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Morphometrics and viability rates support a case of hybrid vigour among New Zealand's Mallard and Pārera (Grey Duck)

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ABSTRACT

The introduction of Mallards (*Anas platyrhynchos*) into New Zealand (NZ) established a self-sustaining feral population, with many hybrids arising through ongoing interbreeding with endemic Grey Ducks (*Anas superciliosa superciliosa*; Pārera). We investigated whether NZ Mallards and verified contemporary Pārera × NZ Mallard hybrids exhibit hybrid vigour by comparing morphometrics (body mass, wing chord and culmen length) and viability metrics (fecundity and nest success) against Pārera. Pārera were generally smaller than NZ Mallards, while hybrids were intermediate, with backcrossed individuals tending towards the size of their respective parent species. Importantly, a binomial generalised linear model of daily nest survival revealed that hybrid females outperform NZ Mallards, with female age, body size and condition also significantly influencing survival. Despite clear morphological differences among genetic groups, these results indicate that hybrids gain a measurable advantage in nest viability. Given that NZ Mallards and contemporary hybrids are at least as viable as Pārera, and that hybrids show higher daily nest survival than Mallards, our findings are consistent with expectations of hybrid heterosis. In the Anthropocene, understanding the adaptive potential of hybrids is critical as anthropogenic hybridisation rises. For Pārera, hybridisation with Mallards represents one of the multiple existential threats, alongside habitat loss, overharvest and exotic predators. However, the elevated survival of hybrid populations suggests that if Pārera were lost, hybrids could successfully occupy their ecological niche, with implications for conservation management of endemic waterfowl.

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Introduction

Human-induced ecological changes have resulted in many once allopatric species being able to hybridise in secondary contact (Muhlfeld *et al.* 2014; Gómez *et al.* 2015). Biologically, hybridisation can threaten species by either decreasing breeding potential in cases where hybrids are infertile or less fit than their parent species, or through gene flow when hybrids are fertile and capable of backcrossing to one or both parental taxa (Todesco *et al.* 2016). It is the latter case that has the potential to threaten species generationally, as hybrids continue to breed into the parental gene pool across time. In fact, extensive gene flow can result in the eventual genetic extinction of endemic species and/or the creation of hybrid population(s) (Wells *et al.* 2019; Lavretsky *et al.* 2023). Generally, hybrid populations are predicted to be less fit than their parental taxa occupying the same niche space as a result of outbreeding depression (Gilk *et al.* 2004). However, there are some cases in which hybrids have shown an increase or shift in niche space that their parental taxa could not fully realise on their own (e.g. hybrid heterosis or hybrid vigour; Baranwal *et al.* 2012; Hristakieva *et al.* 2014; Labroo *et al.* 2021), and this has been documented across lineages including fish (Selz and Seehausen 2019; Šimková *et al.* 2021), plants (Da Re *et al.* 2020; Manzoor *et al.* 2020; Moore *et al.* 2021), birds (Pfennig *et al.* 2016) and mammals (Thornton and Murray 2014; Taylor and Larson 2019). Among growing concerns regarding anthropogenic hybridisation is the interbreeding between domestic individuals and their wild ancestors (Levin 2002). Specifically, distinct selective forces acting on domestic (i.e. artificial selection) and wild (e.g. natural selection) populations result in highly differentiated groups of individuals and variable adaptive outcomes – for example, domestic × wild hybrids may show decreased adaptive capacity in wild settings while realising higher fitness in more urban environments (Beninde *et al.* 2018). Consequently, evaluating the fitness consequences (e.g. adult or offspring survival

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and breeding success) of hybridisation requires understanding the extent of hybridisation and how variation in genetic diversity relates to reproductive outputs relative to source populations.

