

The changing relative abundance of grey duck (*Anas superciliosa*) and mallard (*A. platyrhynchos*) in New Zealand

MURRAY WILLIAMS

68 Wellington Road, Paekakariki 5034, New Zealand

Abstract Change in the relative abundance of grey duck (*Anas superciliosa*) and mallard (*A. platyrhynchos*) in New Zealand, from 1950 to the present day, is summarised from trapping records, hunters' kills, and field studies. Mallards achieved numerical ascendancy over grey duck throughout most of New Zealand by the late 1970s, merely 20 years after the cessation of mallard releases by historic acclimatisation societies. Post-1990, the relative abundance of mallard in almost all districts, as recorded from hunters' kills, appears to have stabilised at 90%, or higher. Uncertainty about hunters' and the public's ability to discriminate between grey ducks, their hybrids with mallard, and variably-plumaged mallard females is demonstrated and most modern (post-1990) records of relative species abundance must be regarded as quantitatively suspect. Ducks identified as grey ducks by hunters are now a relative rarity throughout New Zealand, except in Northland and West Coast. Post-1990 duck trapping in North Island indicates that grey ducks, where reported, are patchily rather than generally distributed. The absence of genetically-validated criteria for discriminating ducks of grey duck x mallard hybrid ancestry continues to confound field identifications of both species.

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INTRODUCTION

The deliberate introduction of mallard (*Anas platyrhynchos*) to New Zealand, by historic acclimatisation societies for amenity and sporting purposes (McDowall 1994; Dyer & Williams 2010), placed a widely-distributed northern-hemisphere species deep within the range of a southern ecological equivalent, the grey (Pacific black) duck (*A. superciliosa*). Distributed throughout the landmasses and islands of the western and southern Pacific (north-south from the Mariana Islands to Macquarie Island, west-east from Australia and Papua, New Zealand to Tahiti), *A. superciliosa*, along with Philippine duck (*A. luzonica*), constitutes the Pacific sub-clade of the so-called "mallard complex" of large *Anas* ducks. The mallard, and spotbill ducks of Asia (*A. poecilorhyncha* / *A. zonorhyncha*), represent its historic old world grouping (Johnson

& Sorenson 1999; Lavretsky *et al.* 2014). Except for a presumed modern genetic recombination reported from Mariana Islands (Yamashina 1948; Reichel & Lemke 1994) these clades appear to have maintained geographic separation, at least throughout the Pleistocene, while significant introgression with existing new world taxa followed the mallard's dispersal into continental North America during that period (Gonzalez *et al.* 2009; Lavretsky *et al.* 2014).

From first contact in New Zealand, mallard and grey duck, species of similar size and ecology, interbred (*e.g.*, WAS 1913, Thomson 1922; Dyer & Williams 2010), the hybridisation leading to introgression of each species' mitochondrial DNA into the other (Rhymer *et al.* 1994) and producing a diversity of phenotypes displaying characteristics of both species (Sage 1958; Braithwaite & Miller 1975). As mallard numbers increased, fuelled initially by concerted breeding and release programmes (Balham 1952; Dyer & Williams 2010), grey duck

abundance reportedly declined (Balham 1952; Caithness *et al.* 1991). The mallard's demographic and competitive ascendancy over grey duck, excessive hunting of grey ducks, and different responses by the 2 species to wetland drainage, pastoralism and human disturbance, have been suggested as factors contributing to the mallard's present numerical dominance (Balham & Miers 1959; Caithness 1982a; Barker *et al.* 1991; Williams & Basse 2006).

The numerical ascent of mallard and concomitant decline of grey duck appears to have varied regionally within New Zealand. For example, Balham (1952) recorded mallards contributing more of hunters' quarry in Manawatu 1947–49 than did grey duck, initial duck trapping in coastal Otago in 1950 recorded equal numbers of the 2 species (Balham & Miers 1959), whereas Caithness *et al.* (1991) reported mallards comprised only 5% of the combined grey duck-mallard population in Waikato in 1957. Historic accounts of some acclimatisation societies (e.g., Lamb 1964; Watt 1967; Wellwood 1968; Sullivan 1997), and the history of mallard introductions (Dyer & Williams 2010) indicate how, in regions where post-1945 mallard propagation and releases were concerted and extensive, mallard numbers increased rapidly.

In this paper, I summarise and interpret the documented change in the perceived relative abundance of grey duck and mallard. I stress the word "perceived". There has been long-standing confusion about phenotypic characteristics of the 2 species, and of their hybrids, dating at least from the commencement of Balham & Miers' (1959) duck trapping and exemplified by most "hybrids" recorded in 1950s banding records having been sexed as females (see Discussion).

Historically, recognition of mallards by New Zealand observers has been based on published descriptions (e.g., Falla *et al.* 1966; Marchant & Higgins 1990) which emphasise the drake's distinctive nuptial plumage and curled tail feathers, the overall mottled brown plumage of the duck, orange legs and feet of both sexes, and the upper wing's characteristic iridescent blue (or purple) speculum prominent on the secondary feathers which is bounded fore and aft by broad white stripes. Descriptions of grey duck (e.g., Falla *et al.* 1966; Marchant & Higgins 1990) emphasise the dark malar and superciliary stripes across an otherwise cream face, a pale cream chin and throat, the upper wing's green speculum bordered anteriorly by black, and posteriorly by a thin white band, and olive/khaki legs and feet.

While the 2 species are distinctive, field identifications can become confused by the highly variable plumages of many mallard females (a consequence of the variable plumages of the

game-farm stock from which the population arose; Dyer & Williams 2010), by the eclipse plumage of mallard males during summer months and their incomplete transition to a nuptial plumage in autumn and winter, and by the immediate post-fledging plumages of young mallards. Adding further confusion is the apparently variable phenotype of ducks of mixed parentage, which has led to subjective and unverified assessments of what is a mallard, a hybrid, and a grey duck (e.g., Gillespie 1985), and depictions of birds, labelled as grey ducks, which display plumage characteristics not reported in historic descriptions of the species (e.g., Fitter & Merton 2012). There are no published accounts of grey duck x mallard hybrid plumage characteristics that have been verified by genetic appraisal.

This confusion inevitably casts a long shadow over attempts to evaluate past and present records of the relative abundance of the 2 species, their present-day distributions (especially of grey duck; Robertson *et al.* 2007), and assessments of grey duck conservation status (e.g., Hitchmough *et al.* 2007; Robertson *et al.* 2013, 2017).

METHODS

Data sources

Estimates of the relative abundance of grey duck and mallard were obtained from the following 3 sources: (1) Species composition and numbers of ducks reported shot by duck hunters during the annual duck hunting season (usually May and June). Data were extracted from diaries maintained by individuals or groups of hunters, from national gamebird recording schemes (by Wildlife Service, Department of Internal Affairs 1968–90 and recorded by Caithness (1968 *et seq.*) and Caithness (1982b), and by regional Fish & Game Councils 1992–present (unpublished data provided by NZ Fish & Game Council), and from reports lodged in historic Internal Affairs Department files archived at Archives New Zealand (e.g., IAD 46/5/23, 25/4/4, 46/2); (2) Numbers of grey ducks and mallards trapped by Wildlife Branch (later Service), Department of Internal Affairs (see IAD 46/5/32, 46/2/2), by historic acclimatisation societies, and by regional Fish & Game Councils, most details of which are recorded in banding schedules now held by the Department of Conservation bird banding office (DOC banding); (3) Records from field studies of the 2 species. These comprised unpublished data from breeding season pair counts on Waikato wetlands (Aka Aka drains, Lake Ohinewai, Whangamarino wetland, Waikato River) 1960–71 conducted by Wildlife Branch (IAD 25/4/4, 46/2), and from weekly counts of waterfowl at Lake Pukepuke (Manawatu) 1968–82 conducted

by Wildlife Branch (Service) (Caithness & Pengelly 1973; IAD 31/4/53).

For inclusion in this study, counts of the 2 species at any site, or assembled totals of duck hunters' kills, had to exceed 50 birds.

All data are presented as reported by the observers or recorders. Potential biases arising from the different sampling methods, or from inaccurate species identifications by hunters or observers, are discussed later.

Data analyses

Data are assembled and examined in 3 time-periods: pre-1970, 1970–90 and post-1990. The pre-1970 period embraces the extensive propagations and releases of mallards by historic acclimatisation societies (Dyer & Williams 2010). It also includes the initial trapping of grey ducks and mallards, and associated field studies, by R. W. Balham from 1947 (Balham 1952), and by Wildlife Branch from 1950 (Balham & Miers 1959; IAD 46/2). Field observations of the time assiduously discriminated the 2 species. Trapping totals were mostly without species targets, and relative species abundance is calculated directly from the totals of each species caught. Where species targets were employed (between 1965–70, and obvious in the records from the round number e.g., 1,500 or 2,000 of 1 species having been banded), I have checked original banding schedules and used records from the first 2 days of trapping (when most ducks were first caught) to establish the relative abundance of the 2 species.

