HYBRIDIZATION, INTROGRESSION, AND MORPHOMETRIC DIFFERENTIATION BETWEEN MALLARD (*ANAS PLATYRHYNCHOS*) AND GREY DUCK (*ANAS SUPERCILIOSA*) IN OTAGO, NEW ZEALAND

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ABSTRACT.—Small numbers of Mallard (*Anas platyrhynchos*) were introduced into New Zealand from Great Britain and North America over 100 years ago. Both sexes have undergone differentiation in size and plumage characters as a consequence of hybridization with the indigenous Grey Duck (*A. superciliosa*). Pure forms of both species, as documented by early descriptions, appear to be disappearing, particularly the Grey Duck. In Otago, the Mallard and Grey Duck are introgressively hybridizing, and the majority of intergrades are Mallard-like in appearance. Separation of Mallards, hybrid birds, and Grey Ducks was achieved using a stepwise cluster analysis of mensural characters. The observed morphometric differentiation was not continuous throughout the Otago population, and a total of 5 discontinuities (groups of morphologically similar birds) were distinguished: male Mallards, female Mallards, Grey Ducks, and 2 groups of hybrid birds. The use of bivariate scattergrams of skull length and eye-lens weight provided the most useful illustration of the distinctions among Mallard, hybrid, and Grey Duck populations. As a consequence of hybridization, two morphologically distinct hybrid populations have been produced: one resembles the Grey Duck and the other the Mallard. This situation is discussed in relation to the two hybrid forms of the Marianas Mallard (*A. oustaleti*).

The Mallard was so successful in newly created agricultural habitat that by 1958 this species constituted 53% of the Mallard-Grey Duck population. Prior to 1958 the observed hybrid frequency was less than 3% and the reduction in the proportion of the Grey Duck most probably was the result of habitat reduction. In 1977 the Mallard comprised 82% of the Mallard-Grey Duck population, and there was concern over the number of pure Grey Ducks remaining in Otago. By 1981-1982 levels of hybridization, based on plumage analysis, had reached 51%, and the proportion of pure Grey Ducks had dropped to 4.5%, which is below the level suggested for the maintenance of a species. In the absence of reproductive isolation or antihybridization mechanisms between these two species, the Mallard and hybrid populations represent a potential threat to the conservation of the New Zealand Grey Duck.
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AVIAN hybridization and the phenotypes exhibited by hybrid individuals within particular areas (suture-zones: Remington 1968) and along geographic gradients have received considerable attention in recent years (Sibley 1957, Johnsgard 1960, Bigelow 1965, Wilson 1965, Short 1969, Mayr 1970, Uzzell and Ashmole 1970, Dobzhansky et al. 1977, Greig 1980, Ford 1981, Alatalo et al. 1982, Scherer and Hilsberg 1982). The rate of hybridization between introduced exotic species and closely related indigenous species, as measured by morphological change, can provide critical insight into the dynamic processes of evolution (Baker 1980). Hybridization resulting from introductions by man often is termed "unnatural" by taxonomists, but forms such as the Marianas Mallard (*Anas oustaleti* Salvadori), which is unlisted in several taxonomic treatments of waterfowl (Delacour 1956, Mayr and Cottrell 1979) because of its hybrid affinities, are of potential importance to our understanding of waterfowl evolution (Milstein 1979, Weller 1980, King 1981).

Interspecific hybrids among birds are rare, occurring at a frequency of about 1 in 50,000 individuals (Mayr 1970). Alatalo et al. (1982) suggested that many isolating mechanisms exist to select against this type of hybridization, which often "wastes genes." These mechanisms appear to be restricted in the Anatidae, for which interspecific hybridization is well documented (Gray 1958, Johnsgard 1960). Re-

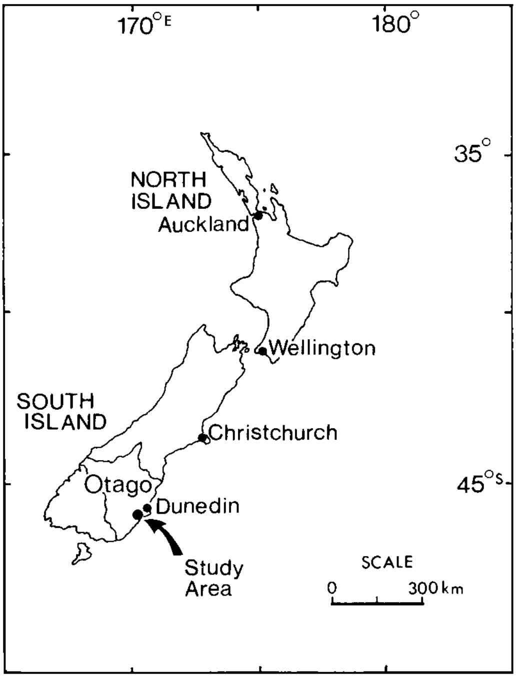

Fig. 1. Map of New Zealand showing the Taieri Plains study area where duck samples were collected. Imported Mallards were liberated in Dunedin, Christchurch, Wellington, and Auckland.

cently, Scherer and Hilsberg (1982) recorded 418 interspecific hybrids, 20% of which were fertile, which emphasizes the close taxonomic relationships of the ducks within this family.

The problem of distinguishing previously distinct species after hybridization occurs has been reported often (West 1962; Delacour 1964; Johnsgard 1967, 1975; Short 1969; Mayr 1970; Gill 1980). However, quantitative information on the degree of hybridization, the rate of morphological change, and the proportion of mixed as opposed to "pure" forms is necessary before aspects of feeding behavior, diet diversity, and competitive overlap can be studied (Alerstam et al. 1978).

