river showed a high degree of genetic similarity.

Even totally unrelated individuals share some bands. This is to be expected, as only a finite number of DNA fragments can be scored for a fingerprint. However, DNA-fingerprint bands of similar mobility (molecular weight) in unrelated individuals are not necessarily isoallelic (Hill 1987). Blue Ducks from the different islands or from geographically separate regions share a "background" level of genetic similarity of $D = 0.17$–0.24 (Table 2). A slightly higher degree of similarity was found between regions within North Island than between North and South Islands ($P < 0.01$ for 33.15).

Individuals from within the same region, but from different rivers or catchments were more similar to one another ($D = 0.25$–0.30) than to individuals from other regions. This was significant for two of four comparisons (Table 3).

The highest degree of genetic similarity ($D = 0.36$–0.46) was found among individuals from the same river. The genetic similarities within rivers were significantly higher than those between rivers for both probes (Table 3). There is evidence of a decrease in genetic similarity with increasing distance between samples within a single river, the Manganuiateao. The highest degree of similarity recorded occurred between individuals from within the lower section of the Manganuiateao ($D = 0.45$–0.51). Comparisons between individuals from different sections of the Manganuiateao yielded significantly lower values ($D = 0.34$–0.39). We consider the very high values of genetic similarity in the lower Manganuiateao a demographic response to the catastrophic volcanic lahar of 1975. Recolonization of this section of river seems to have been through settlement of a small number of related individuals, with little immigration of fledglings raised elsewhere on the river into the vacant habitat (Triggs et al. 1991, Williams 1991).

The Blue Ducks of the Takaputahi River also show a very high degree of genetic similarity to each other relative to birds from different catchments or regions. The genetic similarity within the Takaputahi sample was less than that in the lower Manganuiateao River (significant for both probes), although the influence of nat-

TABLE 3. Statistical differences between *D*-values calculated by Student's *t*-tests.

Comparison	Probe	
	3'HVR	33.15
Between North Island regions vs between Islands		
Wanganui/East Cape vs North/South Island	ns	**
Between rivers within regions vs between regions		
Motu/Waioeka vs Wanganui/East Cape	*	ns
Manganuiateao/Wanganui vs Wanganui/East Cape	ns	***
Within rivers vs between rivers within regions		
Within Manganuiateao vs Manganuiateao/Wanganui	***	***
Within Takaputahi vs Motu/Waioeka	*	**
Within a section vs between sections of the Manganuiateao		
Within lower vs lower/middle	*	**
Within lower vs lower/upper	**	***
Within different rivers		
Within lower vs within Takaputahi	**	***
Within lower + middle vs within Takaputahi	ns	***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, $P > 0.05$.

ural recolonization in the lower Manganuiateao may have affected this result. A more valid comparison may be with the combined middle + upper and lower + middle sections of the Manganuiateao River, which when combined represent a comparable length of river (although not a continuously sampled length) to the sampled length of the Takaputahi River. The Takaputahi sample had a slightly lower genetic similarity than either of these combined sections, but the difference was significant for only one probe in one comparison (Table 3). We infer from these results that highly interrelated populations of Blue Ducks occur even in unmodified habitats, where intermixing of genotypes from a large population is possible. However, a slightly greater degree of genetic similarity may occur within the smaller population on the more modified Manganuiateao River than occurs under more natural conditions.

DISCUSSION

The two probes independently showed similar levels of variability and gave similar results. The genetic similarity between Blue Ducks from geographically separated populations ($D = 0.17$–0.24) is comparable to unrelated individuals from within populations of five other species of birds ($D = 0.13$–0.28, probes 33.15 and 33.6; Burke and Bruford 1987, Wetton et al. 1987) and humans ($D = 0.21$, probe 33.15; Jeffreys et al. 1985b). In contrast, the average genetic similarity within populations of Blue Ducks was very high ($D = 0.36$–0.46). Comparable results have been found only in an inbred laboratory population of Japanese Quail (*Coturnix coturnix japonica*; $D = 0.47$, probe 33.6; Burke and Bruford 1987), a pair of wild Corn Buntings (*Miliaria calandra*; $D = 0.42$, probe 33.6; Burke and Bruford 1987), and Forbes Parakeet (*Cyanoramphus forbesi*; $D = 0.52$, probe 33.15; Marshall, Triggs, and Chambers, unpubl. data), a species known to have gone through a recent bottleneck of fewer than 20 individuals (Taylor 1975). The high genetic similarity of the Blue Ducks we sampled indicates that populations consist of related individuals, which inevitably results in extensive local inbreeding. Earlier (Triggs et al. 1991), we reported that all of the family groups in the lower section of the Manganuiateao were interrelated, and several examples of close inbreeding were found.

Because a high degree of genetic similarity was found in the more undisturbed Takaputahi population, as well as in the potentially isolated Manganuiateao population, we conclude that inbreeding per se is a natural feature of the Blue Duck social system and that limited dispersal of fledglings is the major demographic factor responsible for this population structure. For example, of 54 fledglings banded in the lower section of the Manganuiateao River, only one is known to have dispersed from its natal river (to the adjacent Whakapapa River). Of the 30

known survivors which established territories, 19 (63%) did so close to their natal range, separated from it at the time of settlement by two pairs or fewer (Williams 1991). An earlier (1972–1974) study of Blue Duck dispersal in Urewera National Park, North Island (Williams unpubl. data) found no movement of banded birds between catchments. A greater genetic similarity between adjacent rivers than between geographically isolated regions suggests that these populations are interconnected by a small degree of gene flow. The much higher similarity between individuals within a river compared to between rivers, and the decrease in genetic similarity with increased separation between samples even within a river, support the observational data. Our interpretation is that almost all gene flow (dispersal followed by successful territory establishment and breeding) occurs only over very short distances.

