Lingering genetic evidence of North American mallards (*Anas platyrhynchos*) introduced to New Zealand

Patrick-Jean Guay[1*], Murray Williams[2] and Randall W. Robinson[1]

[1] Institute for Sustainability and Innovation, College of Engineering and Science, Victoria University – Footscray Park Campus, PO Box 14428, Melbourne, VIC 8001, Australia
[2] School of Biological Sciences, Victoria University, PO Box 600, Wellington, New Zealand
*Author for correspondence (Email: patrick.guay@vu.edu.au)

Published online: 21 November 2014

Abstract: Introduced species are becoming part of the landscape around the world. Unfortunately, in many cases, the exact source population for these introduced species is not known, which can hamper their proper management. Genetic investigations can shed light on the introduction process and we used the New Zealand mallard (*Anas platyrhynchos*) population as a case study to demonstrate the insights that genetics can provide. The mallard (*Anas platyrhynchos*) was introduced to New Zealand from the United Kingdom (UK) and the United States (USA) for recreational hunting in the late 19th and early 20th centuries. We used mitochondrial DNA (mtDNA) sequencing to detect any enduring genetic evidence of the two small US-sourced introductions, both of which came from the same game farm. If the US-sourced introductions were pivotal in establishing mallards in New Zealand, as has been suggested, we expected that the North-American-specific haplotypes (type-B) would be common in New Zealand's present-day mallards. From a nationally distributed sample of 122 mallards, we identified 11 mallard mtDNA haplotypes, comprising 10 type-A haplotypes but only one North-American-specific haplotype, which was shared by six ducks. Mallards displayed low nucleotide and haplotype diversity. We also detected weak genetic structure between North and South Island populations ($\Phi_{ST} = 0.0961$). We conclude that the concerted breeding and release of mallards between 1940 and 1960 that followed the US-sourced introductions was fuelled largely by descendants of previous UK-sourced introductions. Furthermore, we speculate that some of the US-sourced mallards may have been descended from game-farm mallards imported from Europe and therefore may not have been representative of wild US ducks.

Keywords: acclimatisation; introduction; introgression; mitochondrial DNA

Introduction

The identification of source populations is increasingly being seen as critical to understanding the processes of biological invasions (Ahlroth et al. 2003). The success or otherwise of introduced organisms depends not only on the physical and ecological tolerances of the species, but also on a host of genetic factors (Vasquez et al. 2006; Mirnezhad et al. 2012). It is widely recognised that populations founded by a small number of individuals will have lower genetic diversity than the source population (Nei et al. 1975). This, in turn, will reduce the invader's ability to respond to selection (Falconer & Mackay 1989), which can potentially compromise their success in establishing permanent populations. Conversely, genetically diverse invading populations are likely to be more successful. For example, multiple introductions of multiple strains of the wetland grass *Phalaris arundinacea* from Europe to the United States (USA) has resulted in a highly genetically diverse population that is able to adapt to a wider range of habitats than the source populations, due to the formation of new genotypes through hybridisation between strains (Lavergne & Molofsky 2007). In contrast, low genetic diversity caused by a low number of founders has allowed Argentine ants (*Linepithema humile*) to thrive due to decreased intraspecific aggression (Tsutsui et al. 2000). Epidemiological molecular techniques, while commonly used to trace diseases of various virulence (Zelner et al. 2010), are not commonly used to trace animal and plant invasions (Durka et al. 2005; Darling et al. 2008).

Knowledge of the source population can provide important information for management of introduced species. For example, investigations into the genetic make-up of red foxes (*Vulpes vulpes*) on Phillip Island in Victoria, Australia, demonstrated strong genetic differentiation between the island and the mainland, suggesting that most island foxes are locally bred and not immigrants from the mainland (Lade et al. 1996). Extirpation of foxes from Philip Island may thus be possible. Unfortunately, knowledge about the source population(s) of introduced species is often lacking, especially in cases where multiple introduction events are suspected (e.g. multiple introductions of HIV in South America (Artenstein et al. 1995); multiple introductions of giant reed in North America (Tarin et al. 2013)). In this study, we investigated the genetic make-up of the mallard (*Anas platyrhynchos*) population in New Zealand as a case study to demonstrate how genetic investigations can provide insights into the introduction process.