New Zealand (NZ) is home to the Pacific Black Duck subspecies *Anas superciliosa superciliosa* (a.k.a. 'Pārera' or Grey Duck; hereafter referred to as Pārera), for which a primary conservation concern is genetic extinction via introgressive hybridisation with the introduced but highly adaptive Mallard (*Anas platyrhynchos*) population (Rhymer *et al.* 2004). In short, over 30,000 game-farm Mallards (a domestic breed) were introduced between the 1860s and the 1950s into NZ (Dyer and Williams 2010). Although game-farm Mallards continue to be released to some extent, and while the exact number is extremely difficult to determine due to inconsistent identification of Mallards and hybrids in the wild, census estimates suggest a self-sustaining feral population of approximately 4.5 million Mallards across NZ today (New Zealand Fish and Game 2022). Although game-farm Mallards from Europe and a mix of wild and game-farm Mallards from North America were used across stocking efforts, genetic assignment has recently confirmed these populations to be of game-farm Mallard ancestry (Lavretsky *et al.* 2023; Brown *et al.* 2025). However, in addition to being genetically distinct from endemic Pārera, NZ Mallards are also genetically distinct from their original source populations (Brown 2021; Lavretsky *et al.* 2023; Brown *et al.* 2025). Landscape genomic analyses suggest that the genetic uniqueness of NZ Mallards may be partially attributable to adaptive introgression from Pārera (Brown *et al.* 2025). This unique genetic combination appears to have expanded the adaptive niche space of NZ Mallards, and it is now estimated that approximately 4.5 million individuals across NZ are Mallards or Pārera × NZ Mallard hybrids, whereas Pārera are considered nearly extinct on the two main islands (Williams 2017; Brown *et al.* 2025).

Here, we take advantage of hundreds of genotyped samples representing known Pārera, NZ Mallards and Pārera × NZ Mallard hybrids (i.e. contemporary hybrids), with available morphological and viability rate data (i.e. fecundity and/or nest success), to test for differences among these groups. Previous morphological studies have shown Pārera and NZ Mallards to be significantly different (Gillespie 1985), whereas contemporary hybrids exhibit morphological intermediacy. However, unlike previous studies that lacked genetic data to determine true ancestry, we conduct similar morphological comparisons using genetically vetted individuals. If NZ Mallards have indeed undergone regional adaptation and/or adaptive introgression, then we expect NZ Mallards to exhibit comparable or higher viability rates than Pārera under a scenario of hybrid vigour. Similarly, contemporary hybrids may also show similar viability rates; however, if hybrid vigour requires multiple generations of selective events, contemporary hybrids may still exhibit maladaptive properties. Under this scenario, we expect viability rates to correlate with ancestry estimates, such that F1 hybrids have lower values than later-generation (e.g. F4) hybrids. Together, we aim to understand how a game-farm-derived feral population became so successful in NZ and whether NZ Mallards represent a case of naturalisation.

Methods

Field sampling methods & defining ancestry groups

A total of 560 Pārera, NZ Mallards and Pārera × NZ Mallard hybrids were sampled as part of several projects across 10 regions in the North and South Islands of NZ from 2014 to 2018. First, 295 samples came from live captures conducted as part of two concurrent projects and the NZ banding programme, including: (1) 96 samples from the Waikato and Southland regions (2014–2015); and (2) 198 samples collected from five regions of the North Island (including Waikato) during the annual summer duck banding programmes run by the NZ Fish and Game Council (2017). Live capture and banding followed methods outlined in Sheppard (2017). Next, 266 birds were salvaged during the 2018 hunting season across five regions of the South Island (including Southland). In all cases, sex and age were determined through cloacal examination (Hochbaum 1942), and birds were aged as juvenile (hatch year) or adult (after hatch year) based on the development of the bursa of Fabricius. We used the bursa of Fabricius because birds are typically around 3–4 months of age during summer banding, which coincides with peak bursa size (Gille and Salomon 1999; Mather and Esler 1999). Additionally, with experience, the bursa can still be identified even as it regresses prior to the first reproductive cycle. Moreover, due to high rates of hybridisation with Pārera, Mallard wing identification is insufficient for ageing birds, as no key has yet been developed or tested to age Pārera and Pārera × NZ Mallard hybrids. Finally, we used genetic assignments for each bird as determined in Brown *et al.* (2025) to categorise samples as genetically pure NZ Pārera ($N = 15$), NZ Mallard ($N = 84$), or NZ Pārera × Mallard hybrid ($N = 461$). For hybrids, we either treated all individuals as a single category or subdivided them into more specific groups as genetically determined in Brown *et al*. (2025), including F1 hybrids ($N = 99$), NZ Pārera-backcrossed individuals ($N = 67$) and NZ Mallard-backcrossed individuals ($N = 295$).