During 1968–90, a national waterfowl hunters' diary scheme (Caithness 1968 *et seq.*) recorded the number and species identity of ducks shot by 1,200–2,000 hunters nationally (with results summarised regionally). Most diary contributors did so over multiple years, with *c.* 20% of them contributing a diary for at least half of the scheme's 23-year duration. In these diaries, hunters recorded their success during the first 2 days of the hunting season (opening weekend, when most hunters participate and *c.* 60% of the season's duck harvest occurs; Balham & Miers 1959) and throughout the remainder of the season. From those annual regional opening weekend and full season totals for each species relative species abundance was calculated; this paper reports relative species abundances based on full season totals.

Hunting returns from the post-1990 period derive from multiple telephone-based surveys of hunters undertaken by regional Fish & Game Councils throughout each hunting season (Barker & McKenzie 1999; McDougall & Amundsen 2017). This sampling methodology differs from that of Caithness (1968 *et seq.*) and sought to estimate, annually, the numbers of each species shot within

each of 13 regions. The relative abundances of grey duck and mallard presented in this paper were calculated using mean regional whole season estimates for each species but do not incorporate sampling variances (standard errors of mallard estimates were mostly <10% of the mean, for grey duck between 10–25% of the mean). As with hunting returns from the previous period, there is no recognition of hybrids between the 2 species.

Trappings of grey ducks and mallards during the 1970–90 and post-1990 periods were all without species-specific targets and relative species abundances were calculated directly from the totals of each species caught. These data were sourced from the Department of Conservation bird banding office (DOC banding) unless stated otherwise.

All references to "ducks" refer to grey ducks and mallards combined, unless stated otherwise.

Places named in the text may be located in the online Gazetteer provided by Land Information New Zealand (<http://www.linz.govt.nz>). Boundaries of historic acclimatisation societies in the 1970s are depicted in McDowall (1994:368) and present-day Fish & Game Council regions are illustrated on New Zealand Fish & Game Council's website (<https://fishandgame.org.nz>).

RESULTS

Pre-1970

Waikato

Wetlands of the lower Waikato River catchment (especially Lakes Waahi, Whangape, Waikare, and nearby Whangamarino wetland) were the locations of early waterfowl studies (Balham & Miers 1959). Initial duck trapping at Lake Waikare in 1950 and 1951 captured just 12 mallards alongside 1,958 grey ducks. When annual duck trapping recommenced there in 1957, mallards comprised 5% of 1,194 ducks trapped and this percentage remained similar over the subsequent 4 years ($n = 1,500\text{--}2,000$ ducks annually). In 1962, trapping shifted to Lake Whangape where 21% of 1,971 ducks caught were mallards. Thereafter at Lake Whangape the relative abundance of mallard increased rapidly, to comprise 50% of the ducks caught in 1967 and, 5 years later, 70% ($n = c. 1,500$ ducks annually; Fig. 1).

In breeding season counts of duck pairs on adjacent Waikato wetlands (IAD 25/4/4, 46/2), the relative abundance of mallard increased from 17% in 1960 to 70% in 1970 (Fig. 1). The total number of duck pairs observed on these wetlands remained roughly constant throughout this decade (Williams & Basse 2006), indicating that a genuine replacement of grey duck by mallard was occurring.

Waikato duck hunters also recorded this change. In May 1964, 45 hunters at Lake Karapiro had 10

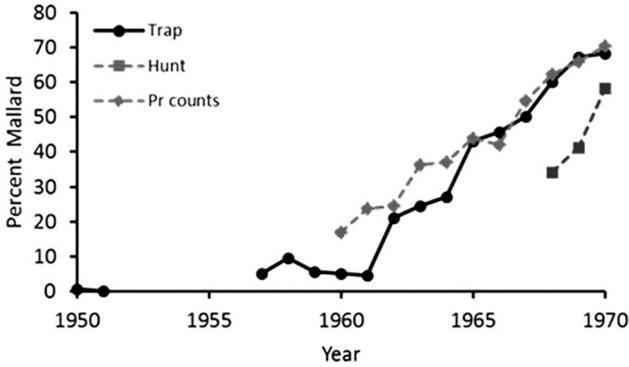


Fig. 1. Percentage of mallards in the combined grey duck and mallard duck population in Waikato 1950–70, as recorded from trapping (trap), in hunters’ kills (hunt), and from breeding season pair counts (pr).

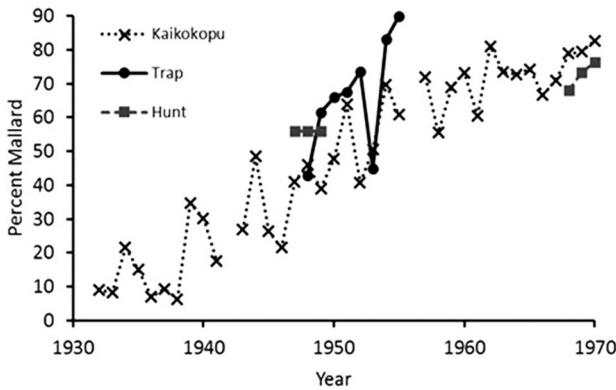


Fig. 2. Percentage of mallards in the combined grey duck and mallard duck population in Manawatu 1932–70, as recorded from trapping (trap) and in hunters’ kills at Lake Kaikokopu, and regionally (hunt; 1947–49 combined and 1968–70).

(10%) mallards amongst 98 ducks shot, and at Lake Arapuni 20 hunters had 10 (6.6%) mallards amongst their 152 ducks (IAD 46/2). In kills by hunters near other upper Waikato River hydro dams, mallards comprised 9% of 118 ducks examined in 1963, 4% of 143 ducks in 1964, 6.5% of 614 ducks in 1967 and 13% of 452 ducks in 1968 (IAD 2/4/10). In 1967, 28% of 246 ducks shot on the lower Waikato River (i.e., below Huntly) were mallards (IAD 46/2). In 3 years of records supplied by 29–131 Waikato hunters (Caithness 1968 *et seq.*) the species ratio changed from 34% mallard (n = 993 ducks) in 1968, to 41% (n = 671 ducks) in 1969, and to 58% (n = 2,951 ducks) in 1970.

Manawatu

R. A. Wilson and his descendants maintained a hunting diary in which they recorded all ducks shot at Lake Kaikokopu (Hunia) in coastal Manawatu between 1932 and 1981 (see Dawber & Haylock 2010). This diary, which recorded 87–170 ducks shot annually (Fig. 2), also chronicles mallards

increasing steadily from <10% of the kill initially to almost 80% by 1970 (and 90% by 1981).

Elsewhere in lowland Manawatu, mallards comprised 56% of hunters’ kills of mallards and grey ducks in 1947–49 (Balham 1952). Mallard relative abundance amongst ducks trapped then, and subsequently, increased from 44% in 1948 to almost 90% by 1955 (Balham & Miers 1959; Fig. 2).

Further hunters’ records from Manawatu were reported by Caithness (1968 *et seq.*; IAD 31/4/53) and differentiated kills at Lake Pukepuke (a sand-dune lake immediately north of Lake Kaikokopu) from those obtained more widely throughout the Manawatu region. In the 1968–70 period, mallards comprised 60–73% of ducks shot on Lake Pukepuke (n = 309–584 ducks) and 67–76% (n = 998–1,433 ducks) regionally (Fig. 2), results akin to those recorded in Wilson’s diary. In a field check of hunters’ kills throughout coastal Manawatu wetlands in 1968 mallards comprised 515 (57.8%) of 891 ducks examined (IAD 46/2).

Table 1. Percentage of mallards in the combined total of grey ducks and mallards (n) shot by hunters in Bay of Plenty (BoP), Taupo, and East Coast regions of North Island, 1963–68 (data from IAD 46/2, 45/5/32).

Area	1963		1964		1967		1968	
	%	n	%	n	%	n	%	n
Wairoa coastal lakes	48	624	36	206	50	239	52	126
Gisborne flats, Lake Repongaere	34	675	25	211	33	278	22	198
Coastal BoP wetlands	7	148	9	278	14	299	32	235
Lake Taupo and surrounds	7	117	10	352	20	566	24	576
Upper Waikato River	9	116	7	393	7	614	13	738

North Island regions

In central Hawkes Bay, mallards comprised 41% of 394 ducks shot in 1961, 70.2% of 1,003 ducks in 1963, 79% of 1,554 ducks in 1967 (IAD 46/2), and 86% of 1,449 ducks in 1969 (Caithness 1968 *et seq.*). At Lake Wairarapa mallards comprised 23% of 311 ducks shot in 1959 (IAD 46/2) but 83% of 130 and 81% of 283 ducks shot in 1969 and 1970 respectively (Caithness 1968 *et seq.*).