The mallard (*Anas platyrhynchos*), a dabbling duck ubiquitous throughout Eurasia and North America, was introduced to New Zealand as sporting quarry from the late 19th century (Thomson 1922; Dyer & Williams 2010). Hybridisation with its local ecological equivalent, the grey (Pacific black) duck (*Anas superciliosa*) was soon reported (Thomson 1922). Due to hybrids being fertile (Phillips 1915), very few pure grey ducks may now exist in New Zealand and the species is on a pathway to extinction in New Zealand via introgression (Gillespie 1985; Rhymer & Simberloff 1996; Williams & Basse 2006; Guay & Tracey 2009). Initial mallard introductions

were sourced from game farms in the United Kingdom (UK). Dyer and Williams (2010) identified 14 importations totalling 115 birds prior to 1910 and 3 further importations to 1930, totalling at least 400. Despite their subsequent extensive captive breeding and release in many parts of New Zealand these mallards only established locally. This prompted two private importations (by C. A. Whitney) of 50 pairs (one male died in transit and thus 99 birds were received) in 1937 and 45 eggs in 1941, both importations from Connecticut, USA. Whitney had long argued that introductions of wild, migratory stock were needed to establish mallards as a widespread sporting bird in New Zealand (Whitney 1942; Dyer & Williams 2010). These importations initiated a vigorous release effort of least 25 000 mallards between 1940 and 1960 (table 2 in Dyer & Williams 2010) and, by 1960, mallards had become more numerous than grey ducks throughout all agricultural landscapes. Mallards, and mallard-like hybrids, are now New Zealand's most numerous and widespread waterfowl (Robertson et al. 2007).

The increase in mallard abundance has led to the contention that Whitney was correct; wild birds from the USA – with more mobile (i.e. migratory) habits – were necessary for the widespread establishment of mallards in New Zealand (e.g. Caithness 1982; McDowall 1994). However, the high numbers released during the 1940s and 1950s may have been the most important determinant of the mallard's success just as numbers released has been shown to be the key determinant for other successful avian introductions (Veltman et al. 1996; Cassey et al. 2004; Lockwood et al. 2005).

In this paper we test the hypothesis that introductions of wild birds from the USA played a significant role in the naturalisation of mallards in New Zealand. We predict that if this was the case, a large number of New Zealand's present-day mallards will carry an mtDNA haplotype reflecting their North American ancestry. Our evaluation arises from Avise et al.'s (1990) identification of two primary haplotype lineages (type-A and type-B) in mallards. Type-A haplotypes occur throughout the mallard's entire natural range. Type-B haplotypes are unique to North American mallards and other members of the mallard complex (American black duck *Anas rubripes*, mottled duck *A. fulvigula*, and Mexican duck *A. diazi*) and the Eastern spot-billed duck (*A. zonorhyncha*) from Asia (McCracken et al. 2001; Kulikova et al. 2004; Hou et al. 2012). The present-day occurrence of type-A haplotypes in North America is considered to be due to the extensive releases of game-farm mallards for recreational shooting in the USA since the 1930s (Kulikova et al. 2005; Harrigan 2006; Kraus et al. 2011). For example, close to half a million game-farm-bred mallards are thought to have been released to the wild by 1940 in the State of New York alone (Bump 1941). This contention is supported by the low frequency of type-A haplotypes observed in pre-1930 mallard samples from the east coast of the USA (Harrigan 2006).

Methods

Sample collection

Tissue samples were collected from ducks shot by hunters during the 1991 and 1998 shooting seasons. The locality of each sample was recorded at the regional level to match the regional locality detail of the original mallard releases (Dyer & Williams 2010). The phenotype of each duck was scored using the protocol of Rhymer et al. (1994), which produces low scores (minimum 1) for ducks most similar to grey ducks and higher scores (maximum 25) for ducks most similar to mallards. We report results from 122 specimens obtained from throughout New Zealand with phenotype scores greater than 15 (Fig 1). Scores in the 15–25 range are clearly indicative of mallard-like hybrids or pure mallards.