Morphometric data and statistical analyses

Across all 560 birds, weight was obtained using Pesola or electronic scales (±10 g), right wing chord (±1 mm) was measured flattened from the end of the carpometacarpus to the tip of the longest primary feather using a ruler, and the culmen (i.e. total length of the upper part of the bill) was measured with an electronic or vernier caliper (±0.1 mm). Note that mass and wing measurements were missing for 12 individuals, and culmen length was missing for one sample.

Prior to comparing morphological data from all 560 samples, we standardised the three morphometric variables by converting each sample's measurements into z-scores, expressing their distance from the mean in units of standard deviations, using IBM SPSS (IBM Corp 2020). The per-sample z-scores were then summed into a single composite score. Subsequently, we used a one-way ANOVA to test for significant differences in measurements among genetic groups. Once a significant difference was confirmed ($\alpha = 0.05$), a set of independent-sample t-tests was conducted with a 95% confidence interval while testing for equality of variance distributions between samples and independent sample size effects. Culmen length showed unequal variances between groups according to Levene's test for equality of variances. Therefore, significance was assessed using Welch's t-test, in which equal variances are not assumed, and results remained significant. Similarly, unpaired t-tests were performed on historical morphometric data obtained from Balham (1952) (hereafter referred to as Historic) and compared with data used in this study (hereafter referred to as Contemporary). In addition to comparable methodologies used to collect measurements, comparison with data from Balham (1952) was ideal because these measurements were obtained prior to Mallard establishment and widespread hybridisation. We tested contemporary and historical measurements of mass, right wing chord length and culmen length between males and females in paired comparisons presented in Table 1.

Finally, we visualised distribution patterns for any trait found to be significant by plotting the per-sample z-scores, which standardised the measurements of each trait relative to its mean and standard deviation.

Nesting data

Nest data were collected for 91 females (total nest observations = 134) that were either radio-marked prior to breeding or located at nests found during systematic nest searches, for which females were subsequently trapped and marked. Once discovered, eggs were

Table 1. T-statistics, degrees of freedom and *p*-values for unpaired *t*-test for historic and contemporary mass, wing chord and culmen measurements between male NZ Mallards and Pārera. Bold text indicates significance ($p < 0.05$). Sample sizes (N) are: *Contemporary Mallard Female* N = 48, *Contemporary Pārera Female* N = 6; *Historic Pārera Female –* $_{\text{Mass}}$N = 140, $_{\text{Wing chord}}$N = 121, $_{\text{Culmen}}$N = 120; *Historic Mallard Female –* $_{\text{Mass}}$N = 156, $_{\text{Wing chord}}$N 120, $_{\text{Culmen}}$N 120; *Contemporary Mallard Male* N = 36, *Contemporary Pārera Male* N = 9; *Historic Pārera Male –* $_{\text{Mass}}$N = 112, $_{\text{Wing chord}}$N = 97, $_{\text{Culmen}}$N = 101; *Historic Mallard Male –* $_{\text{Mass}}$N = 171, $_{\text{Wing chord}}$N = 147, $_{\text{Culmen}}$N = 146.

	MALE			FEMALE		
	t-stat	df	*p*-value	t-stat	df	*p*-value
MASS	11.99	281	**<0.00**	9.99	394	**<0.00**
Historic NZ Mallard vs. Historic Pārera						
Historic NZ Mallard vs. Contemporary NZ Mallard	2.79	205	0.01	0.98	202	0.33
Historic NZ Mallard vs. Contemporary Pārera	5.32	178	**<0.00**	2.62	160	**0.01**
Contemporary NZ Mallard vs. Contemporary Pārera	4.77	43	**<0.00**	2.46	52	**0.02**
Historic Pārera vs. Contemporary Pārera	1.96	119	0.05	0.09	144	0.93
WING CHORD						
Historic NZ Mallard vs. Historic Pārera	17.70	242	**<0.00**	15.92	239	**<0.00**
Historic NZ Mallard vs. Contemporary NZ Mallard	3.79	181	**<0.00**	3.47	166	**<0.00**
Historic NZ Mallard vs. Contemporary Pārera	6.96	154	**<0.00**	4.54	124	**<0.00**
Contemporary NZ Mallard vs. Contemporary Pārera	4.64	43	**<0.00**	3.19	52	**<0.00**
Historic Pārera vs. Contemporary Pārera	0.98	104	0.33	0.03	125	0.98
CULMEN						
Historic NZ Mallard vs. Historic Pārera	11.54	245	**<0.00**	7.92	238	**<0.00**
Historic NZ Mallard vs. Contemporary NZ Mallard	1.82	180	0.07	1.33	166	0.18
Historic NZ Mallard vs. Contemporary Pārera	6.04	153	**<0.00**	1.66	124	0.10
Contemporary NZ Mallard vs. Contemporary Pārera	4.08	43	**<0.00**	1.02	52	0.31
Historic Pārera vs. Contemporary Pārera	2.21	108	**0.03**	0.85	124	0.40