Wildlife Branch staff undertook extensive hunting season surveys in parts of the Rotorua/Taupo, and East Coast regions. Their records (IAD 46/2, 45/5/32, 2/4/10, 8/4/0) are the most extensive North Island records from this period. In 1956, mallards were rarely recorded on coastal Bay of Plenty wetlands (e.g., Matata 3%, n = 302 ducks), Kaituna wetlands/Opotiki 2% (n = 594 ducks) and at Lake Repongaere, Gisborne (1 of 176 ducks). However, on Wairoa's coastal lakes where mallards comprised 29% of 547 ducks trapped in 1953–54 (Balham & Miers 1959), they were more common (39%, n = 137 ducks). Later sampling (Table 1) recorded the steady increase in the relative abundance of mallards at all sites, as well as on and adjacent to Lake Taupo and the upper Waikato River.

Duck trapping at Matata Lagoon, coastal Bay of Plenty in 1968 and 1969, recorded 38% (n = 491 ducks) and 32% (n = 498 ducks) mallards respectively while at Wairoa coastal lakes in 1969 65% of 491 ducks trapped were mallards.

South Island regions

South Island records chronicle relative abundance changes even in regions where mallards were already well established. For example, in Otago, trapping which caught 1,000–1,500 ducks annually at coastal Lake Tuakitoto 1961–69, recorded the proportion of mallards changing from an initial 70% to almost total dominance in 1968 and 1969 (DOC banding). The identity of 1,505 ducks shot at this lake in 1968 comprised 95% mallard (IAD 46/2). At

Lake Waiholo, 54% of 1,436 ducks trapped in 1950–51 were mallards (Balham & Miers 1959) and in 1959, mallards comprised 68% of 572 ducks shot by 31 hunters there, with another 35 ducks considered to be hybrids (IAD 46/2). Thus, by 1970, grey ducks were already very uncommon in coastal Otago and outnumbered in wetlands of the lower Taieri River basin. In hunting diary records for 1968–70, and based on fewer than 800 birds annually (Caithness 1968 *et seq.*), c. 80% of ducks shot in wider Otago were identified as mallards.

In Canterbury, 110 ducks trapped at Woodend Lagoon in 1951 comprised 45% mallards, and at a Waimakariri River site in 1952, 59% of 662 ducks captured were mallards (Balham & Miers 1959). In the capture of 500 ducks annually at Harts Creek, Lake Ellesmere 1967–69, mallards dominated (86–96%). Hunters' diaries reported by Caithness (1968 *et seq.*) for 1968–70 from throughout North Canterbury record 74–77% mallards (n = 254–305 ducks), and 66–72% mallards (n = 606–1,428 ducks) from South Canterbury.

From elsewhere in South Island, limited data show regional variation. For example, in Southland 1969, of 1,013 ducks trapped, just 15 (1.5%) were identified as grey ducks. In the same year when hunters reported the identities of 2,396 ducks shot, 340 (14.2%) were as grey ducks (Caithness 1968 *et seq.*). At Wairau Lagoon (Blenheim) in 1952, mallards comprised 45.3% of 507 ducks trapped with an additional 45 ducks labelled as hybrids (DOC banding). Hunters' diaries from Marlborough in 1969 and 1970 recorded 37% and 48% mallards amongst 331 and 398 ducks respectively. On West Coast, trapping at Lake Ryan in 1953 obtained 139 ducks, all grey ducks (Balham & Miers 1959; DOC banding). Diaries of hunters shooting at this lake and in its environs during 1968–70 record c. 17% mallards (n = 377–760 ducks) in all 3 years (Caithness 1968 *et seq.*) while 13 (9.4%) of 138 ducks obtained by hunters in the Okarito area in 1969 were identified as mallards (IAD 46/2).

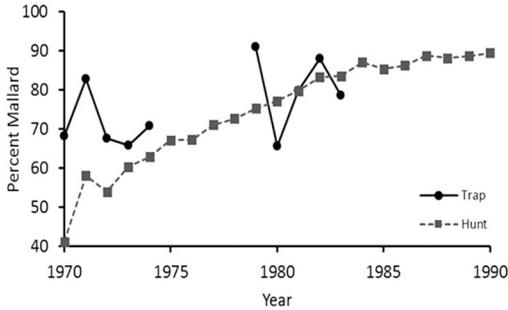


Fig. 3. Percentage of mallards in the combined grey duck and mallard duck population in Waikato 1970–90, as recorded from trapping (trap) and in hunters' kills (hunt).

Summary

During the period 1950 to 1970, multi-year duck trapping in Waikato, Manawatu and Otago, and spasmodic trapping in Canterbury, Southland, West Coast and Marlborough all captured annually increasing numbers of mallards relative to grey ducks. The gathering ascendancy of mallards was also reported by duck hunters from these regions, and more widely in the central and eastern North Island. By 1970, the relative abundance of mallards, as reported in duck hunters' kills, had just exceeded that of grey ducks in Waikato, but outnumbered grey ducks 2:1 in Manawatu, and by 3:1, or more, in lowland eastern and southern South Island.

1970–90

Waikato

Mallards comprised 75.6% of 3,103 ducks trapped at Lake Waahi 1970–71, 68.5% of 4,456 ducks at Lake Whangape 1972–74, and 79.4% of 5,142 ducks at Lake Whangape 1979–83. The influence of trapping site was apparent in 1980 when traps were placed at 4 locations around Lake Whangape instead of at the 1 used in all previous years, and subsequently: grey ducks comprised 34.2% of 989 ducks trapped in 1980 and accounted for one-third of all grey ducks trapped ($n = 1,056$) in the 1979–83 period (Fig. 3).

Hunters' diaries, sourced from throughout the wider Waikato region (annually from 220–320 hunters and totals of 5,368–9,002 ducks), recorded an average 2.4% annual increase in mallard relative abundance from 1971 to 1983, and thereafter a consistent 85–90% relative abundance of mallard (Fig. 3).

Manawatu

Sources of hunting and trapping data for this period were the Wilson hunting diary from Lake

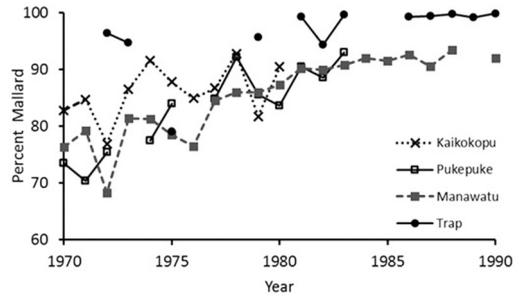


Fig. 4. Percentage of mallards in the combined grey duck and mallard duck population in Manawatu 1970–90, as recorded from trapping (trap) and in hunters' kills at Lake Kaikokopu, Lake Pukepuke, and regionally (Manawatu).

Kaikokopu 1970–80 ($n = 50$ –120 ducks annually), diaries of hunters ($n = 22$ –35) at nearby Lake Pukepuke 1970–83 ($n = 450$ –700 ducks annually; IAD 31/4/53), diaries of hunters ($n = 96$ –160) throughout Manawatu 1970–90 ($n = 1,600$ –4,000 ducks annually) (Caithness 1968 *et seq.*), and totals of ducks trapped ($n = 1,000$ –1,700 ducks) on coastal Manawatu lakes.

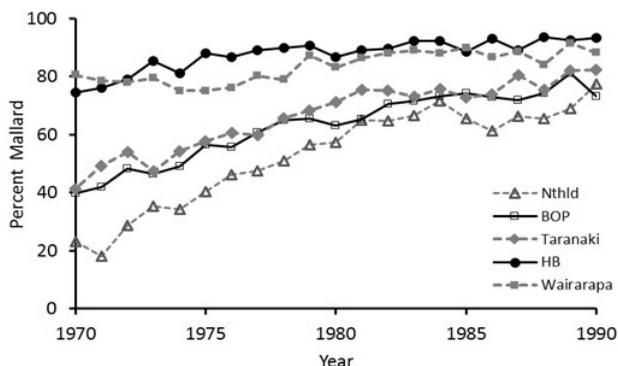
Mallards comprised >90% of the ducks captured in each of 12 annual trappings during this 20-year period (Fig. 4), and throughout the 1980s only 127 of 1,1485 ducks trapped were not recorded as mallards. The relative abundance of mallards, as recorded by hunters, was conspicuously lower during the 1970s (80.5% of 18,530 ducks) but was consistently above 90% during the 1980s (mean 91.1% of 29,432 ducks). All 3 sets of hunter records evince the same steady increase in mallard relative abundance throughout the 1970s (Fig. 4).