In New Zealand, the taxonomy of two species of dabbling duck, the Mallard (*Anas platyrhynchos*), which was introduced in the 1860's, and the indigenous Grey Duck (*A. superciliosa*), has become confusing because of interbreeding between the two populations and the subsequent production of viable hybrid forms (Williams 1981, Haddon 1984). The earliest reference to hybridization between these species was documented by Thomson (1922), who reported that ducks shot in Christchurch in 1917 were thought to be Mallard-Grey Duck hybrids. Sage (1958), using plumage characters, estimated that the proportions of hybrids in Auckland, Wellington, Christchurch, and Dunedin (Fig. 1) were 0.3, 0.4, 4.3, and 3.0%, respectively. His figures, based on trapping returns, indicated that hybrids were more frequent on South Island than on North Island. Buchan (1977) recorded an average hybrid frequency of 6.1% (range 0.0–12.5%) based on the plumage characters of wings collected from the Taieri Plains. He suggested that the incidence of hybridization was increasing.

I present an analysis of morphometric variation in Otago populations of Mallards, Grey Ducks, and associated hybrids. An attempt was made to quantify the degree of interspecific hybridization, statistically assess patterns of variability within populations, and investigate the possible significance of the morphological differentiation exhibited among these birds.

Materials and Methods

All duck samples were collected from the Taieri Plains study area (Fig. 1) during the first two weeks of the 1981 and 1982 shooting seasons (May–July). First-year birds were excluded from the analyses because of obvious size variations. Yearlings were recognized by notched tail feathers (with attached down), comparatively narrow, pointed tertial coverts, the presence of a bursa (with small unsheathed penis) in young males, and a small oviduct opening (often invisible) in young females (Owen and Cook 1977, Schemnitz 1980).

The remaining birds were sexed in the field by cloacal examination (Schemnitz 1980). The head and wings of each bird were removed and placed in labeled plastic bags. All samples were frozen within 3 h of collection.

The degree of hybridization was assessed by two methods. First, a hybrid-index system was constructed based on plumage and soft-part characteristics (Anderson 1949, Johnsgard 1961, Braithwaite and Miller 1975, Hubbard 1977). Plumage categories were constructed from descriptions given for Mallards by Delacour (1956), Kortright (1962), and Palmer (1976); for Grey Ducks by Buller (1888) and Oliver (1930); and for hybrids by Sage (1958), Soper (1963), Falla et al. (1970), and Williams and Roderick (1973). Duck samples were divided into Grey Ducks, hybrids, and Mallards by allocating a score based on plumage and soft-part characters (Table 1). Ducks with scores of 0–9 were designated Grey Ducks and those with 25–35 were designated Mallards. The remaining birds, with scores of 10–24, were considered hybrids. Male and female birds were scored separately. The results were pooled and the overall frequencies calculated. Establishing absolute scores for "pure" Grey Duck (0–4) or "pure" Mallard (30–35) was difficult, even when based on direct comparisons with representative specimens and species descriptions. This may be attributable to the natural, intrinsic variation inherent in most populations (Hubbard 1977).

The second method utilized morphometric parameters and multivariate techniques in an attempt to achieve a quantitative measure of the degree of hybridization and morphological differences. Six parameters were used: (1) Wing length. The wing was flattened and measured from the flesh at the "bend" to the tip of the longest primary feather (Palmer 1976). (2) Skull length. The head was measured from the bill tip to the base of the cranium (feathers included; Owen and Montgomery 1978, Thomas 1982). (3) Eye-lens weight. The eyeballs were removed from the skull and placed in 10% formalin for 2 weeks. This soaking fixed and hardened the lenses to minimize any subsequent damage (Friend 1968, Morris 1972). The lenses were removed from the eyeball casings and left to soak for a further 4 weeks in the formalin solution. After this soaking period any ciliary material still attached to the lenses was carefully removed. The lenses were dried in a convection oven at 55°C for 48 h, placed in a desiccator to cool, and weighed on an electronic balance to the nearest 1 mg (Friend 1968, Morris 1972, Wheeler and King 1980). (4) Bill length. The bill was measured in a straight line along the dorsal surface of the exposed culmen (Baldwin et al. 1931). (5) Neck length. The neck was measured on a flat surface, but not stretched, from the base of the cranium to the junction of neck and thorax (Thomas 1982). (6) Body length. The body was measured on a flat surface from the junction of the neck and thorax to the anterior junction of the leg and body (Thomas 1982). Measurements of all characters except eye-lens weight were recorded to the nearest 0.1 mm with dial calipers or to the nearest 1 mm with a ruler.

A stepwise cluster analysis of cases, based on average linkage between merged groups (Anderberg 1973), was used to distinguish birds with similar morphometrics (Rosenberg et al. 1982). To improve the accuracy of this technique, it was necessary to choose morphologically independent parameters that would minimize the effects of age or the environment. Variations in morphological measurements were influenced by age, season, and environmental conditions (Owen and Cook 1977, Owen and Montgomery 1978). Skull length was preferable to bill length, as the exact position of the tip of the feathering often is indistinct (Owen and Montgomery 1978). Measurements of retrapped Mallards in Britain indicated that wing measurements were preferable to neck and body parameters. The elasticity of the neck and the difficulty of measuring body length accurately indicated that such measurements were useful only for comparative analyses (Owen and Montgomery 1978). Studies with Mallard and Blue-winged Teal (*Anas discors*) in the Northern Hemisphere have shown that eye-lens growth is slow, increasing linearly from hatching and leveling off at about 100 days, and continued weight changes in the eye lens, if any, are insignificant (Friend 1963, 1968). Thus eye-lens weight could be used in the analyses as an age-independent parameter, thereby minimizing the clustering of individuals of similar size with

TABLE 1. The hybrid index used for the detection of Mallard–Grey Duck hybrids (modified from Braithwaite and Miller 1975).