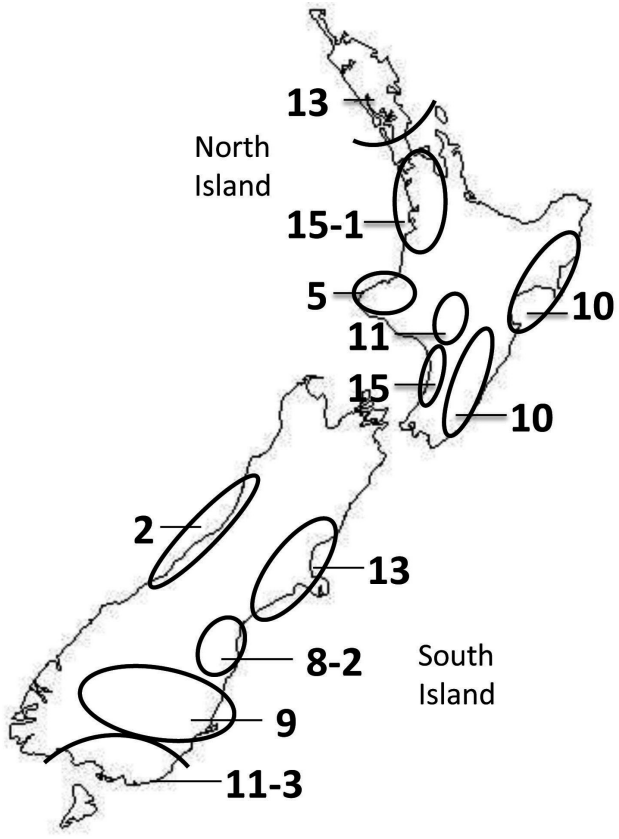

Figure 1. Distribution of samples collected from duck hunters during the 1991 and 1998 hunting seasons. For each region, we indicate the number of specimens followed by the number carrying the type-B haplotype where detected. Two specimens from the Chatham Islands are not depicted.

Sequencing

We extracted DNA from tissue samples using the salting-out method (Bruford et al. 1992). We amplified the 5' end of the mitochondrial genome control region (positions 79–773 in the chicken genome) using primers L78 (Sorenson & Fleischer 1996) and H774 (Sorenson et al. 1999). We performed polymerase chain reactions (PCR) on a BIO-RAD MyCycler thermal cycler using standard recipes (Guay et al. 2010). Betaine (1.0 M) was added to PCR reactions to increase yield (Johnson & Dunn 2006). We performed PCR amplification as follows: one cycle at 94°C for 7 min followed by 45 cycles at 94°C for 20 s, 52°C for 20 s and 72°C for 60 s, and one cycle at 72°C for 7min. The products of PCR were separated by agarose gel electrophoresis, gel-purified using the QIAquick Gel Extraction Kit (Qiagen, Valencia, CA), and sequenced commercially (Macrogen, Seoul, Republic of Korea). We sequenced both strands of the mtDNA.

The region targeted (667 bp) contains most of Domain I and all of Domain II of the control region (Quinn & Wilson 1993). Sequences from complementary mtDNA strands were

reconciled using SEQUENCHER 3.1 (Gene Codes, Ann Arbor, USA). Sequences were archived in GenBank (accession numbers: KJ755705–KJ755826).

Five specimens showed a single ambiguous site in their mtDNA, suggesting heteroplasmy. To confirm the polymorphism, DNA from all five samples was re-extracted in a different laboratory and the mitochondrial region was re-amplified. In all cases, identical results were obtained suggesting that these samples may represent genuine cases of heteroplasmy. Both haplotypes for these five specimens were considered separately in the analysis. We calculated haplotype ($h \pm SD$) and nucleotide diversity ($\pi \pm SD$) using ARLEQUIN 3.01 (Excoffier et al. 2005). The HKY model (Hasegawa et al. 1985) was identified using MODELTEST 3.7 (Posada & Crandall 1998) as the best-fit model of nucleotide substitution for mtDNA in our dataset. To investigate genetic structure between the North and South Islands, we calculated pairwise Φ_{ST} values for mtDNA between the two islands using the closely related K80 (Kimura 1980) nucleotide substitution model in ARLEQUIN 3.01, as the HKY model is not available in this software. We confirmed the haplotype groupings (mallard type-A, mallard type-B, and grey duck) by comparing with other published sequences. We calculated unrooted networks using the software NETWORK 4.2.0.1 (Fluxus Technology) to infer relationships between haplotypes.

Results

We found 16 distinct haplotypes (A–P in Fig. 2). Eleven mallard haplotypes were identified, 10 (from 111 birds) were type-A and 1 (from 6 birds) was type-B. Thus, there is little evidence of the widespread distribution of North-American-specific haplotypes in current mallard populations in New Zealand.

Both haplotype (0.5926 ± 0.0418) and nucleotide diversities (0.0032 ± 0.0020) were low compared with mallards sampled in their natural ranges (e.g. table 1 in Kraus et al. 2011).

Of the three common type-A haplotypes (H, I, J; Fig. 2), I was identified from throughout the country, 25 (93%) of 27 haplotype H samples were from the North Island, and haplotype J was more common in the South Island than the North Island. The most common haplotype (I) corresponded with Kulikova et al.'s (2005) haplotype A7. Of the ducks with type-B haplotypes, three were from Southland, two from the central South Island, and one from the Waikato (Fig. 1). The haplotype frequency differences were confirmed by significant Φ_{ST} between the North and South Island ($\Phi_{ST} = 0.09617$; $P < 0.001$).

Even though all ducks showed phenotypic characters indicative of mallard or mallard-like hybrids, five unique haplotypes (from five birds) were clearly of grey duck origin. These birds had phenotype scores of 19–25.