Monthly counts of grey ducks and mallards present at Lake Pukepuke were conducted between 1968 and 1982 (IAD 31/4/53). Counts of pre-breeding aggregations in June–August of each year were summed and the relative abundance of mallards in these totals were 75% ($n = 3,070$ ducks) in 1969, 73% ($n = 3,891$ ducks) in 1970, 80% ($n = 1,834$ ducks) in 1971, and 82% ($n = 1,823$ ducks) in 1972. A decade later, in 1982, when data were recorded only as monthly averages, grey ducks were rarely seen and mallards comprised 94% of the unspecified number of ducks observed.

June–August counts at nearby Lake Kaikokopu recorded 93% mallards amongst 918 ducks in 1969 and 91% of 384 ducks in 1970 (IAD 31/4/53).

Of newly-hatched broods of grey ducks and mallards observed at Lake Pukepuke, mallards comprised 69% of 45 broods in 1968, 87% of 61 broods in 1969, 70% of 33 broods in 1970 and 69% of 65 broods in 1971 (Caithness & Pengelly 1973). In

Fig. 5. Percentage of mallards in the combined grey duck and mallard kill reported by hunters from Northland (Nthld), Bay of Plenty (BOP), Taranaki, Hawkes Bay (HB) and Wairarapa regions 1970–90 (data from Caithness 1968 *et seq.*). Refer to Table 2 for explanation of regional composition



1976, 85% of 35 broods observed were mallards, 87% of 44 broods in 1981, and all 41 broods identified in 1982 were mallard (IAD 40/7/14, 31/4/53).

North Island regions

Trapping

At Lake Wairarapa in 1970, 95% of 143 ducks trapped were mallards. Between 1974 and 1980, 5,206 ducks were trapped there also, of which 86.5% were mallard. However, annual species composition varied between 71–97% mallard as different trapping sites around the lake and on its adjacent wetlands were used. Contemporaneous hunting returns from the wider Wairarapa region record a broadly similar relative species abundance (Fig. 5).

At Matata, Bay of Plenty, trapping initiated in 1968, continued, with 48.1% of 495 and 57.2% of 498 ducks trapped in 1970 and 1971 respectively being mallards; across all 4 years of trapping the mallard's relative abundance almost doubled. Trapping at Taupo in 1971 captured 477 ducks of which 27% were mallards, and at Wairoa coastal lakes in 1970–71 combined, 82% of 615 ducks trapped were mallards.

Hunting

The relative abundance of mallards in the combined grey duck and mallard harvest is illustrated for 5 regions in Fig. 5, and changes between the first and last 2-year periods (and including Waikato and Manawatu for comparison) are presented in Table 2. There were substantial increases in mallard relative abundance in all regions over this 20-year period, although less so for the drier pastoral areas of Hawkes Bay and Wairarapa than elsewhere and where mallards were already relatively common.

South Island regions

Trapping

At Lake Tuakitoto, coastal Otago, trapping continued during 1970 and 1971 when 95% and 99%

of c. 1,000 ducks caught, respectively, were mallard, essentially the same as in the previous 5 years. In North Canterbury, 200 ducks were trapped at Hart's Creek on Lake Ellesmere in 1985, of which 97% were mallard, a similar percentage to that recorded in 1967–69 (see above).

In Southland, the dominance of mallard as recorded in hunters' kills (Fig. 6, Table 2) was further highlighted in trappings during 1969–74. For example, at Thompson's Crossing, an inland site, c. 1,000 ducks were trapped annually but only 5 grey ducks were ever caught; at coastal Waituna Lagoon 1,500 ducks were trapped each year of which 90–98% were recorded as mallards, although in 1 year 28 ducks were designated as hybrids. Trapping at lowland Southland sites (e.g., Thornbury) was undertaken between 1987 and 1990; 3,833 ducks were trapped of which just 3 were grey duck. At Kakapo Swamp, near Te Anau, trapping of c. 500 ducks annually occurred between 1971–73, of which 71–83% were mallards.

Hunting

The relative abundance of mallards in the combined grey duck and mallard harvest is illustrated for 5 regions in Fig. 6, and changes between the first and last 2-year periods presented in Table 2. There were reported increases in mallard relative abundance in all regions over this 20-year period, most dramatically so in West Coast and Nelson.

Summary

Within the 1970–90 period, dramatic regional increases in the relative abundance of mallards were reported by duck hunters, although rates of increase (as illustrated in Figs. 5, 6) were less in regions where mallards already comprised >80% of the duck population by 1970 than elsewhere. Trapping programmes were not sufficiently widespread geographically to corroborate these reported increases, but in Waikato and Manawatu the mallard's relative abundance in the total of

Table 2. Percentage of mallards in the combined total of grey ducks and mallards (n) reported shot by hunters in North and South Island regions in the first and last 2-year periods of 1970–90 (data from Caithness 1968 *et seq.*).

Region	1970-71		1989-90		Data amalgamated from Acclimatisation Society districts
	%	n	%	n	
<i>North Island</i>					
Northland	20.5	3,009	71.8	5,869	Whangarei, Hobson, Manganui-Whangaroa, Bay of Islands
Bay of Plenty	45.8	2,827	81.0	2,266	Tauranga, Rotorua and Taupo segments of the Central North Island Wildlife Conservancy
Taranaki	23.5	3,040	82.2	3,530	Taranaki, Stratford, Hawera
Hawkes Bay	75.5	2,882	96.7	2,504	
Wairarapa	79.6	525	90.0	3,048	Eastern segment of Wellington
Waikato	55.5	8,319	89.5	15,534	Auckland, Waikato;
Manawatu	78.0	2,665	92.6	4,651	Western segment of Wellington
<i>South Island</i>					
Nelson	35.0	869	72.8	1,413	
West Coast	17.7	1,786	58.1	2,553	Westland and West Coast
North Canterbury	69.9	1,138	89.0	1,168	
Otago	80.7	2,888	97.2	6,506	
Southland	89.2	9,231	99.0	10,751	

ducks trapped generally exceeded that being reported by hunters. The sole field study, at Lake Pukepuke in Manawatu, provided evidence of the mallard's long-established local ascendancy and of the grey duck's gradual extirpation.

Post-1990

Trapping data are limited because no duck trapping occurred in South Island, while in North Island it was limited to Auckland-Waikato and Eastern Fish and Game districts. Hunting records for this period are not directly comparable with those for the previous 2 periods because of the different survey methodology used. Relative species abundance has been calculated from mean estimated totals of hunters' kills rather than from totals declared by hunters (see Methods). Nevertheless, trend over time should be directly comparable with the 1970–1990 period. Additionally, some regional designations were altered following the establishment of regional Fish and Game Councils in 1990 to administer and enact gamebird management. Most significantly, the Eastern Fish and Game region encompasses Gisborne-East Coast, much of central North Island and the Bay of Plenty area referred to earlier, Wellington combines Manawatu and Wairarapa,

and Nelson-Marlborough is an amalgam of the 2 formerly separate administrative areas.

North Island regions

Trapping

Ducks were trapped annually 1997–2015 at sites in Hawkes Bay, Gisborne-East Coast, and Bay of Plenty. In Hawkes Bay, mallards dominated at all 3 sites trapped over multiple years: Lake Rotokare 2000–15, 99.4% (n = 4,168); Eskdale lakes 2001–14, 90.4% (n = 1,774); Ohuia Lagoon (coastal Wairoa) 1998–2011, 92.7% (n = 1,743). There was similar dominance of mallards at small (locally-named) Gisborne-East Coast sites near Gisborne: Dods 1998–2009 98.4% (n = 1,500); McLaurins 1998–2014 99% (n = 1,027); Holdsworth 2000–14 82% (n = 1,023).

At 3 long-term trapping sites in Bay of Plenty, considerable variation in relative abundance of mallards caught annually occurred. At Lake Aniwhenua on the Rangitaiki River 1999–2009, 2,367 ducks were trapped of which 82.7% were mallards, with annual variations of 63–94%. On ponds c. 2km distant, 64.8% of 3,362 ducks trapped 1999–2015 were mallards, with annual variations of 53–80%. At the coastal Kaituna River wetlands 1997–2015, 92.0% of 6,319 ducks trapped were mallards, the percentage varying annually between

Fig. 6. Percentage of mallards in the combined grey duck and mallard kill reported by hunters from Southland (Sthld), Otago, North Canterbury (NCant), West Coast (WC) and Nelson, 1970–90 (data from Caithness 1968 *et seq.*). Refer to Table 2 for explanation of regional composition.