Characteristic	Degree of character assessment	Value[a]
Face striping		
Grey Duck	Two clear black stripes on a cream background	0–1
Hybrid	Obscured face stripes	2–3
Mallard	No face stripe to a thin black eye stripe in the female	4–5
Speculum borders—anterior		
Grey Duck	No white bar	0–1
Hybrid	Thin white bar (2 mm)	2–3
Mallard	Broad white bar (5 mm)	4–5
Speculum borders—posterior		
Grey Duck	Faint white line	0–1
Hybrid	Thin white bar (2 mm)	2–3
Mallard	Broad white bar (5 mm)	4–5
Bill		
Grey Duck	Slate gray	0–1
Hybrid	Gray-yellow	2–3
Mallard	Yellow-orange	4–5
Nape		
Grey Duck	Cream	0–1
Hybrid	Creamy brown	2–3
Mallard	Dark brown, varying from a dark green to a purple-green in the male	4–5
Tail		
Grey Duck	Slate gray	0–1
Hybrid	Gray-brown	2–3
Mallard	Creamy brown, varying from a dark green to a purple-green in the male	4–5
Leg		
Grey Duck	Gray-brown	0–1
Hybrid	Gray-yellow	2–3
Mallard	Yellow-orange	4–5

[a] The index gives a score of 0 for the purest Grey Duck and 35 for the purest Mallard.

TABLE 2. The phenotypic frequencies, as distinguished by plumage and soft-part characters, of ducks collected from the Taieri Plains during the 1981 and 1982 shooting seasons.[a]

	Scores	Sample size	Percent of total
Grey Duck			
Pure	0–4	10	4.5
Very like	5–9	16	7.2
Like	10–14	18	8.1
Hybrid			
Intermediate	15–19	20	9.0
Mallard			
Like	20–24	23	10.4
Very like	25–29	37	16.7
Pure	30–35	98	44.1
Combined categories[b]			
Grey Duck-like	0–9	26	11.7
Hybrids	10–24	61	27.5
Mallard-like	25–35	135	60.8
Total	35	222	100.0

[a] Ducks were compared with typical specimens and original descriptions.
[b] Birds divided into three categories based on pooled scores.

respect to age (Humphries et al. 1981). Collection of all samples within a 2-week period minimized any seasonal differences in morphology (e.g. abrasion, molting).

The ecological implications of the various body parameters, in relation to feeding, were investigated. Skull, neck, and body measurements were summed to compare the average potential reach of Mallards, hybrids, and Grey Ducks while feeding on submerged foods (Thomas 1982). Morphological differences were tested using the Student's *t*-test with separate variances (Zar 1974); the standard deviation and coefficient of variation also were calculated. Multivariate analyses were performed on a Digital VAX/VMS computer using a BMDP program package (Dixon 1977, Hill 1979).

RESULTS

Discernment of hybrid birds.—Using the hybrid-index system, samples were divided into 7 categories ranging from pure Grey Duck to pure Mallard (Table 2). The number of birds in each category gradually increased from Grey Duck to Mallard. Pure Grey Ducks, hybrids, and pure Mallards constituted 4.5%, 51.4%, and 44.1% of the total sample. However, by combining categories of like birds, it was evident that 11.7% of the specimens were essentially similar to the Grey Duck, 27.5% were variously intergrade, and 60.8% were essentially like the Mallard (Table 2). These three combined groupings were considered representative of the overall phenotypic frequency, as Mallard-Grey Duck hybrids with fewer than 5% Grey Duck or Mallard genes appear to be indistinguishable from pure Grey Ducks and pure Mallards, respectively (Williams 1970, Williams and Roderick 1973).

A range of plumage patterns was evident during analysis, especially among male and female Mallards. A total of 61 birds were identified as hybrids, and they exhibited diagnostic features of both species. Within the hybrid sample 61% of the birds were female. This higher frequency of females in hybrid populations has been reported previously (Braithwaite and Miller 1975, Hubbard 1977), although Williams (1981) maintains that many of these females are not hybrids but simply birds of variable plumage.

Skull morphology generally was similar in Mallards and Grey Ducks. A highly arched skull, smoothly curved cheeks, and a rounded lower chin were characteristic of these birds (Fig. 2). The hybrids had narrower and more elongated skulls. Braithwaite and Miller (1975) also found such elongated skulls in hybrids between the Mallard and Black Duck (*Anas superciliosa rogersi*) in New South Wales, Australia.

Degree of hybridization.—A dendrogram was constructed, by cluster analysis, to assess the degree of hybridization and indicate the proportion of ducks that exhibited similar morphological features. The stepwise clustering of wing, skull, and eye-lens parameters revealed a more or less steadily decreasing dissimilarity among groups (Fig. 3). Groups of ducks within this population exhibited a range of wing, skull, and eye-lens sizes that gradually increased from the smaller Grey Duck to the larger Mallard males. This progression in size of body parameters was not continuous, however; ducks of very similar morphology were evident, although the groups themselves differed substantially.