counted and candled to determine incubation status, calculate nest initiation dates and estimate hatch dates. Nests were revisited every 7–10 days to monitor clutch size and determine fate. Hens were genotyped as either NZ Mallard ($N = 26$, total nests = 42) or hybrid ($N = 65$, total nests = 99), with some nests representing re-nesting attempts. Nest fate was classified as (1) successful if at least one egg hatched; (2) abandoned if the nest was deserted following investigator disturbance or partial depredation of less than half the clutch; (3) destroyed if at least half of the clutch was removed or consumed, or if the female was killed while nesting; or (4) non-viable if eggs showed no sign of embryo development. Complete clutch size was known for all 142 nests (i.e. no evidence of partial depredation, the female was not killed during laying, and females did not abandon prior to incubation). For the purposes of the generalised linear model, nest outcomes were consolidated into a binary success/failure variable. We applied a chi-square test to the data, grouping by genotype, to determine whether nest success differed between NZ Mallards and hybrids, whereby hybrids were analysed as a single group or further partitioned as first-generation (F1; $N = 9$) or NZ Mallard-backcrossed ($N = 58$) hybrids. The chi-square test was implemented in R (R Core Team 2024) to determine significant differences in composite z-scores from morphological analyses (see above) and nest. Note that we used percentage totals to properly compare the distribution of clutch size (number of eggs laid) to account for uneven sampling between the groups.

We used a generalised linear model (GLM) in R (R Core Team 2024) with a binomial error distribution and logit link function to evaluate factors influencing daily nest survival in female ducks. Exposure days for each nest were calculated as the number of days from discovery to the end of the nest (hatching or last known alive), plus 1 day to include the day of discovery. This provides a nest-level measure of exposure similar to Mayfield's (1961) nest-day approach, which accounts for both the number of nests and the duration each nest is observed. However, because exact loss dates between nest checks were not available, we could not fully apply the Mayfield method. Specifically, the dataset from Sheppard (2017) and Sheppard et al. (2019) did not include precise timing of nest loss within observation intervals. As a result, we could not assign fractional exposure for nests lost between visits and instead used the approach described above to approximate total exposure for each nest.

The response variable for the GLM was nest fate (1 = successful, 0 = failed), weighted by the number of exposure days for each nest. Predicted daily survival rates (DSR) for each nest were generated from the binomial GLM using the logit link function, with predicted values on the logit scale back-transformed to probabilities using R's predict function. Cumulative nest survival over the observed exposure period was calculated as $S_t = \mathrm{DSR}^t$, where t represents the number of exposure days, providing an estimate of the probability that a nest survived the entire observation interval. Survival curves with 95% confidence intervals were plotted to visualise differences between genetic groups. Explanatory variables included hen age, study area, nesting attempt, female size, female condition and genotype. Random effects were tested using band number as a grouping variable to account for re-nesting attempts, but mixed models did not improve model fit, so a standard GLM was retained. Likewise, clutch size distributions were assessed separately for hybrid and Mallard females. For each group, skewness and kurtosis were calculated to assess the distribution shape, and the Shapiro–Wilk test (Shapiro and Wilk 1965) was used to test for normality. Interquartile range (IQR) was also computed to describe variability in clutch size.

Results

Morphological assessments

Morphometric measurements were evaluated across 15 Pārera, 84 NZ Mallards and 461 contemporary hybrids. Historic and contemporary data indicated that male and female Pārera had significantly lower mass and shorter wing chord lengths compared to NZ Mallards (Table 1). Culmen length in Pārera was shorter for both historic males and females, but only significantly shorter for contemporary males (Table 1). NZ Mallards also exhibited significantly longer wing chord lengths than contemporary hybrids, although they did not differ significantly in mass or culmen length. Evaluation of specific filial classes (i.e. F1, F2 backcrosses, etc.) revealed significant differences among hybrids, with measurements reflecting the parental species to which they were backcrossed; specifically, NZ Mallard-backcrossed hybrids were relatively larger, whereas Pārera-backcrossed hybrids were relatively smaller (Table 2). Finally, plotting standardised z-scores for each measurement revealed that NZ Mallards and contemporary hybrids differed significantly in wing chord length, whereas Pārera differed significantly across all measurements relative to both NZ Mallards and contemporary hybrids (Figure 1).