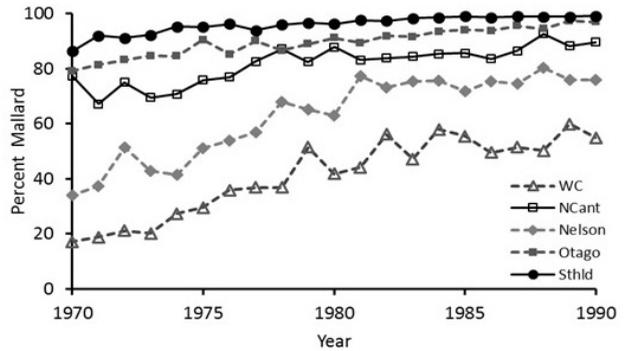
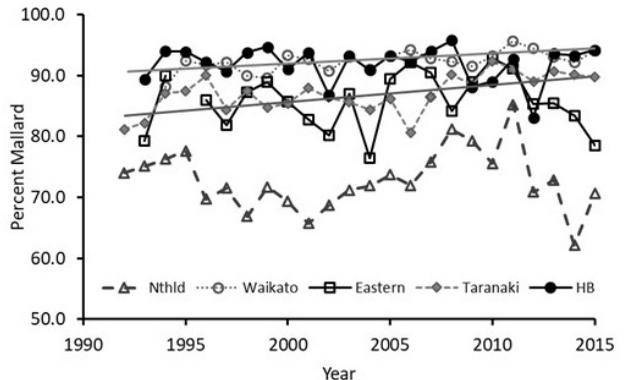


Fig. 7. Percentage of mallards in the combined grey duck and mallard kill reported by hunters from Northland (Nthld), Auckland-Waikato (Waikato), Eastern, Taranaki and Hawkes Bay (HB) Fish and Game regions 1992–2015 (data from NZ Fish & Game Council). Calculated trendlines shown for Waikato (upper line) and Taranaki (lower line) are statistically significant (see text).



83–95%. The calculated trendlines for all 3 sites do not indicate any significant change in mallard relative abundance over this period (Aniwhenua $r = -0.123$, $t_8 = 0.349$, n.s.; Ponds $r = -0.168$, $t_{13} = 0.614$, n.s.; Kaituna $r = 0.228$, $t_{16} = 1.15$, n.s.). The 2 Rangitaiki River valley sites consistently provided the highest relative abundances of grey ducks in the Bay of Plenty region (M. McDougall *pers. com.*)

In the Auckland-Waikato region 2003–12 trapping included sites at Helensville, Te Awamutu, Hauraki Plains, and Lake Whangape. Grey ducks comprised just 56 (1.3%) of 4,329 ducks trapped at Helensville, 5 (0.1%) of 3,772 ducks trapped at Te Awamutu, and 44 (0.25%) of 17,653 ducks trapped at 3 Hauraki sites. At Lake Whangape and nearby, site-specific differences were apparent; trapping on the lake's shore 2002–07 yielded 108 (2.9%) grey ducks amongst 3,772 captures whereas, at the nearby tree-fringed Opuatia wetland reserve, grey ducks comprised 11.2% of 5,949 ducks trapped 2002–14. Within this landscape of intensive agriculture, ducks perceived as grey ducks have become extremely rare.

There was no trapping of ducks in Manawatu or the wider Wellington region (including Wairarapa), except in 2012 when 564 ducks were caught near Foxton; just 3 were recorded as grey ducks.

Hunting

The relative abundance of mallards reported in hunters' kills from 5 North Island regions for the period 1992–2015 are illustrated in Fig. 7. All regional graphs display more annual variability than recorded in the previous era (Fig. 5) undoubtedly a reflection of the different sampling methodology employed. Only for Taranaki and Waikato do calculated trendlines (depicted) indicate a significant increase in mallard relative abundance over this time-period (Taranaki $r = 0.598$, $t_{22} = 3.499$, $0.01 > P > 0.001$; Waikato $r = 0.615$, $t_{20} = 3.485$, $0.01 > P > 0.001$). The conspicuous annual variability in mallard relative abundance, particularly for Eastern and Northland regions, is primarily a consequence of an annually consistent estimated kill of grey ducks and an oscillating estimated kill of mallards (Fig. 8 A, B).

South Island regions

Hunting

The relative abundance of mallards in hunters' kills from 5 South Island regions for the period 1992–2015 is illustrated in Fig. 9. There was considerably less annual variability than from North Island regions but in Southland, Otago and North Canterbury this was a consequence of few grey ducks being

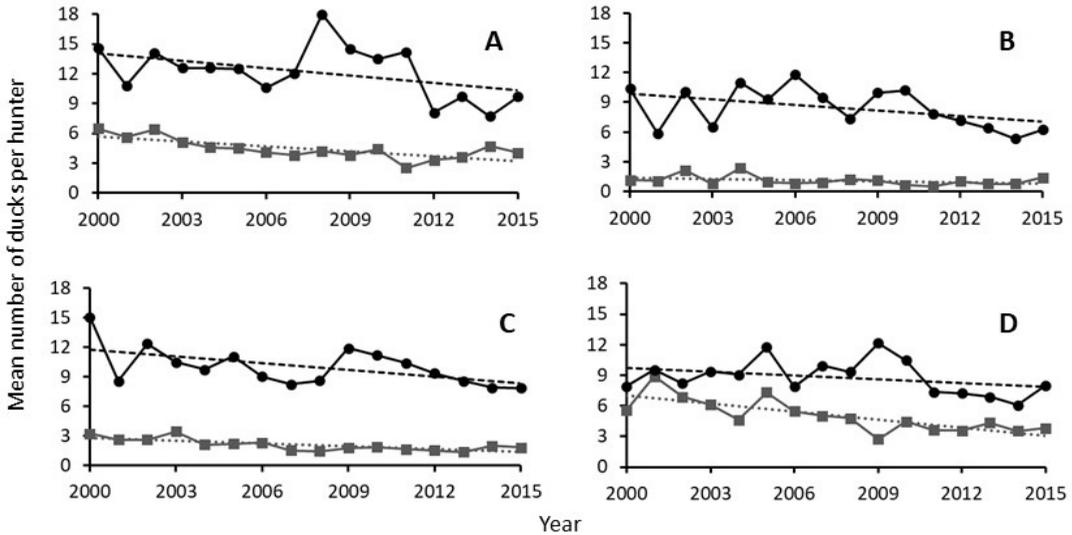


Fig. 8. Estimated mean number of grey ducks (grey square) and mallards (black dot) shot annually by each of 1,911–2,370 hunters in Northland (A), 3,365–3,958 hunters in Eastern (B), 827–1,023 hunters in Nelson-Marlborough (C) and 418–634 hunters in West Coast (D) Fish & Game regions 2000–15 (data from NZ Fish & Game Council). Depicted trendlines indicate a statistically significant trend only for Northland grey ducks ($r = -0.734$, $P < 0.001$), Nelson-Marlborough mallards ($r = -0.551$, $0.02 > P > 0.01$), Nelson-Marlborough grey ducks ($r = -0.759$, $P < 0.001$) and West Coast grey ducks ($r = -0.762$, $P < 0.001$).

reported in any year. Nelson-Marlborough and West Coast hunters reported a significant grey duck contribution to their seasonal kill but only in West Coast did the relative abundance of the 2 species change significantly over time (West Coast $r = 0.755$, $t_{22} = 3.499$, $P < 0.001$; Nelson-Marlborough $r = 0.325$, $t_{22} = 1.613$, n.s.). Annual variability in mallard relative abundance in Nelson-Marlborough was influenced by fluctuations in numbers of mallards reported shot whereas in West Coast, the reported kills of both species varied considerably between years and seldom in synchrony (Fig. 8 C, D).

Summary

Post-1990, the mallard's relative ascendancy, as reported in hunters' kills and in limited North Island trapping, consolidated. By 2015, grey ducks were rarely reported by hunters in Southland, all of eastern South Island, and from southern and eastern North Island. North Island trapping indicates grey duck occurred in enclaves rather than being widely distributed. In the 2 regions in which relative abundance of grey ducks was reported to be highest in 1990 (West Coast, Northland), grey ducks retained a conspicuous presence in reported hunter kills but the gradual ascendancy of mallards in West Coast was not matched in hunting statistics from Northland.

DISCUSSION

Interpreting the data

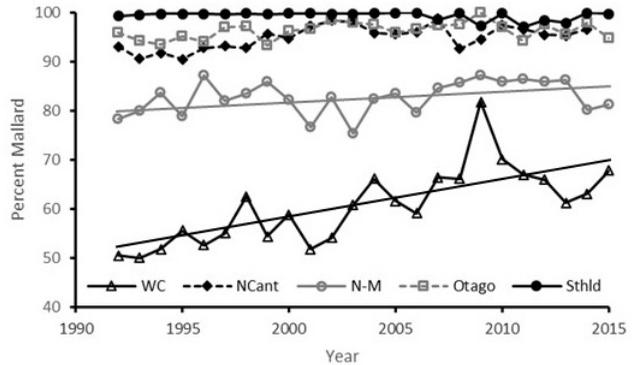
Three factors influence interpretation of the data presented: species identification, trapping and hunting biases, and inference arising from using a ratio as a statistic.