By adopting a morphological dissimilarity threshold of greater than 0.8, 5 distinct clusters of ducks with similar wing, skull, and eye-lens parameters were defined (Fig. 3). Cluster 1 was composed of 75 male Mallards and cluster 3 of 65 female Mallards. Clusters 2 and 4 contained a total of 57 hybrid birds of both sexes, and

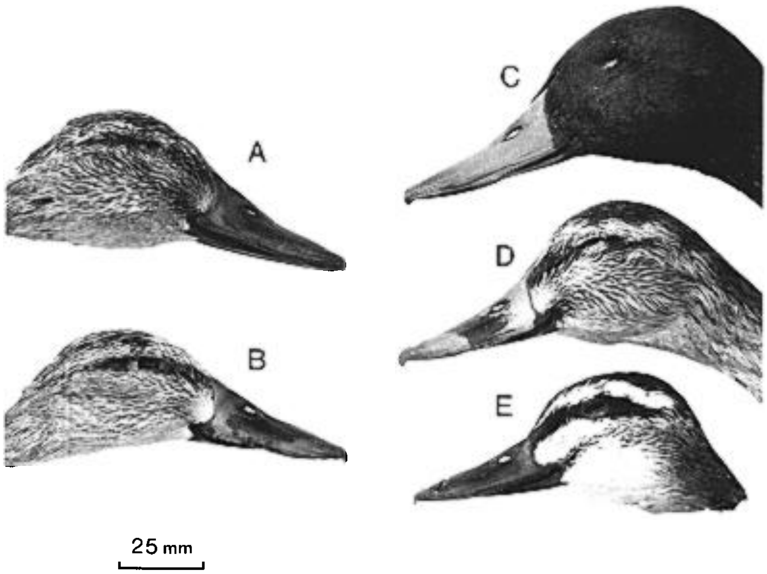

Fig. 2. Morphology of the head of hybrids, Mallards, and Grey Ducks collected from the Taieri Plains, 1981. A = male hybrid, B = female hybrid, C = male Mallard, D = female Mallard, E = male Grey Duck.

cluster 5 contained 14 male and 11 female Grey Ducks. Using these groupings, Mallards constituted 63%, hybrids 26%, and Grey Ducks 11% of the population collected from the Taieri Plains.

The similarity of individuals within the Mallard, hybrid, and Grey Duck groupings varied greatly. The most similarly clustered group was the male Mallards, with 19 (25.3%) identical individuals present (Fig. 3). In the female Mallard, hybrid, and Grey Duck groups only 18.5%, 15.8%, and 20% of the individuals were identical.

A discontinuity was evident in the clustering of hybrid individuals, and two distinct groups were present. One group resembled the Mallard (cluster 2), and the other resembled the Grey Duck (cluster 4; Fig. 3). The Mallard-like group (2) contained male and female birds that were larger in size than the males and females of the Grey Duck-like group (4). Sexual dimorphism in relation to wing, skull, and eye-lens parameters was not evident within either of the two hybrid groups.

Bivariate scattergrams of body parameters were constructed to compare the groups, as determined by cluster analysis, and to illustrate which of the three parameters was the most important in the discernment of hybrid individuals. Wing length and eye-lens weight separated the female Mallards from the hybrids and Grey Ducks. Male Mallards were separated from Grey Ducks, but there was considerable overlap between all 5 groups (Fig. 4A). Wing length and skull length, on the other hand, divided the birds into 3 groups: male Mallards, female Mallards and hybrids, and Grey Ducks (Fig. 4B). Complete separation of the 5 groups was obtained using skull-length and eye-lens weight parameters (Fig. 4C). In this scattergram, skull length divided Grey Ducks and male Mallards from female Mallards and hybrids, while eye-lens weight separated the hybrids from the female Mallards. A similar pat-

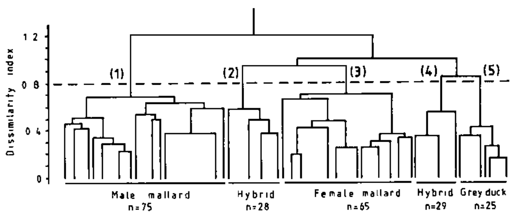

Fig. 3. Dendrogram, constructed by cluster analysis, indicating the degree of similarity of ducks collected from the Taieri Plains based on skull, wing, and eye-lens parameters. Numbers in parentheses indicate distinct clusters, as determined by the dissimilarity threshold (dashed line).

tern of morphological groups was evident in the cluster analysis, but skull length and eye-lens weight were more important than wing length in the discernment of Mallards, Grey Ducks, and hybrid birds.

Morphological differentiation in relation to hybridization.—Body morphology parameters within the Mallard, hybrid, and Grey Duck groups, as determined by cluster analysis, were compared. Male Mallards were significantly larger than female Mallards in all 6 body parameters (Table 3). Hybrid males had larger wing, neck, and eye-lens measurements, while the male Grey Ducks had longer bill, neck, and body measurements than their respective females.

The greatest variance in body parameters was evident among the hybrids. Eye-lens weight was particularly variable, as indicated by the high coefficients of variation for male and female hybrids (Table 3). Skull length was the most consistent measurement for all groups and had the lowest coefficients of variation.

Mallards had a longer reach and presumably are able to feed at greater depths than Grey Ducks (Fig. 5). Hybrid birds had a maximum reach that was intermediate between Mallards and Grey Ducks. Sexual differences in bill, skull, neck, and body morphology were evident in all groups. Males had the longest reach, and differences between the sexes of 16.4% for Mallards, 4.7% for hybrids, and 9.3% for Grey Ducks were recorded. Significant sexual differences were evident in the reach parameters of both the Mallards and Grey Ducks (Table 3). Mallard and Grey Duck males had longer skull, neck, and body parameters and therefore could feed at greater depths than their respective females (Fig. 5). The reduced sexual dimorphism in the reach parameters of the hybrids enabled both