Independent-sample t-tests were first conducted among the three major categories, including NZ Mallards, Pārera

Table 2. Averages and standard deviation of total body mass, right wing chord length, and culmen lengths of NZ Mallards, F1 hybrids, Pārera-backcrossed hybrids, NZ Mallard-backcrossed hybrids and Pārera sampled in New Zealand from 2014 to 2018. Note we provide estimates across all samples and partitioned by age-sex cohort.

			Mass (grams)	Wing (mm)	Culmen (mm)
Pārera	Male	All (*n* = 9)	1013.9 (±163.9)	258.6 (±11.5)	50.1 (±2.4)
		Juvenile (*n* = 7)	1045.0 (±143.3)	261.9 (±8.4)	50.1 (±2.3)
		Adult (*n* = 2)	905.0 (±247.5)	247.0 (±17.0)	50.1 (±3.8)
	Female	All (*n* = 6)	976.7 (±151.1)	248.5 (±13.6)	50.7 (±0.9)
		Juvenile (*n* = 4)	900.0 (±106.1)	249.8 (±2.9)	50.5 (±1.0)
		Adult (*n* = 2)	1130.0 (±99.0)	246.0 (±29.7)	51.1 (±0.8)
NZ Mallard	Male	All (*n* = 36)	1208.3 (±92.6)	275.4 (±9.3)	54.75 (±3.2)
		Juvenile (*n* = 19)	1220.9 (±88.5)	276.0 (±6.3)	56.2 (±3.2)
		Adult (*n* = 17)	1194.3 (±97.7)	274.7 (±11.9)	53.2 (±2.3)
	Female	All (*n* = 48)	1101.8 (±113.4)	259.5 (±7.2)	51.7 (±2.3)
		Juvenile (*n* = 25)	1068.8 (±114.2)	257.8 (±8.1)	51.9 (±2.6)
		Adult (*n* = 23)	1137.3 (±103.4)	261.4 (±5.6)	51.5 (±2.0)
F1 hybrid	Male	All (*n* = 65)	1123.7 (±123.9)	265.6 (±10.0)	52.8 (±2.6)
		Juvenile (*n* = 31)	1085.3 (±113.6)	265.0 (±10.2)	52.9 (±2.7)
		Adult (*n* = 34)	1158.6 (±124.2)	266.0 (±10.0)	52.7 (±2.6)
	Female	All (*n* = 34)	1037.9 (±91.9)	253.5 (±10.9)	50.0 (±2.0)
		Juvenile (*n* = 20)	1003.3 (±79.6)	251.4 (±12.3)	49.6 (±2.2)
		Adult (*n* = 14)	1087.3 (±87.8)	256.4 (±8.1)	50.5 (±1.8)
Pārera-backcrossed hybrid	Male	All (*n* = 35)	1110.8 (±98.2)	263.9 (±7.9)	54.3 (±2.4)
		Juvenile (*n* = 17)	1080.7 (±99.4)	262.5 (±7.9)	53.7 (±1.8)
		Adult (*n* = 18)	1139.3 (±90.7)	265.2 (±7.9)	53.8 (±2.8)
	Female	All (*n* = 32)	963.7 (±88.9)	250.3 (±6.5)	50.4 (±2.8)
		Juvenile (*n* = 21)	941.9 (±85.0)	249.2 (±6.6)	50.3 (±3.0)
		Adult (*n* = 11)	1005.3 (±84.5)	252.3 (±6.2)	50.4 (±2.5)
NZ Mallard-backcrossed hybrid	Male	All (*n* = 130)	1218.7 (±129.7)	273.0 (±8.7)	54.4 (±2.6)
		Juvenile (*n* = 71)	1206.1 (±132.8)	272.4 (±7.2)	54.7 (±2.4)
		Adult (*n* = 59)	1233.9 (±125.2)	273.7 (±10.3)	54.1 (±2.7)
	Female	All (*n* = 165)	1102.6 (±111.8)	256.7 (±8.7)	51.2 (±2.2)
		Juvenile (*n* = 88)	1071.3 (±112.3)	255.2 (±9.5)	51.0 (±2.1)
		Adult (*n* = 77)	1138.3 (±100.5)	258.5 (±7.4)	51.4 (±2.4)