Discussion

Importance of the North American mallard introductions

If wild North American mallards played a significant role in the naturalisation of mallards in New Zealand, we predicted a large number of New Zealand's present-day mallards would carry the type-B haplotype. Contrary to our prediction, we found a very low (5%) frequency of type-B haplotypes in our sample. Our data thus clearly demonstrate that wild North American mallards played a role in the establishment of mallards in New Zealand, but the low frequency of type-B haplotypes suggests that that role was minor.

Two non-mutually-exclusive explanations may explain the low frequency of type-B haplotypes in contemporary New Zealand mallards: the mallards sourced by Whitney were not all of wild origin and/or the extensive breeding programmes initiated following importations resulted in dilution of the type-B haplotypes in the resulting progeny.

Both of Whitney's importations were obtained from the same supplier (C. L. Sibley, Sunnyfield Game Farm,

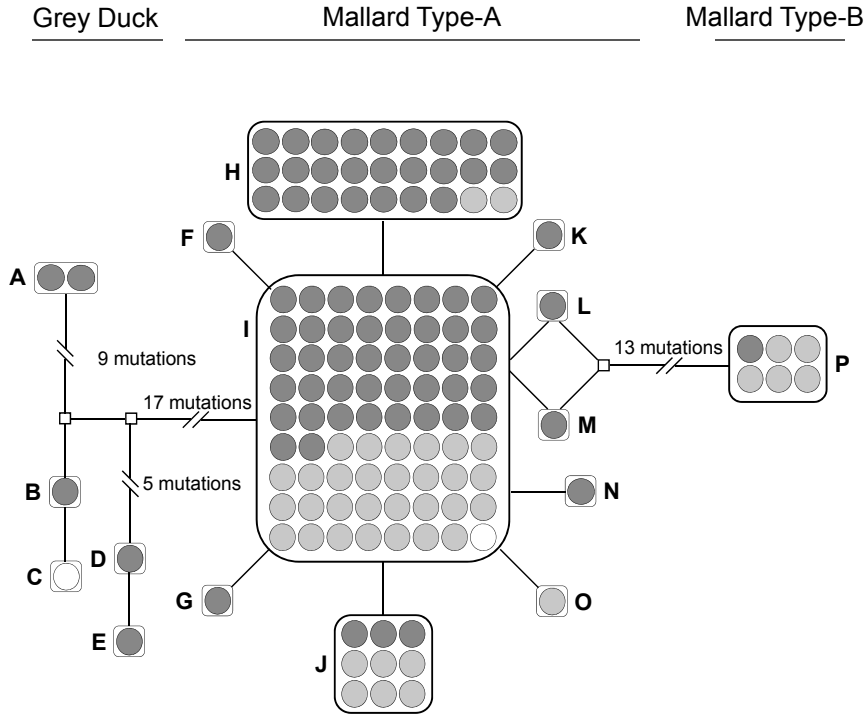

Figure 2. Unrooted haplotype network for the 16 unique mitochondrial control region haplotypes detected in our sample of 122 individuals. Dark grey circles represent sequences from the North Island, light grey represent sequences from the South Island, and white circles represent sequences from the Chatham Islands. Haplotypes are labelled from A to P. A total of 127 sequences are presented, as five individuals contributed two sequences.

Wallingford, CT; Dyer & Williams 2010). This single population of origin may sufficiently explain why only one type-B haplotype was identified in our study, but C. L. Sibley was noted for his exotic waterfowl importations, especially from sources in Holland. Therefore, there is a good chance that he had captive mallards sourced from Europe and was using these to supply mallards to local hunting clubs for release, rather than acclimatising wild-caught mallards to captivity (Ian Gereg, Livingston Ripley Waterfowl Conservancy, USA, pers. comm.). Thus, although they were clearly imported from North America, quite possibly not all of the birds received by Whitney were of exclusive North American wild ancestry. Given that only one of 100 birds died during the 6 weeks of rail and ship travel to New Zealand, then all ducks probably had a long captive ancestry.

Present-day game-farm mallards in the eastern USA have type-A haplotypes including our haplotype I (which corresponds with haplotype A7; Kulikova et al. 2005) (Harrigan 2006). Furthermore, wild mallards in the eastern USA contain this and other type-A haplotypes (Kraus et al. 2011) because of the millions of game-farm mallards released in this region since the 1930s (e.g. Foley et al. 1961; Osborne et al. 2010). Although the current frequency of type-A haplotypes in wild mallards is high in the eastern USA (70%), preliminary results based on historical samples suggest that type-A haplotype frequency was much lower (14%) prior to the 1930s (Harrigan 2006). Thus if only wild mallards were imported and if these wild mallards played a crucial role in the naturalization of the species in New Zealand, a greater diversity of type-B haplotypes would have been expected.