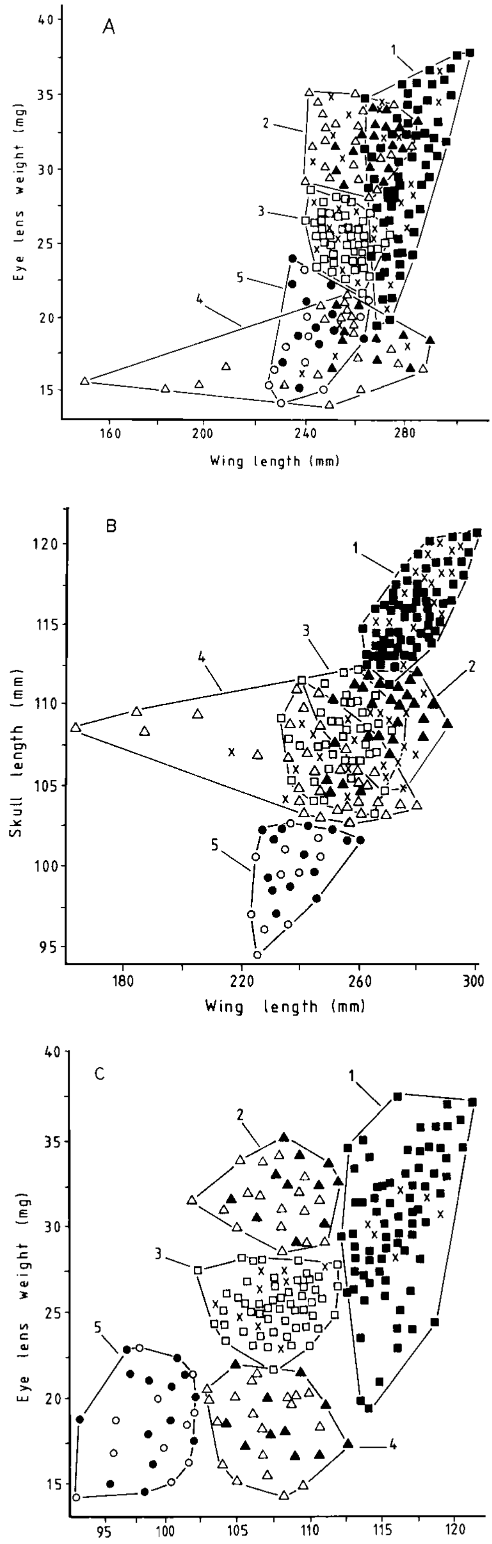

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Fig. 4. Bivariate plots of morphological measurements for Mallards, hybrids, and Grey Ducks collected from the Taieri Plains during the 1981 and 1982 shooting seasons. Lines indicate groups of individuals as determined by cluster analysis. ■ = male Mallard, □ = female Mallard, ▲ = male hybrid, △ = female hybrid, ● = male Grey Duck, ○ = female Grey Duck, X = overlap of 2 or more data points. (A) eye-lens weight and wing length ($r = 0.65$, $n = 222$, $P < 0.001$), (B) skull length and wing length ($r = 0.73$, $n = 222$, $P < 0.001$), (C) eye-lens weight and skull length ($r = 0.51$, $n = 222$, $P < 0.001$).

TABLE 3. Parameters of body morphology, as determined by cluster analysis, for Mallards, hybrids, and Grey Ducks collected from the Taieri Plains during 1981 and 1982.

	Wing	Skull	Eye lens	Bill	Neck	Body
Mallard						
Males (n = 75)						
Range	259–298	111–121	19–37	48–60	110–231	171–193
Mean	275.2	116.3	30.8	55.1	222.5	184.6
SD	18.0	2.2	4.2	2.1	7.5	6.1
CV[a]	6.6	1.9	13.6	3.8	3.4	3.3
Females (n = 65)						
Range	236–273	103–112	21–28	47–59	183–201	138–157
Mean	254.2	110.1	24.5	50.1	194.1	146.2
SD	17.5	2.4	1.8	1.9	6.8	5.8
CV	6.9	2.2	7.4	3.8	3.5	4.0
Value of t[b]	16.97***	15.84***	11.80***	14.79***	23.49***	38.14***
Hybrid						
Males (n = 22)						
Range	247–293	104–112	16–35	47–53	189–235	159–192
Mean	276.7	110.1	29.6	51.2	211.7	177.9
SD	21.7	3.3	6.8	3.5	18.1	12.3
CV	7.8	3.0	23.0	6.8	8.6	6.9
Females (n = 35)						
Range	143–285	103–111	14–35	47–54	164–226	154–193
Mean	264.9	109.6	25.8	50.8	198.8	172.6
SD	20.3	4.6	6.4	2.7	16.3	13.1
CV	7.7	4.2	24.8	5.3	8.2	7.6
Value of t	2.05*	0.48	2.10*	0.46	2.72**	1.54
Grey Duck						
Males (n = 14)						
Range	229–263	96–102	15–24	46–56	155–174	139–161
Mean	248.3	100.7	20.2	50.1	165.4	152.5
SD	19.7	1.9	2.5	2.9	6.3	6.0
CV	7.9	1.9	12.4	5.8	3.8	3.9
Females (n = 11)						
Range	221–265	92–102	14–23	44–50	130–152	129–151
Mean	241.0	100.1	19.4	47.0	141.7	146.6
SD	18.8	1.6	2.2	1.6	6.1	6.1
CV	7.8	1.6	11.3	3.4	4.3	4.2
Value of t	0.94	0.86	0.85	3.40**	9.50***	2.42*

[a] Coefficient of variation (%).

[b] Student's t-test, with separate variances, for male and female (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

sexes to feed at approximately the same maximum depth.

DISCUSSION

Plumage indices and mensural characters were utilized in the discernment of Mallards, hybrids, and Grey Ducks. Cluster analysis of three independent parameters separated the ducks into 5 groups based on individuals of similar morphology. Skull and eye-lens characters were the two most important parameters in this analysis. Skull length separated Grey Ducks and Mallards, while eye-lens weight separated the hybrids. These results indicate that the degree of hybridization or range of intergrading forms is not continuous. Two distinct hybrid groups were present, and both contained individuals of both sexes. They exhibited a range of plumage patterns, but sexual dimorphism in both plumage and mensural characters was reduced considerably compared with the Mallards.