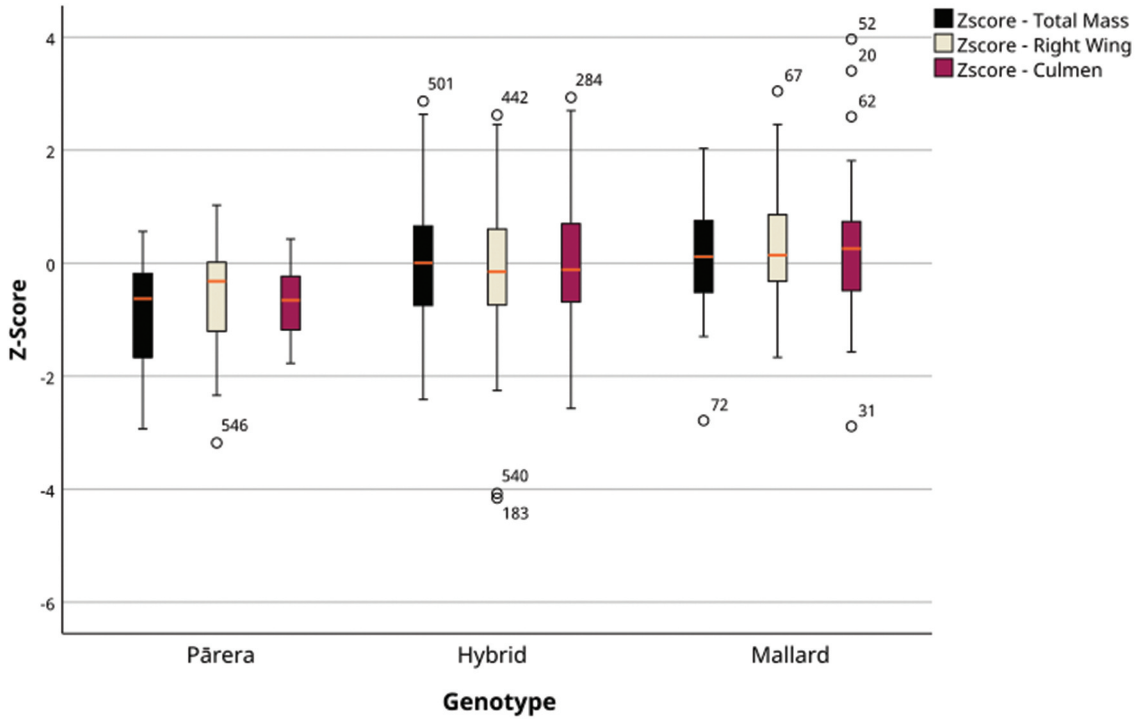

Figure 1. Standardized z–score distribution measuring distance from average in standard deviations for total mass (g), right wing chord length (mm) and culmen length (mm) measurements between NZ Mallards, Pārera, and their hybrids, collected during 2014–2015 in New Zealand.

and F1 hybrids. All three morphometric traits differed significantly between NZ Mallards and Pārera, including mass ($p < 0.001$; $\bar{x} = 148.36$ g; sd = 34.53 g), wing chord length ($p < 0.001$; $\bar{x} = 11.79$ mm; sd = 3.23 mm) and culmen length ($p < 0.001$; = 2.64 mm; sd = 0.83 mm) (Table 5). Comparisons involving hybrids revealed significant differences in wing chord length relative to NZ Mallards ($p < 0.001$; $\bar{x} = 3.91$ mm; sd = 1.39 mm), as well as significant differences in mean total mass ($p < 0.001$; $\bar{x} =$ 125.50 g; sd = 35.66 g), wing chord length ($p = 0.01$; $\bar{x} =$ 7.87 mm; sd = 3.11 mm) and culmen length ($p < 0.001$; $\bar{x} =$ 2.05 mm; sd = 0.51 mm) when compared to Pārera (Table 3). Regression analyses revealed significant genotype × mass interactions ($p < 0.001$), indicating that the relationship between body mass and wing chord length differed among NZ Mallards, Pārera and hybrids. NZ Mallards and Pārera exhibited steeper scaling slopes (0.060 and 0.061, respectively) compared to hybrids (0.051) (Figure 3).