Species identification

The ducks were identified as either grey duck or mallard because that was what the trapper, hunter or field observer perceived them to be. Because it is not possible to seek confirmation of the identifications, those perceptions are this paper's reality. Nevertheless, a cloak of uncertainty must lie across all species assignments.

Missing from the statistics is recognition of ducks displaying a hybrid phenotype. While those operating the duck traps, professional gamebird managers mostly, could be expected to discriminate the 2 species accurately, and to be able to recognise an obvious hybrid, this is not always the case. For example, of a sample of ducks designated as "hybrids" in the banding records 1950–66, 82% ($n = 178$) were sexed as females (DOC banding), indicating the variable mallard female plumage was already a source of confusion. A change of trapping operators sometimes occasioned a sudden spike of birds being identified as hybrids e.g., at Wairau

Fig. 9. Percentage of mallards in the combined grey duck and mallard kill reported by hunters from North Canterbury (NCant), Southland (Sthld), Otago, Nelson-Marlborough (N-M) and West Coast (WC) Fish and Game regions 1992–2015 (data from NZ Fish & Game Council). Calculated trendlines shown for Nelson-Marlborough (upper line) and West Coast (lower line) are statistically significant (see text).



Lagoon 1952, Waituna Lagoon 1969–74, and Lake Wairarapa 1974–80 (DOC banding; IAD 46/2). Even modern trappers report uncertainty and resort to designating, as a grey duck, a duck that “looks like a grey duck” (M. McDougall *pers. com*).

Can hunters discriminate the 2 species correctly? This is examined in Appendix 1. Soulsby’s (1982) testing of 48 Otago hunters, the only empirical test reported in New Zealand, found 10% of 328 mallards were identified as grey ducks (all were females) and 6 (12.5%) of the hunters made erroneous identifications.

Hunters’ identifications provided when reporting a retrieved band to the Banding Office emphasise how widespread this difficulty may be (Appendix 1: Table A.1). Whereas in 1971–72, 90% of hunters’ species identifications of both grey ducks and mallards matched that of the banders’, post-1980 almost 75% of banded grey ducks were misidentified by hunters as mallards. As the reported relative abundance of grey ducks declined, fewer hunters would have encountered them, and most hunters who commenced their sport post-1990 may not have encountered a grey duck at all. This means that data obtained from hunters will underestimate the relative abundance of grey ducks, and perhaps increasingly so over time.

Sampling bias

Data were obtained using 2 sampling methods: trapping and hunting. The expectation is that, throughout each time-period, both methods will produce similar trends in relative species abundance, although not necessarily of the same magnitude. Furthermore, any set of consistent field observations should provide a trend that also broadly matches those provided by trapping and

hunting. Figs. 1–4 support this expectation.

Interest in short-term change, however, invariably requires a consideration of magnitude, so it is important to recognise each method’s bias.

Trapping

Totals of each species trapped generally overestimate the relative abundance of mallards amongst ducks visiting the traps. Mallards, being larger than grey ducks, physically dominate them whenever the species aggregate, and especially so at concentrated feeding sites (Williams & Basse 2006). The smaller grey ducks are timid when amongst mallards and it is the observation of duck trappers that mallards can exclude grey ducks from the traps by physically and aggressively blocking their access to the traps’ funnels and food.

Trap site location can influence the numbers of each species trapped; sites on exposed shorelines of large lakes, or at sites close to, or within, urban precincts, tend to trap many more mallards than those on smaller wetlands or those with generally occluded margins. For example, the early 1960s trappings in Waikato reported relatively few mallards initially but a change of site, from Lake Waahi to Lake Whangape, quadrupled the percentage of mallards in the total capture. Similar site-specific variation occurred during 1974–80 trapping at Lake Wairarapa (see Results), and was a feature of post-2000 Fish & Game Council trapping in Bay of Plenty, and about Lake Whangape and nearby wetlands (see above).

What is uncertain is the area from which a trap site draws its ducks and thus how representative the species ratio at the trap site is of the wider population. Duck trapping during the pre-1970 and 1970–90 periods routinely used just few trap sites

and placed on edges of large lakes, so that the ducks caught were probably more representative of local, rather than regional, populations. Thus, inferring region-wide relative species abundance from sampling few sites may be problematic. Post-1990 trapping sites in Bay of Plenty and Waikato were more numerous and more widely dispersed, and may have sampled their regional populations more comprehensively.

Hunting

Reported hunters' kills over-estimate the relative abundance of grey duck in the wild population because of the grey duck's tendency to flight directly into hunters' decoys and the mallard's renowned caution at doing so (Balham & Miers 1959; Barker *et al.* 1991). Recovery rates of banded grey ducks are significantly higher than those from banded mallards (Balham & Miers 1959, Caithness *et al.* 1991; Barker *et al.* 1991); grey ducks are simply "easier" to shoot.

Counteracting this is the effect of hunting site. Hunters at sites in expansive pastoral landscapes, and where wetlands may have grazed or sparsely-vegetated margins, will encounter fewer grey ducks simply because of the species' preference for wetlands in more occluded or wooded environments. Over time, and reflecting the modern intensification and expansion of pastoral farming on New Zealand lowlands (NZOYB 1990, 2010), more hunting sites will have become wetland islands in the pastoral ocean.

Relative species abundances for the 1970–90 period were obtained directly from the cumulative totals of grey ducks and mallards reported killed by a sample of hunters (Caithness 1968 *et seq.*). Those for the post-1990 period were derived from regional estimates of hunters' kills of each species occasioned by periodic telephone surveys of hunters throughout the hunting season (Barker & McKenzie 1999). Whereas the former is a direct measure, the latter is an estimate (with accompanying variance), the means of which were then used to calculate relative species abundance. These 2 sets of statistics are not directly comparable.

Whilst these potential sampling biases will be at play in the data presented, I have not attempted to quantify them or determine how they might interact. However, they offer 1 explanation why trends based on each method, as illustrated in Figs. 1–6 and in Figs. 7–9, are of conspicuously different form.

Interpreting the relative abundance measure

The measure of relative abundance reflects change between grey duck and mallard populations. Change in this ratio, when determined from hunters' kills, may arise from change in harvest of

just 1 species (e.g., as in Nelson-Marlborough 2000–15 and Eastern 2000–15; Fig. 8 B, D) or changes in both simultaneously (e.g., West Coast 2000–15; Fig. 8 C). Change in this statistic more reliably reflects true changes in species abundances when considered over multi-year rather than year-to-year time spans (e.g., Taranaki 1992–2015, Waikato 1994–2015; Fig. 7).

Changes in relative species abundance

There is a consistent trend in reported or observed grey duck and mallard relative abundance over the time-periods analysed: it is of progressive mallard ascendancy. Waikato and Manawatu records for the 1950–70 period (Figs. 1–4) and most regional graphs for the 1970–90 period (Figs. 5, 6) indicate the rate of change was remarkably steady everywhere. Thereafter, the regional trends, based exclusively on estimated hunters' kills, are more equivocal; although influenced by increased uncertainty of hunters' species identifications, their descriptive accuracy may be compromised by their derivation.

In Waikato, the best-monitored region in the pre-1970 period, an obvious change in relative abundance occurred in the 1960s (Fig. 1). During this decade mallards achieved their numerical ascendancy over grey duck, an outcome identified at the duck trap, at the hunter's maimai, and in the field. Field counts demonstrated that the mallard's ascent was accompanied by a rapid numerical decline of the grey duck. Population models compiled by Williams & Basse (2006) using survival and fecundity data from the era (Balham & Miers 1959; Nichols *et al.* 1990; Caithness *et al.* 1991), and informed by field counts, suggest that during this period, mallard productivity was 15% above replacement while, for grey ducks, it was 5% below.

In Manawatu, however, the extensive breeding and releases of mallards from the late 1920s, and boosted again during the early 1940s (Balham 1952; Dyer & Williams 2010), had established mallards as the dominant species in coastal Manawatu by the late 1940s, and perhaps even more widely in the district (Andrews *in* WAS 1939). The Wilson diary from Lake Kaikokopu (Fig. 2) provided a unique perspective on the change in relative abundance of the 2 species during an era when mallards were being released into the region by the Wellington Acclimatisation Society. Lake Kaikokopu, then fringed by raupo (*Typha orientalis*), as were most other Manawatu sand country lakes, contrasted with the open surroundings of the initial sites of mallard releases and early abundance in Manawatu (e.g., Hokowhiti (Centennial) Lagoon in Palmerston North, Levin, Marton, Lake Horowhenua, upper Manawatu River; Dyer & Williams 2010). Thus, it provided a refuge of sorts for grey ducks in pre-

World War 2 years. Although it was not until after 1950 that Wilson recorded mallards consistently outnumbering grey ducks in his kill, elsewhere mallards may have done so earlier. For example, Andrews (*in WAS 1937*) reported “the mallard duck has increased remarkably in the Manawatu district and in a very few years will be more numerous than the native grey duck”, and shortly thereafter (*in WAS 1939*) commented that, “they (mallard) now outnumber the grey duck on inland waters about the Manawatu and are numerous in the lower Rangitikei”.