Most species of Anatidae tend to disperse widely (Greenwood 1987), and inbreeding on an extensive scale is rare (Anderson et al. 1991). Among other species of birds there are few examples of extensive inbreeding (Greenwood 1987), other than in some communally-breeding birds (Rowley et al. 1986, Craig and Jamieson 1988). However, this may be partly due to the difficulty, prior to the development of molecular genetic techniques, of documenting inbreeding. Exceptional studies include intensive, long-term banding studies (e.g. Greenwood et al. 1978, van Noordwijk and Scharloo 1981). Philopatry is common in avian species (Greenwood 1987, Anderson et al. 1991), implying that the potential for inbreeding is widespread.

Our findings have several implications for the conservation of Blue Duck. The Manganuiateao population, although large by present Blue Duck standards, may be unnaturally isolated from other Blue Duck populations by downstream agricultural and riverine development. If the natural structure of Blue Duck populations and, in particular, the amount of dispersal or gene flow between them are disrupted by fragmentation into small groups in river headwaters, then the probability of long-term survival of this species may be decreased by environmental, genetic, and stochastic effects (Soule 1987).

The deleterious genetic effects of isolation and small population size include inbreeding depression and loss of genetic variation. Inbreeding is usually deleterious in species that normally outbreed (Ralls et al. 1986, 1988, Charlesworth and Charlesworth 1987) due to the increased expression of a high accumulated load of deleterious recessive alleles and a loss of fitness associated with increased homozygosity (Frankel and Soule 1981, Templeton 1987). When inbreeding is part of the natural social system of a species, inbreeding depression is far less severe, as the genetic load is usually low (Templeton and Read 1983, Templeton 1987). Inbreeding appears to be a natural characteristic of the Blue Duck social system, although small remnant populations may have higher levels of inbreeding than occurs naturally. While Blue Ducks in small isolates are unlikely to be affected severely by inbreeding depression, even a small increase in inbreeding over that occurring naturally may produce harmful effects (Charlesworth and Charlesworth 1987).

Loss of genetic variation (heterozygosity and allelic diversity) is also predicted for small isolated populations and may be associated with loss of fitness and adaptability (Frankel and Soule 1981, Mitton and Grant 1984, O'Brien et al. 1985, Allendorf and Leary 1986). However, very little gene flow between populations is needed to prevent genetic isolation (Allendorf and Phelps 1981). Recent simulation studies (Boecklen 1986, Varvio et al. 1986) suggest that subdivided populations linked by a small amount of gene flow (as little as 1 migrant per generation) may preserve more genetic variation than an intact population of the same total size. We cannot estimate rates of gene flow in Blue Duck populations from our data. Gene flow into the Manganuiateao population appears to be lower than that into the less-modified Takaputahi population, but it may still be sufficient to prevent genetic isolation. Further studies are underway to investigate this possibility. Fortunately, the Manganuiateao population is large compared to many other remnant populations of Blue Duck, especially in North Island and, thus, may be less severely affected by isolation.

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APPENDIX. Allozyme electrophoresis of Blue Ducks.

Red cell and serum components were subjected to horizontal starch gel electrophoresis in gels of 12% Sigma starch. We followed the staining methods of Selander et al. (1971), Harris and Hopkinson (1976), and Allendorf et al. (1977), as described by Triggs et al. (1989). We resolved 24 allozyme loci: Ada (EC no. 3.5.4.4), Ak (2.7.4.3), Est (2 loci; 3.1.1.1), general proteins and hemoglobin (6 loci), Gd (1.1.1.49), Gpi (5.3.1.9), Icd (1.1.1.42), Ldh (2 loci; 1.1.1.27), Mdh (1.1.1.37), Me (1.1.1.40), Mpi (5.3.1.8), Pep (3.4.11), Pgd (1.1.1.44), Sod (3 loci; 1.15.1.1), and unidentified dehydrogenase.

Only two loci (Gd and Gpi) were polymorphic, and each was represented by a single heterozygote in the Takaputahi sample. We estimated that in the Takaputahi sample the extent of polymorphism (P) was 0.083 and heterozygosity (H) was 0.007. Overall for the Blue Duck, polymorphism was 0.083 and heterozygosity was 0.002. No variation was detected in other populations, which were fixed for the same alleles; therefore, no estimate of genetic differentiation between populations (F_{ST}; Nei and Chesser 1983) could be made. The level of allozyme variation detected in Blue Ducks was very low compared to the average for 26 other species of Anatidae ($H = 0.033$; Patton and Avise 1986). Low levels of allozyme polymorphism have been described for many species that have gone through severe bottlenecks in population size (Bonnell and Selander 1974, Schwaeregle and Schaal 1979, O'Brien et al. 1983). Although the Blue Duck is presently listed as threatened, investigators have not determined whether it has gone through any major recent bottlenecks that would affect all populations studied. However, historical records of Blue Ducks are sparse and catastrophic events, such as the major volcanic eruptions centered on Lake Taupo within the last 2,000 years (Challies 1978), almost certainly would have decimated many Blue Duck populations in the central and eastern portions of North Island. A few other avian species also have low levels of variation ($H < 0.01$) for which no explanation is given (Guttman et al. 1980, Guttierez et al. 1983, Patton and Avise 1986).