A similar situation has been documented for the Marianas Mallard. This bird also is considered to be a hybrid of the Mallard and the Grey

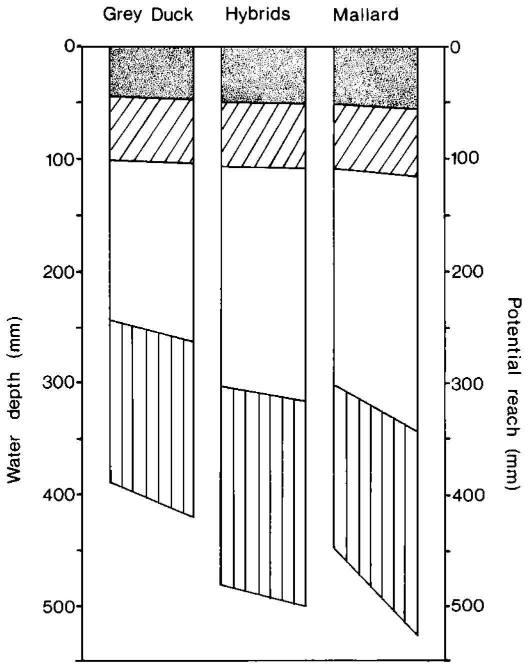

Fig. 5. Average reach morphometrics of Grey Ducks, hybrids, and Mallards in relation to feeding postures (after the method of Thomas 1982). Female measurements are given on the left of each histogram and male measurements on the right. The cumulative proportions of the various parameters are illustrated. Shaded area = bill length, diagonal lines = skull length (excluding bill), open area = neck length, vertical lines = body length.

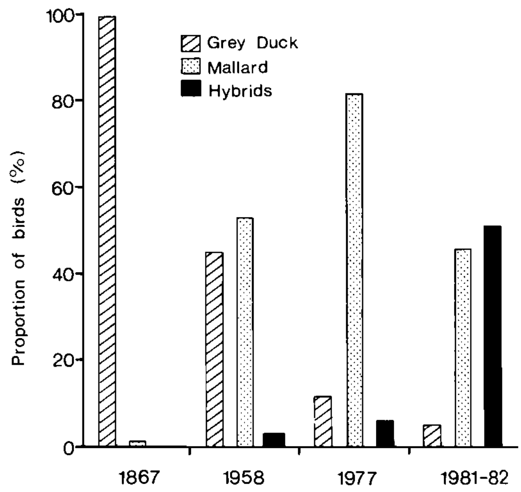

Fig. 6. The proportion of Grey Ducks, Mallards, and hybrids as determined by plumage characters in samples collected from the Taieri Plains area after the introduction of the Mallard in the 1860's.

Duck (Yamashina 1948, Amadon 1966). The literature is confusing because there are two intergrading plumage forms: one resembles the northern Mallard male in eclipse and the other the New Zealand Grey Duck (Yamashina 1948, Weller 1980, King 1981). Yamashina (1948) concluded that these two forms of the Marianas Mallard arose from hybridization of Mallards that arrived accidentally in areas inhabited by the Grey Duck. If these conclusions are correct, it appears that a similar situation has occurred in Otago, where two distinct hybrid forms also have developed as a result of hybridization between these two species.

The significance of hybridization.—The proportion of pure Grey Ducks in Otago has declined from 100% prior to the introduction of the Mallard in 1867 (Thomson 1922) to less than 5% in 1981 (Fig. 6). The number of Mallards in Otago appears to have increased proportionally. Buchan (1977) estimated that Grey Ducks constituted only 7.3% of the total population. This figure is a little higher than the arbitrary 5% level suggested by Short (1969) to ensure that some pure parents were present in the population and not just extreme hybrid phenotypes that appeared as pure individuals. Since 1977, levels of hybridization, which previously had been less than 3% (Sage 1958), have increased substantially from 7.2 to 51.4% (Table 2). The proportion of pure Mallards (44.1%) appears to have decreased in response to increasing hybrid levels, while the proportion of pure Grey Ducks has continued to decline (Fig. 6).

The discernment of hybrids produced between these two species is complex for a number of reasons. First, the Mallard and Grey Duck are closely related forms and probably of similar origin. This common genetic heritage may produce similar phenotypic characters at different times. Further, male hybrids beyond the first backcross (75% one species, 25% another) are often difficult to recognize because of Mallard dominance in plumage characters. Finally, female Mallard populations exhibit high levels of intrinsic variation, and the resulting forms are often difficult to distinguish from hybrid forms.

Recently, several workers have expressed concern that the New Zealand Grey Duck may be disappearing because it is hybridizing with the introduced Mallard (Weller 1969, 1980;

Dorst 1970; Greig 1980). In New Zealand, however, the attitude is somewhat different; for example, Caithness (1975) stated: "Hybridization certianly occurs but is probably confined to those areas where Greys [Grey Ducks] are persisting in low numbers on what is for them marginal habitat." Williams (1981) denied the claim that Mallards were replacing Grey Ducks through hybridization and stated: "What little evidence there is, suggests that Grey Duck are retaining their purity while Grey [Duck] blood has more strongly infiltrated the Mallard."

Introgression as described by Anderson (1949, 1953) undoubtedly occurs among the Mallard and Grey Duck populations of Otago. Three stages are necessary for this process: (1) initial formation of F_1 hybrids, (2) backcrossing to either of the parental groups, and (3) selection of certain recombinant types. Introgressive hybridization between the Mallard and the Grey Duck has been enhanced by the reduction of conspecific mates, the instinctive drive to reproduce, and the inevitability of forced copulations with larger, more aggressive birds. As a result, a large number of hybrid and recombinant forms now constitute a significant proportion of the population (Haddon 1984).