The impact of Whitney's importations may also have been diluted after arrival into New Zealand. Of the 45 eggs imported, only 20 (44%) hatched and 19 birds survived to be distributed to two hunters' clubs (Whitney 1942). The birds' fates were unrecorded, but if they were bred and their progeny released, it would only have been locally. Whitney's 1937 live-bird importation comprised 50 pairs. Therefore, the type-B mtDNA haplotype introduction arises from a maximum of 50 hens. However, almost half of this importation by Whitney was distributed immediately to interested breeders and a government game farm (Dyer & Williams 2010). Little is known about the fate of these birds distributed to the government other than that they bred and that their progeny was released locally for about 10 years.

Whitney retained some of the imported birds and commenced a concerted breeding programme. He distributed over 2000 eggs during 1938–39 to the Northland, Auckland, Wellington, and Otago acclimatisation societies. During 1940 and 1941 he sent an unspecified number (numbering in hundreds) of eggs to the Southland, North Canterbury, South Canterbury, Nelson and West Coast acclimatisation societies in the South Island, provided at least 5000 eggs to the Auckland and Northland acclimatisation societies, and released 1200 ducks in the Waikato region. He continued to supply eggs and release birds annually until 1948 (Dyer & Williams 2010). In short, Whitney distributed many thousands of mallard eggs to most regions of New Zealand, but not all of the eggs Whitney distributed would have carried the type-B haplotype. To achieve his high egg production Whitney caged a single male with up to five females and sought to improve the local birds by crossing them with the North American birds (Whitney 1942). Many of the females in his breeding programme must have carried a type-A haplotype, and so too the eggs Whitney distributed. It would not have been possible for the few North American females Whitney retained to have produced all the eggs distributed. Whitney's larger post-1940 egg distributions, those that stimulated a resurgence of mallard breeding and release nationwide, may thus have contained a smaller percentage of type-B haplotypes than his distributions in the first 2–3 years immediately after the North American birds reached New Zealand.

Introgression

The presence of grey duck haplotypes in our sample indicates that introgression between mallards and grey ducks had progressed extensively in New Zealand at the time the samples were collected (1991, 1998). Rhymer et al. (1994) previously reported introgression of mallard mtDNA into grey duck populations and of grey duck mtDNA into mallard populations and our results confirm the latter.

Genetic diversity and structure

Low genetic diversity in New Zealand mallards compared with mallards from Europe, Eurasia, Asia and North America (Kulikova et al. 2004, 2005; Harrigan 2006; Kraus et al. 2011; Hou et al. 2012) is indicative of a low number of founding individuals or of the founders reaching New Zealand from just a few sources which in themselves may have had low founder numbers. The low number of founders hypothesis is supported by Dyer & Williams' (2010) narrative, which identified 14 UK-sourced importations (of 115 birds) during the initial (pre-1910) period of mallard acclimatisation attempts, and 3 (also UK-sourced) importations thereafter to 1930. Although the precise UK sources of most importations cannot be determined, it is likely all of the birds came from game farms, had a lineage of captive confinement (and limited mtDNA haplotype diversity), and were mostly sourced from south-eastern England close to London, the principal port of embarkation to New Zealand.

The observed genetic structure between North and South Islands might indicate that some geographic differences persist from the initial introductions, possibly a consequence of the mallard's initially sedentary nature. Band recoveries in the 1950s demonstrated that mallards were then much less dispersive than grey ducks and that most birds were recovered within 40 km of their banding site (Balham & Miers 1959). Grey ducks also display some level of genetic differentiation within their range (Rhymer et al. 2004).

Management of introduced species

There are many different reasons why knowledge of the source population of an introduced species is very important. Different source populations may have different behaviours and thus may need to be managed accordingly. This is clearly demonstrated in the case of the mallard. Worldwide mallard introductions can be either from wild or domestic stocks. While wild mallards are released for recreational shooting (e.g. Foley et al. 1961; Dyer & Williams 2010), domestic mallards often escape captivity and become established in the wild (e.g. Braithwaite & Miller 1975). Both strains differ markedly in behaviour, with domestic mallards being more conspicuous and relying heavily on forced copulation to obtain mating, which likely results in higher hybridisation threat (Desforges & Wood-Gush 1976; Guay & Tracey 2009; Guay et al. 2014). Similarly, the justification behind the importations of mallards from North America was that the North American mallards were more migratory than the Eurasian mallards and thus were

required for the naturalisation of the species in New Zealand (Whitney 1942). Although naturalisation did take place after the large-scale introduction programme following the North American importations, it is not clear whether the success was the result of having a population of more mobile ducks or due to releasing more ducks into the countryside (Dyer & Williams 2010).