In Waikato and Manawatu, the supplanting of grey duck by mallard appears to have proceeded apace. By 1990, grey ducks in Manawatu had been reduced to a level of numerical uncertainty in hunters’ diaries, were rarely observed in the field, and were no longer encountered during trapping. In Waikato, there was an obvious geographic retrenchment of grey ducks to wetlands of the lower Waikato River and its delta from about 1980 onwards (IAD 46/2, MW pers. obs.) and post-2000 trapping data indicates that everywhere in the pastoral Waikato and Hauraki landscapes, grey ducks are very rarely encountered.

Whilst pre-1970 data from beyond Waikato and Manawatu indicate mallards were approaching, or already were in, relative ascendancy in many parts of New Zealand, data from the 1970–90 period demonstrates the relative demise of grey duck everywhere. Records of hunter’s kills from early and late years of this interval (e.g., Table 2) emphasise that the extent of the perceived change was dramatic in some places (e.g., Northland, Taranaki, Nelson, West Coast). In Southland, Otago, North Canterbury, Hawkes Bay, and Wairarapa mallards approached the total dominance exemplified in post-1990 records. These relative abundance records, however, mask what was a burgeoning mallard population during this time, a feature unreported other than in anecdotal literature (e.g., Williams 1981; Caithness 1982a). By 1980, mallards were in such abundance in grain and pea cropping regions of Southland, South Canterbury and Wairarapa that consideration was being given to declaring the duck a pest of local importance and subjecting it to additional control (IAD 46/2, Williams 1981). Extended hunting seasons combined with no daily limits were trialled in some of the affected regions. It was the drought-inducing effects of a strong El Nino weather system in 1982–83 (see <http://www.bom.gov.au/climate/current/soi2.shtml>) that curtailed mallard population growth in eastern regions of New Zealand. The ensuing slow recharge of ephemeral wetlands, or their loss to intensive pastoral farming, removed habitat previously used by mallards for brood rearing (NZOYB 1990, 2010; P. Taylor, *pers. comm.*; MW, *pers. obs.*).

Interpreting data from the post-1990 period is problematic. The considerable (10–15%) annual variability in the relative abundance of mallards reported in some regional hunters’ kills (Figs. 7, 9) is outwardly disconcerting, as is the calculated long-term trend for these same regional datasets to indicate no change. To conclude long-term stability, albeit with considerable short-term variability, in the relative abundance of the 2 species in North Island regions, defies expectation following such a consistent trend of mallard ascendancy in the previous time-periods, and is counter-intuitive when such extensive landscape change and intensification of pastoral land use would be more favourable to mallards than to grey ducks. Short-term catastrophic breeding performance by 1 species while the other retains average or above productivity, only for a subsequent reversal in species’ fortunes, is simply not a credible explanation.

This period is also problematic because other sources of field information are so limited, or unavailable. For example, trapping in North Island has been limited to the Eastern Fish & Game Region 1997–2015 and Auckland/Waikato 2003–15, and not undertaken at all in South Island. No field studies to quantify population size or duckling production and from which relative species abundance may be calculated, have been reported from any region. In regions from which present-day hunters report grey ducks being a significant proportion of their kill (e.g., Northland, Nelson, West Coast) no complementary field checks of hunters’ kills to corroborate species identification have been conducted.

In short, nearly all information on the relative abundance of grey ducks and mallards for the entire post-1990 period is based on hunter statistics and is cloaked in uncertainty about species identification.

Interpreting grey duck distribution and status

The data examined in this paper can contribute to an understanding of distributional change of grey duck over the past 60 years, and is of potential relevance to ongoing conservation status assessments of the species (e.g., Hitchmough *et al.* 2007). Grey duck is accorded “nationally critical” status, the highest category of conservation concern, predicated not on abundance records but on the likely outcome of demonstrated introgressive hybridisation with mallard (Rhymmer *et al.* 1994), whilst ducks that “effectively resemble grey ducks” have been categorised as “not threatened” (Robertson *et al.* 2017).

Post-1990 trapping of ducks throughout the Eastern Fish & Game region indicates ducks perceived as grey ducks may have a restricted distribution within that region, because they have

been captured at only a few sites. Although grey ducks comprised c. 14% of ducks trapped region-wide 1997–2012 (McDougall & Amundsen 2017), most captures were from 2 adjacent sites in the Rangitaiki River valley, and at 1 site near Gisborne. Such a disjunctive distribution across an expansive region was replicated in the Auckland-Waikato region where most grey ducks were trapped at Opuatia, but only rarely encountered elsewhere. Thus, relative abundance statistics derived from region-wide trapping may mask the possible presence of remnant concentrations of grey ducks. Furthermore, trapping may select for mallards by being limited to sites where large late-summer aggregations of ducks are known but which behaviourally more timid and more solitary grey ducks may simply avoid.

Post-1990, region-wide hunters' kill statistics similarly fail to detect localised concentrations of grey ducks unless survey records can be scrutinised at fine geographic detail. Presently, the sampling net is widely cast and statistical reporting is at a large regional scale (NZ Fish & Game Council, *unpubl.*). Nevertheless, uncertainty about species identification renders the kill statistics of doubtful utility for assessing grey duck distribution and status except, perhaps, to help corroborate the nationwide distribution of grey ducks as recorded by members of the Ornithological Society of New Zealand (OSNZ) between 1999 and 2004 (Robertson *et al.* 2007).

The OSNZ fine-scale survey recorded grey duck presence in 10 km x 10 km grid squares based on NZ Mapping Series 262. Whereas mallard presence was recorded in 84.8% of 1,412 grid squares covering North Island and 60.6% of 1,647 grid squares in South Island, grey ducks were reported from 59.1% of North Island grid squares and 34.7% of South Island grid squares. In North Island, grey duck records were concentrated in Northland, the Waikato River delta, Taranaki, King Country, and Gisborne-East Coast, and well represented on the Volcanic Plateau, in southern Hawkes Bay, and in southern Wairarapa. Although reported from the Kapiti Coast, there were few sightings recorded from Horowhenua and Manawatu, and inland Hawkes Bay (Robertson *et al.* 2007: 123). In South Island, Fiordland, West Coast, and the eastern alpine foothills were regions of concentration, with more scattered records from lower Waitaki Valley, Nelson, Marlborough and North Canterbury (Robertson *et al.* 2007:122).

The reported North Island grey duck distribution is at variance with data obtained from contemporaneous regional hunter kill surveys (e.g., Fig. 7), especially in Gisborne-East Coast, Wairarapa, and Hawkes Bay, and with trapping records from Eastern and Auckland-Waikato Fish

and Game regions. Similarly, in South Island, the grey duck's recorded presence in South Canterbury-Waitaki Valley and in coastal North Canterbury is not corroborated by hunter-sourced data (Fig. 9).

The OSNZ survey is not without interpretative problems of its own. For example, the reported species occurrences in half of all grid squares nationally were based upon 5, or fewer, independent bird surveys within the square (Robertson *et al.* 2007: 12). For grey duck, in each of 491 (58.8%) of the 835 North Island grid squares in which it was reported, fewer than 25% of the independent surveys actually recorded its presence. In South Island, the same limited recording applied to 347 (60.7%) of the 571 grid squares in which grey ducks were reported present. In effect, more than half of all grid squares in which grey ducks were reported nationally may be based upon just a single, or 2, records. With such limited corroboration that a grey duck was indeed observed, and given the uncertainty in species identification shown by hunters with ducks in their hands, how robust were the identifications of OSNZ survey participants when viewing a duck at distance? Even allowing for grey ducks lingering in low abundance, the possibility of confusion with mallard females, and with grey-like ducks of hybrid ancestry, can fairly be raised when the OSNZ survey reported them from such modified environments as urban and peri-urban regions (e.g., Wellington-Kapiti Coast, greater Auckland, Christchurch-Pegasus Bay), and regions of pastoral or viticultural intensification (Marlborough, North Canterbury, Waitaki Valley, Gisborne). Hunters may not be the only observers to find species discrimination challenging.

Hybridisation between grey ducks and mallards

Uncertainty about species identification by trapper, hunter, and field observer has excluded consideration of an ecological outcome of considerable interest, the extent of hybridisation between the 2 species. How extensive has it become? Where grey ducks linger, are hybrids observed also? Are the phenotypically-confusing ducks all of hybrid ancestry? Indeed, do any pure grey ducks remain?