Whether or not the New Zealand Grey Duck will continue to exist as a distinct species under these circumstances is uncertain, but given the extremely low proportion of pure stock and the present levels of introgression, the Mallard poses a threat to Grey Duck conservation in agricultural areas. One factor necessary for a species' continued existence is reproductive isolation (Mayr 1942, Kendeigh 1961, Pettingill 1970, Dobzhansky et al. 1977). Since the Grey Duck's separation from parental stock some time in the Cretaceous (Kear and Murton 1976) and the subsequent introduction of the Mallard into New Zealand over 100 years ago, no prezygotic or postzygotic antihybridization mechanisms have developed. As a consequence, these two species hybridize extensively. The apparent genetic compatibility and hybrid fertility has produced a range of morphologically intermediate hybrid and recombinant forms (Haddon 1984).

I found significant mensural differences in the feeding morphology of Mallards, hybrid birds, and Grey Ducks. Interspecific differences in the size of the feeding apparatus often is interpreted to be a mechanism that allows two species to coexist because they can exploit foods of different sizes (Lack 1971). Differentiation in the bill, skull, neck, and body size of Mallards, hybrids, and Grey Ducks may enable the coexistence of these birds in agricultural habitats and reduce competition by partitioning available resources into different niches (Schoener 1965, 1974). At present, this hypothesis is being investigated in Otago to determine the influence of hybridization on the feeding ecology of Mallard, Grey Duck, and hybrid populations (Gillespie 1983, 1985). Further work is required to elucidate the role of hybridization as an important evolutionary mechanism inherent to waterfowl speciation.

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Literature Cited

ALATALO, R., L. GUSTAFSSON, & A. LUNDBERG. 1982. Hybridization and breeding success of Collared and Pied flycatchers on the island of Gotland. Auk 99: 285–291.

ALERSTAM, T., B. EBENMAN, M. SYLVÉN, S. TAMM, & S. ULFSTRAND. 1978. Hybridization as an agent of competition between two bird allospecies: *Ficedula albicollis* and *F. hypoleuca* on the island of Gotland, in the Baltic. Oikos 31: 326–331.

AMADON, D. 1966. Insular adaptive radiation among birds. Pp. 18–20 *in* Proceedings of the symposium of the Galapagos International Scientific Program (R. I. Bowman, Ed.). Berkeley, Univ. California Press.

ANDERBERG, M. R. 1973. Cluster analysis for applications. New York, Academic Press.

ANDERSON, E. 1949. Introgressive hybridization. New York, J. Wiley & Sons.

———. 1953. Introgressive hybridization. Biol. Rev. 28: 280–307.

BAKER, A. J. 1980. Morphometric differentiation in New Zealand populations of the House Sparrow, *Passer domesticus* (L.). Evolution 34: 638–653.

BALDWIN, S. P., H. C. OBERHOLSER, & L. G. WORLEY. 1931. Measurements of birds, vol. 2. Cleveland, Ohio, Cleveland Mus. Nat. Hist.

BIGELOW, R. S. 1965. Hybrid zones and reproductive isolation. Evolution 19: 449–458.

BRAITHWAITE, L. W., & B. MILLER. 1975. The Mallard, *Anas platyrhynchos*, and Mallard-Black Duck, *A. superciliosa rogersi*, hybridization. Australian Wildl. Res. 2: 47-61.

BUCHAN, G. 1977. Mallard, Grey, and hybrid ducks in Otago and Southland. Unpublished Diploma of Science thesis, Dunedin, New Zealand, Univ. Otago.

BULLER, W. L. 1888. A history of the birds of New Zealand, vol. 2. London, Taylor and Francis.

CAITHNESS, T. A. 1975. The Mallard, Grey situation. Pp. 6-9 *in* Wellington Acc., Soc. Ann. Rept. Wellington, New Zealand, Govt. printer.

DELACOUR, J. T. 1956. The waterfowl of the world, vol. 2. London, Country Life Ltd.

———. 1964. The waterfowl of the world, vol. 4. London, Country Life Ltd.

DIXON, W. J. 1977. BMDP: biomedical computer programs. Berkeley, Univ. California Press.

DOBZHANSKY, T., F. J. AYALA, G. L. STEBBINS, & J. W. VALENTINE. 1977. Evolution. San Francisco, W. H. Freeman and Co.

DORST, J. 1970. Before nature dies (C. O. Sherman, transl.) Boston, Houghton Mifflin Co.

FALLA, R. A., R. B. SIBSON, & E. G. TURBOTT. 1970. A field guide to the birds of New Zealand and outlying islands. London, Collins.

FORD, J. 1981. Hybridization and migration in Australian populations of the Little and Rufous-breasted bronze-cuckoos. Emu 81: 209-222.

FRIEND, M. 1963. The use of eye lens as an indicator of age in game farm Mallards. New York State Conserv. Dept. mimeo.

———. 1968. The lens technique. North Amer. Wildl. Conf. 33: 279-298.

GILL, F. B. 1980. Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97: 1-18.

GILLESPIE, G. D. 1983. The morphology and feeding ecology of Mallard (*Anas platyrhynchos*) in relation to agriculture in Otago, New Zealand. Unpublished M.Sc. thesis, Dunedin, New Zealand, Univ. Otago.

———. 1985. Feeding behaviour and impact of ducks on ripening barley crops grown in Otago, New Zealand. J. Appl. Ecol. 22: 1-10.

GRAY, A. P. 1958. Bird hybrids: a checklist with bibliography. Farnham Royal, England, Common W. Agr. Bur.

GREIG, J. C. 1980. Duck hybridization: a threat to species integrity. Bokmakierie 32: 88-89.

HADDON, M. 1984. A re-analysis of hybridization between Mallards and Grey Ducks in New Zealand. Auk 101: 190-191.

HILL, M. A. 1979. B.M.D.P. user's digest: a condensed guide to the B.M.D.P. computer programs. Los Angeles, B.M.D.P. Statistical Software, Dept. Biomathematics, Univ. California.