Furthermore, it is also very important to understand where the source population is in order to prevent reintroductions following extermination. For example, a study on the genetic diversity of the invasive European green crab (*Carcinus maenas*) on the US west coast suggested that, although the species is now widespread, the current population is the result of a single introduction event (Tepolt et al. 2009). Early detection followed by extermination would thus have been highly successful in controlling this invasive species since ongoing introductions do not seem to be a problem. In cases where there is ongoing migration between the introduced population and the source population, vigilance is even more important. For example, mallards that have colonised Lord Howe Island have driven the local grey duck population to extinction (Tracey et al. 2008). Both banding records (J. P. Tracey & C. Haselden unpubl.) and genetic analyses (A. J. Taysom & P.-J. Guay unpubl.) suggest that mallards self-colonised Lord Howe Island from New Zealand. Extermination of mallards on Lord Howe has been proposed, but any such extermination will be in vain if not coupled with ongoing monitoring since recolonisation will be an ongoing issue (Tracey et al. 2008).

The current mallard population in New Zealand is of mixed European and North American origin. Does this knowledge provide insight into the management of the introduced species or provide information relevant to the protection of the grey duck? Unfortunately, the answer to both questions is no. Mallards are too well established to consider extermination, especially since they are highly prized by hunters (Muller 2009). Furthermore, while there may have been differences in behaviour between the two original strains, there is clear evidence that both strains were hybridised as part of the captive breeding and release programme and thus most mallards in New Zealand today are likely to be of mixed origin (Dyer & Williams 2010). A recent genetic study of the status of the grey duck demonstrated that the species is likely to be extinct in its pure form in New Zealand (Muller 2009). If any pure populations subsist, they should be identified and brought into captivity for preservation with the idea of potentially releasing some individuals on islands like Norfolk, Auckland, or Campbell Island where mallard colonisation could be more easily monitored (Rhymer et al. 2004; Muller 2009).

Conclusion

Overall our results demonstrate the continuing presence of a North American mallard haplotype in the gene pool of New Zealand's mallards. Its low frequency, in addition to being a possible artefact of our sampling and influenced by genetic drift, is most likely a consequence of the multifarious breeding and release programmes that followed the arrival of Whitney's mallards from North America, compounded by the poor survival probability of newly-released captive-raised birds (Balham & Miers 1959).

Was the introduction of US-sourced wild mallards necessary to ensure the establishment of the mallard in New Zealand? The low presence of the type-B haplotype detected in contemporary mallards in New Zealand suggests that few wild females of North American origin participated in the naturalisation of the mallard in New Zealand. A much greater, and more widespread, presence of the type-B haplotype would be necessary to indicate that wild US-sourced mallards, rather than UK-sourced or game-farm mallards, played an essential role in the establishment of the species in New Zealand. Conversely, by importing the North American birds C. A. Whitney stimulated a concerted and persistent mallard breeding and release programme in every region of the country. Without this stimulus, perhaps the spread of mallards and their eventual ecological ascendancy over grey ducks might have taken much longer to occur (Williams & Basse 2006).

Acknowledgements

MW thanks Ian Gereg of the Livingston Ripley Waterfowl Conservancy, Litchfield, Connecticut, USA, for comments about C. L. Sibley, and acknowledges funding support from the Southland, Otago, Wellington and Auckland-Waikato Fish & Game councils. This research was also funded by a Victoria University Fellowship to P-JG.

References

Ahlroth P, Alatalo RV, Holopainen A, Kumpulainen T, Suhonen J 2003. Founder population size and number of source populations enhance colonization success in waterstriders. Oecologia 137: 617–620.

Artenstein AW, Brown AE, VanCott TC, Mascola JR, Burke DS, Coppola J, Galbarini E, Schonbrood P, Carr JK, Sanders-Buell E, McCutchan FE 1995. Multiple introductions of HIV-1 subtype E into the western hemisphere. The Lancet 346: 1197–1198.

Avise JC, Ankney CD, Nelson WS 1990. Mitochondrial gene trees and the evolutionary relationship of Mallards and Black Ducks. Evolution 44: 1109–1119.

Balham RW, Miers KH 1959. Mortality and survival of grey and mallard ducks banded in New Zealand. Wildlife Publication 5. Wellington, New Zealand, Department of Internal Affairs. 56 p.

Braithwaite LW, Miller B 1975. The mallard, *Anas platyrhynchos*, and the mallard–black duck, *Anas superciliosa rogersi*, hybridization. Australian Wildlife Research 2: 47–61.

Bruford MW, Hanotte O, Brookfield JFY, Burke T 1992. Single-locus and multilocus DNA fingerprinting. In: Hoelzel AR ed. Molecular genetic analysis of populations: a practical approach. Oxford, UK, IRL Press. Pp. 225–269.

Bump G 1941. The introduction and transplantation of game birds and mammals into the state of New York. Transactions of the North American Wildlife Conference 5: 409–420.

Caithness TA 1982. Gamebird hunting: problems, questions and answers. Wellington, The Wetland Press. 96 p.