Hybridisation between grey duck and mallard has long been reported (e.g., Thomson 1922), but except for Sage's (1958) reporting of 0.3–4.3% hybrids amongst 634–4,543 ducks trapped at 5 locations in the 1950s, not its frequency or extent. Recognition of a hybrid phenotype, even just the first cross (F.1) has been bedevilled in large part by the plumage variability of mallard females, a consequence of the game farm origins of all New Zealand mallards. Equally, there are no definitive accounts of hybrid plumage characteristics corroborated by genetic

analyses. Presently, Braithwaite and Miller's (1975) schema, modified by Gillespie (1985), and also by Rhymer *et al.* (1994), provides an uncertain method for discriminating hybrids. Results arising from its use by Gillespie (1985), who concluded that 51% of 222 grey ducks and mallards sampled in Otago in 1981–82 were hybrids, remain problematic alongside trap, field and hunting records from the same region and years (Caithness 1968 *et seq.*; Buchan 1977: Table 2; Soulsby 1982: Table 5) all of which report >90% mallard relative abundance. For example, Buchan (1977), using wing characteristics of known captive-reared hybrids, considered 6.1% of 508 ducks collected in Otago and Southland in 1977 to be F.1 hybrids, and Soulsby (1982) identified 10 (2.9%) of 345 Otago ducks collected from hunters in 1982 as hybrids. Green *et al.* (2000), using 2 body measurements, 2 wing characters, and face patterns of known captive-reared hybrids, reported only modestly accurate (76–90%) discrimination between pure grey ducks, F.1 hybrids, and grey-like ($\frac{3}{4}$ and $\frac{7}{8}$ -grey) hybrids, and could not discriminate between mallard-like hybrids and mallards. They assessed F.1 and grey-like hybrids together comprising just 4 (4.6%) of 87 ducks sampled in Otago in 1998, and these hybrid categories being more frequent (up to 14–16% of the combined species population) in regions in which grey ducks had highest relative abundance (Northland, West Coast, Nelson). These divergent appraisals emphasise the need for a genetically-corroborated method for discriminating ducks of hybrid ancestry in the field.

High relative abundance of mallard, and relative rarity of grey duck, should offer fertile ground for inter-specific hybridisation. A numerical imbalance between species in sympatry facilitates hybridisation because of a scarcity of conspecifics for mating (Randler 2002). In *Anas* species, however, forced extra-pair copulatory behaviour, so conspicuous in mallards (McKinney *et al.* 1983), provides another mechanism whereby hybrid offspring are sired (Evarts & Williams 1987; McKinney & Evarts 1998). But as Rhymer *et al.* (1994) identified, introgression of grey duck mitochondrial DNA into the mallard population, as well as the reverse, indicates it is not just mallard male-imposed hybridisation that is occurring. Hybrids were designated to be amongst ducks trapped from the very commencement of trapping programmes in the 1950s (see above) and mixed species pairs were observed during Waikato field studies in the 1960s (Williams & Basse 2006). These observations derive from an era in which, and from places at which, both species were common. Reports of hybridisation have not been limited to times and places where 1 species was conspicuously ascendant.

Perceptions of grey ducks and mallards

The records summarised in this paper derive from the most extensive historic and contemporary accounts of grey ducks and mallards in New Zealand. They indicate that, historically (up to c. 1980), grey ducks were sufficiently abundant to be encountered readily in the field and successfully hunted over much of New Zealand. Post-1980, however, they have dwindled to the point where many hunters and field observers rarely encounter them, and when they do, there is uncertainty about what is being viewed. Ducks perceived to be grey ducks, and many designated as mallards too, may not necessarily be so.

With hybridisation between grey ducks and mallards now having been reported in New Zealand for 100 years, and if hybrids are not selectively disadvantaged, it is possible that the combined grey duck-mallard population in New Zealand is now an extensive genetic admixture. Will the outcome see 2 stable phenotypes, grey-like and mallard-like, persist, as Yamashina (1948) suggested had occurred for the enigmatic *A. (platyrhynchos) oustaleti* from the Mariana Islands, or will a genuinely new hybrid taxon eventually arise, perhaps akin to Hawaiian duck (*A. wyvilliana*; Lavretsky *et al.* 2015)? Alternatively, could mallard simply competitively extirpate *A. superciliosa* from New Zealand with but slight, or no, genetic inclusion? Unravelling the genetic consequences of the mallard's introduction to New Zealand, and thus quantifying this oft-cited example of invasiveness (e.g., Callaghan & Kirby 1996; Rhymer & Simberloff 1996), is a topic of research necessity, as is the need for clarity in the field about what is presently being perceived as a "grey duck" and a "mallard".

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APPENDIX 1: How accurately do hunters discriminate grey duck from mallard?

Duck hunting regulations have never required hunters to demonstrate an ability to identify game and protected species of waterfowl. During years in which hunters have reported their hunting outcomes (1968–present), no test(s) of hunters' abilities to differentiate between waterfowl species has been conducted by those collating the hunting statistics. The reported species identifications have been accepted as correct. The regular inclusion of the protected grey teal (*A. gracilis*) amongst hunters' kills (e.g., Mills 1976; Soulsby 1982; Caithness 1982a) is cause sufficient to suggest that not all hunters can identify their quarry accurately.

Soulsby (1982) is the only reported attempt to test New Zealand hunters' waterfowl identification skills. He asked 48 hunters to record in a diary the species identity of each duck shot, and to keep a wing from each. Those diaries listed the identities of 398 ducks as 302 mallard, 45 grey duck and 51 shoveler (*A. rhynchotis*) whereas Soulsby identified the wings to be from 332 mallard, 10 mallard x grey duck hybrids, 3 grey duck and 53 shoveler. Six (12.5%) of the hunters were responsible for the 43 conflicting identifications. Of the incorrectly identified birds (10.8% of the total), 1 shoveler was listed as mallard and another as grey duck, 1 grey duck as a mallard, the hybrids as grey duck (6) and mallard (4), and 31 mallards (10%) as grey ducks. All mallards incorrectly identified as grey ducks were females.

Soulsby (1982) also asked 41 hunters to identify duck species from colour illustrations: correct identifications were given for mallard male (98%), mallard female (80%), grey duck (61%), shoveler male (85%), shoveler female (83%) and grey teal (46%). There was confusion between grey ducks and mallard females.

Bands retrieved from c. 15%–20% of all grey ducks and mallards banded in New Zealand are

eventually reported to the Banding Office (Balham & Miers 1959; Caithness *et al.* 1991; McDougall & Amundsen 2017). When reporting a banded bird, a minority of hunters indicate the species from which the band was removed. Comparing species assigned at banding with that assigned when reported offers a means to assess accuracy of species identification by those hunters who already believe they can. Archived letters reporting band recoveries during 5 time-intervals were examined (IAD 46/5/32A, 46/2/2, DOC banding), and agreement between bander and hunter species assignments quantified (Table A.1.).

When hunters declared ducks to be mallards, they were invariably correct (92–98%). However, the mallard declaration appears biased. In the 3 tabulated time-intervals between 1971 and 2001, 299 correct mallard identifications were stated as “mallard drake” (56%), “mallard female” (or “hen”) (15%), and “mallard or mallard duck” (29%); the mallard drake's breeding plumage was more readily identified. Over the same time-intervals, 17 (25%) of 69 grey ducks were erroneously identified as mallards (1 as a male, 1 as a female, and the remainder as “mallard”). Of 17 mallards from these intervals erroneously identified as grey ducks, 12 were banded as females and 5 as males. Three “hybrids” reported in 1997–2001 were banded as mallard females. Thus, hunters' abilities to identify grey ducks were poorer than their abilities to identify mallards, and hunters were more accurate identifying a mallard when confronted with a drake.

Hunters' abilities to identify grey ducks correctly changed over time; 81 (89%) of 91 banded grey ducks were correctly identified as such by hunters in the 1961–2 and 1971–2 time-intervals combined whereas only 13 (27%) of 49 from the 3 later time-intervals were, a highly significant difference ($\chi^2 = 56.36$, $P < 0.0001$). There was no complementary decline in hunters' abilities to identify mallards correctly ($\chi^2 = 0.21$, $P = 0.64$).

Table A1. Percentage of banded mallards and grey ducks (n) shot by hunters in 5 time-periods whose species identifications, as reported to the Banding Office, matched that of the duck's bander. Hunter identifications other than the alternate species were: ¹1 (1%) shoveler (*A. rhynchotis*); ²3 (3%) “hybrid”; ³1 (1%) “hybrid”; ⁴1 (7%) “hybrid”.

Year	1961-2		1971-2		1981-2		1997-01		2016	
	%	n	%	n	%	n	%	n	%	n
Mallard	79	24	94	116	92 ¹	104	94 ²	96	98 ³	285
Grey duck	86	57	94	34	67	27	25	8	14 ⁴	14