HUBBARD, J. P. 1977. The biological and taxonomic status of the Mexican Duck. N.W. Dept. Game and Fish Bull. 16: 1-56.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, & S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Syst. Zool. 30: 291-308.

JOHNSGARD, P.A. 1960. Hybridization in the Anatidae and its taxonomic implications. Condor 62: 25-33.

———. 1961. Evolutionary relationships among the North American Mallards. Auk 78: 3-43.

———. 1967. Sympatry changes and hybridization incidence in Mallards and Black Ducks. Amer. Midl. Natur. 77: 51-63.

———. 1975. Waterfowl of North America. Bloomington, Indiana Univ. Press.

KEAR, J., & R. K. MURTON. 1976. The origins of Australian waterfowl as indicated by their photoresponses. Pp. 83-97 *in* The 16th International Ornithological Conference (H. J. Frith and J. H. Calaby, Eds.). Sydney, Australia, Griffin Press.

KENDEIGH, S. C. 1961. Animal ecology. Englewood Cliffs, New Jersey, Prentice-Hall.

KING, W. B. 1981. Endangered birds of the world. The I.C.B.P. bird red data book. Washington, D.C., Smithsonian Inst. Press.

KORTRIGHT, F. H. 1962. The ducks, geese, and swans of North America. Washington, D.C., Amer. Wildl. Inst.

LACK, D. 1971. Ecological isolation in birds. Oxford, Blackwell Sci. Publ.

MAYR, E. 1942. Systematics and the origin of species. Morningside Heights, New York, Columbia Univ. Press.

———. 1970. Populations, species and evolution: an abridgment of animal species and evolution. Cambridge, Massachusetts, Belknap Press.

———, & G. W. COTTRELL. 1979. Birds of the world, vol. 1, 2nd ed. Cambridge, Massachusetts, Mus. Comp. Zool.

MILSTEIN, P. LE S. 1979. The evolutionary significance of wild hybridization in South African Highveld ducks. Ostrich 13(Suppl.): 1-48.

MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Rev. 2: 69-103.

OLIVER, W. R. B. 1930. New Zealand birds, 1st ed. Wellington, New Zealand, Fine Arts (N.Z.) Ltd.

OWEN, M., & W. A. COOK. 1977. Variations in body weight, wing length and condition of Mallard *Anas platyrhynchos platyrhynchos* and their relationship to environmental changes. J. Zool., London 183: 377-395.

———, & S. MONTGOMERY. 1978. Body measurements of Mallard caught in Britain. Wildfowl 29: 123-134.

PALMER, R. S. 1976. Handbook of North American birds. Vol. 2, Waterfowl. New Haven, Connecticut, Yale Univ. Press.

PETTINGILL, O. S., JR. 1970. Ornithology in laboratory and field. Minneapolis, Minnesota, Burgess Publ. Co.

REMINGTON, C. L. 1968. Suture-zones of hybrid interaction between recently joined biotas. Evol. Biol. 2: 321–428.

ROSENBERG, K. V., R. D. OHMART, & B. W. ANDERSON. 1982. Community organization of riparian breeding birds: response to an annual resource peak. Auk 99: 260–274.

SAGE, B. L. 1958. Hybrid ducks in New Zealand. Bull. Brit. Ornithol. Club 78: 108–113.

SCHEMNITZ, S. D. 1980. Wildlife management techniques manual, 4th ed. Washington, D.C., Wildl. Soc.

SCHERER, S., & T. HILSBERG. 1982. Hybridisierung und Verwandtschaftsgrade innerhalbo der Anatidae—eine systematische und evolutionstheoretische Betrachtung. J. Ornithol. 123: 357–380.

SCHOENER, T. W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19: 189–213.

———. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

SHORT, L. L. 1969. Taxonomic aspects of avian hybridization. Auk 86: 84–105.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor 59: 166–191.

SOPER, M. F. 1963. New Zealand bird portraits. Christchurch, New Zealand, Whitcombe and Tombs.

THOMAS, G. J. 1982. Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. J. Zool., London 197: 131–172.

THOMSON, G. M. 1922. The naturalisation of animals and plants in New Zealand. Cambridge, England, Cambridge Univ. Press.

UZZELL, T., & N. P. ASHMOLE. 1970. Suture-zones: an alternative view. Syst. Zool. 19: 197–199.

WELLER, M. W. 1969. Potential dangers of exotic waterfowl introductions. Wildfowl 20: 55–58.

———. 1980. The island waterfowl. Ames, Iowa State Univ. Press.

WEST, D. A. 1962. Hybridization in grosbeaks (*Pheucticus*) of the Great Plains. Auk 79: 399–424.

WHEELER, S. H., & D. R. KING. 1980. The use of eyelens weights for aging wild rabbits, *Oryctolagus caniculus* (L.), in Australia. Australian Wild. Res. 7: 79–84.

WILLIAMS, M. J. 1970. Mallard/Grey hybridization. Wildlife 1970—A review. Pp. 47–48.

———. 1981. The duckshooter's bag. Wellington, New Zealand, Wetland Press.

———, & C. RODERICK. 1973. Breeding performance of Grey Duck (*Anas superciliosa*), Mallard (*Anas platyrhynchos*) and their hybrids in captivity. Intern. Zoo Yearbook 13: 62–69.

WILSON, E. O. 1965. The challenge from related species. Pp. 7–27 *in* The genetics of colonizing species (H. G. Baker and G. L. Stebbins, Eds.). New York, Academic Press.

YAMASHINA, Y. 1948. Notes on the Marianas Mallard. Pacific Sci. 2: 121–124.

ZAR, J. H. 1974. Biostatistical analysis. London, Prentice-Hall.