Cassey P, Blackburn TM, Sol D, Duncan RP, Lockwood JL 2004. Global patterns of introduction effort and establishment success in birds. Proceedings of the Royal Society of London B – Biological Sciences 271 (Suppl. 6): S405–S408.

Darling JA, Bagley MJ, Roman J, Tepolt CK, Geller JB 2008. Genetic patterns across multiple introductions of

the globally invasive crab genus *Carcinus*. Molecular Ecology 17: 4992–5007.
Desforges MF, Wood-Gush DGM 1976. Behavioural comparison of Aylesbury and Mallard ducks: sexual behaviour. Animal Behaviour 24: 391–397.
Durka W, Bossdorf O, Prati D, Auge H 2005. Molecular evidence for multiple introductions of garlic mustard (*Alliaria petiolata*, Brassicaceae) to North America. Molecular Ecology 14: 1697–1706.
Dyer J, Williams M 2010. An introduction most determined: Mallard (*Anas platyrhynchos*) to New Zealand. Notornis 57: 178–195.
Excoffier L, Laval G, Schneider S 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evolutionary Bioinformatics Online 1: 47–50.
Falconer DS, Mackay TFC 1989. Introduction to quantitative genetics. Harlow, UK, Pearson Education.
Foley DD, Benson D, DeGraff LW, Holm ER 1961. Waterfowl stocking in New York. New York Fish and Game Journal 8(1): 37–48.
Gillespie GD 1985. Hybridization, introgression, and morphometric differentiation between Mallard (*Anas platyrhynchos*) and Grey Duck (*Anas superciliosa*) in Otago, New Zealand. The Auk 102: 459–469.
Guay P-J, Tracey JP 2009. Feral Mallards: a risk for hybridisation with wild Pacific Black Ducks in Australia? The Victorian Naturalist 126 (3): 87–91.
Guay P-J, Chesser RT, Mulder RA, Afton AD, Paton DC, McCracken KG 2010. East–west genetic differentiation in Musk Ducks (*Biziura lobata*) of Australia suggests late Pleistocene divergence at the Nullarbor Plain. Conservation Genetics 11: 2105–2120.
Guay P-J, Taysom AJ, Robinson RW, Tracey J 2014. Hybridization between the Mallard and native dabbling ducks: causes, consequences and management. Pacific Conservation Biology 20:41–47.
Harrigan RJ 2006. Global phylogeography of the Mallard complex (genus *Anas*) : speciation, hybridization, and lineage sorting. Unpublished PhD thesis, Boston University, Boston, USA. 231 p.
Hasegawa M, Kishino H, Yano T 1985. Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22: 160–174.
Hou ZC, Yang FX, Qu LJ, Zheng JX, Brun JM, Basso B, Pitel F, Yang N, Xu GY 2012. Genetic structure of Eurasian and North American mallard ducks based on mtDNA data. Animal Genetics 43: 352–355.
Johnson JA, Dunn PO 2006. Low genetic variation in the Heath Hen prior to extinction and implications for the conservation of prairie-chicken populations. Conservation Genetics 7: 37–48.
Kimura M 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120.
Kraus RHS, Zeddeman A, van Hooft P, Sartakov D, Soloviev SA, Ydenberg RC, Prins HHT 2011. Evolution and connectivity in the world-wide migration system of the mallard: Inferences from mitochondrial DNA. BMC Genetics 12: 99.
Kulikova IV, Zhuravlev YN, McCracken KG 2004. Asymmetric hybridization and sex-biased gene flow between Eastern Spot-billed Ducks (*Anas zonorhyncha*) and Mallards (*A. platyrhynchos*) in the Russian Far East. The Auk 121: 930–949.
Kulikova IV, Drovetski SV, Gibson DD, Harrigan RJ, Rohwer S, Sorenson MD, Winker K, Zhuravlev YN, McCracken KG 2005. Phylogeography of the Mallard (*Anas platyrhynchos*): Hybridization, dispersal, and lineage sorting contribute to complex geographic structure. The Auk 122: 949–965.
Lade JA, Murray ND, Marks CA, Robinson NA 1996. Microsatellite differentiation between Philip Island and mainland Australian populations of the red fox *Vulpes vulpes*. Molecular Ecology 5: 81–87.
Lavergne S, Molofsky J 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. Proceedings of the National Academy of Sciences USA 104: 3883–3888.
Lockwood JL, Cassey P, Blackburn TM 2005. The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20: 223–228.
McCracken KG, Johnson WP, Sheldon FH 2001. Molecular population genetics, phylogeography, and conservation biology of the mottled duck (*Anas fulvigula*). Conservation Genetics 2: 87–102.
McDowall RW 1994. Gamekeepers for the nation: the story of New Zealand's acclimatisation societies, 1861–1990. Christchurch, Canterbury University Press.
Mirnezhad M, Schidlo N, Klinkhamer PGL, Leiss KA 2012. Variation in genetics and performance of Dutch western flower thrips populations. Journal of Economic Entomology 105: 1816–1824.
Muller W 2009. Hybridisation, and the conservation of the grey duck in New Zealand. Unpublished PhD thesis, University of Canterburry, Christchurch, New Zealand. 311 p.
Nei M, Maruyama T, Chakraborty R 1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1–10.
Osborne CE, Swift BL, Baldassarre GA 2010. Fate of captive-reared and released mallards on eastern Long Island, New York. Human–Wildlife Interactions 4: 266–274.
Phillips JC 1915. Experimental studies of hybridization among ducks and pheasants. Journal of Experimental Zoology 18: 69–143.
Posada D, Crandall KA 1998. MODELTEST: testing the model of DNA substitution. Bioinformatics 14: 817–818.
Quinn TW, Wilson AC 1993. Sequence evolution in and around the mitochondrial control region in birds. Journal of Molecular Evolution 37: 417–425.
Rhymer JM, Simberloff D 1996. Extinction by hybridization and introgression. Annual Reviews in Ecology and Systematics 27: 83–109.
Rhymer JM, Willams MJ, Braun MJ 1994. Mitochondrial analysis of gene flow between New Zealand Mallards (*Anas platyrhynchos*) and Grey Ducks (*A. superciliosa*). The Auk 111: 970–978.
Rhymer JM, Williams MJ, Kingsford RT 2004. Implications of phylogeography and population genetics for subspecies taxonomy of Grey (Pacific Black) Duck *Anas superciliosa* and its conservation in New Zealand. Pacific Conservation Biology 10: 57–61, 63–66.
Robertson CJR, Hyvönen P, Fraser MJ, Pickard CR 2007. Atlas of bird distribution in New Zealand 1999–2004. Wellington, Ornithological Society of New Zealand.
Sorenson MD, Fleischer RC 1996. Multiple independent transpositions of mitochondrial DNA control region

sequences to the nucleus. Proceedings of the National Academy of Sciences USA 93: 15239–15243.
Sorenson MD, Ast JC, Dimcheff DE, Yuri T, Mindell DP 1999. Primers for a PCR-based approach to mitochondrial genome sequencing in birds and other vertebrates. Molecular Phylogenetics and Evolution 12: 105–114.
Tarin D, Pepper AE, Goolsby JA, Moran PJ, Contreras Arquieta A, Kirk AE, Manhart JR 2013. Microsatellites uncover multiple introductions of clonal giant reed (*Arundo donax*). Invasive Plant Science and Management 6: 328–338.
Tepolt CK, Darling JA, Bagley MJ, Geller JB, Blum MJ, Grosholz ED 2009. European green crabs (*Carcinus maenas*) in the northeastern Pacific: genetic evidence for high population connectivity and current-mediated expansion from a single introduced source population. Diversity and Distributions 15: 997–1009.
Thomson GM 1922. The naturalisation of animals & plants in New Zealand. Cambridge, UK, Cambridge University Press.
Tracey JP, Lukins BS, Haselden C 2008. Hybridisation between mallard (*Anas platyrhynchos*) and grey duck (*A. superciliosa*) on Lord Howe Island and management options. Notornis 55: 1–7.
Tsutsui ND, Suarez AV, Holway DA, Case TJ 2000. Reduced genetic variation and the success of an invasive species. Proceedings of the National Academy of Sciences USA 97: 5948–5953.
Vasquez EA, Glenn EP, Guntensporgen GR, Brown JJ, Nelson SG 2006. Salt tolerance and osmotic adjustment of *Spartina alterniflora* (Poaceae) and the invasive M haplotype of *Phragmites australis* (Poaceae) along a salinity gradient. American Journal of Botany 93: 1784–1790.
Veltman CJ, Nee S, Crawley MJ 1996. Correlates of introduction success in exotic New Zealand birds. The American Naturalist 147: 554–557.
Whitney CA 1942. History of the introduction and establishment of the English wild duck or mallard in New Zealand. New Zealand Fishing and Shooting Gazette (February): 2–5.
Williams M, Basse B 2006. Indigenous gray ducks, *Anas superciliosa*, and introduced mallards, *Anas platyrhynchos*, in New Zealand: processes and outcome of a deliberate encounter. Acta Zoologica Sinica 52 (Suppl.): 579–582.
Zelner JL, King AA, Moe CL, Eisenberg JN 2010. How infections propagate after point-source outbreaks: an analysis of secondary norovirus transmission. Epidemiology 21: 711–718.

Editorial Board member: Craig Barnett
Received 18 September 2012; accepted 24 April 2014