Paired independent *t*-test analyses recovered seven significant pairwise comparisons among hybrid types and between hybrids and parental taxa (Table 4). No comparisons involving NZ Mallards alone resulted in significant differences; however, Pārera differed significantly from F1 hybrids in total mass ($p = 0.01$; $\bar{x} = 96.15$ g; sd = 34.64 g), with no other morphometric differences detected between NZ Mallards and Pārera. Among hybrids, NZ Mallards were larger and had longer wing chord lengths than both NZ Mallard- and Pārera-backcrossed hybrids (mass: $t = 6.41$, $p = 0.02$; $\bar{x} = 113.21$ g; sd = 19.67 g; wing: $t = 4.17$, $p < 0.001$; $\bar{x} = 6.24$ mm; sd = 1.55 mm). Additionally, NZ Mallard – backcrossed hybrids were significantly heavier and larger than F1 hybrids (mass: $t = -3.94$, $p < 0.001$; $\bar{x} = 58.60$ g; sd = 15.03 g; wing: $t = -1.81$, $p = 0.05$; $\bar{x} = 2.68$ mm; sd = 1.35 mm; culmen: $t = -2.39$, $p = 0.03$; $\bar{x} = 0.70$ mm; sd = 0.33 mm).

Historical versus contemporary morphometrics

Comparing our measurements to those of Balham (1952) revealed notable morphometric shifts between Pārera and NZ Mallards. Historically, NZ Mallard and Pārera females differed significantly across all traits, but today they differ only in mass and wing chord, with Mallard females being 12% heavier and having a 4% longer wing chord. Although these differences remain significant, culmen length is no longer significantly different (i.e. a decrease in difference from 5% to 2%; Table 1). Intraspecific and sex-based comparisons showed that

Table 3. Effects of female traits and genotype on daily nest survival and clutch size across all nests between Pārera x NZ Mallard hybrids and NZ Mallards from nests in New Zealand from 2014 – 2015. Nest survival estimates are from a binomial GLM weighted by exposure days. Clutch size is shown as median and interquartile range (IQR).

Genotype	*N*	Median Clutch (IQR)	Mean + SD	Daily Survival %	Significant Predictors
Hybrid	93	0.35 (8.25 – 11)	9.90 ± 2.27	82	Age, Body Size, Body Condition, Genetics
Mallard	41	0.48 (9.00 – 12)	10.46 ± 1.95	74	

Table 4. Statistical significance (*p*-value) for pairwise independent t-tests between all combinations of genetic ancestry of NZ Mallards, F1 hybrids, Pārera-backcrossed hybrids, NZ Mallard-backcrossed hybrids and Pārera sampled in New Zealand from 2014 to 2018. Missing values indicate a lack of significant p-value.

	Body Morphometric	t-stat	df	Significance (*p*-value)
NZ Mallard vs. Pārera	*Mass*	4.30	97	0.00
	Wing Chord	3.65	97	0.00
	Culmen	3.18	97	0.00
NZ Mallard vs. hybrids	*Mass*	1.46	543	–
	Wing Chord	2.81	543	0.01
	Culmen	1.67	543	–
Pārera vs. hybrids	*Mass*	−3.53	474	0.00
	Wing Chord	−2.54	474	0.01
	Culmen	−2.70	474	0.00
F1 hybrids vs. Pārera Backcrossed hybrids	*Mass*	2.82	164	0.00
	Wing Chord	2.29	164	0.04
	Culmen	−1.24	164	–
F1 hybrids vs. NZ Mallard Backcrossed hybrids	*Mass*	−3.94	392	0.00
	Wing Chord	−1.81	392	–
	Culmen	−2.39	392	0.03
NZ Mallard Backcrossed hybrids vs. Pārera Backcrossed hybrids	*Mass*	6.41	360	0.02
	Wing Chord	4.17	360	0.00
	Culmen	0.52	360	–

male NZ Mallards differed from historical samples in wing chord and culmen length, whereas only female wing chord length changed significantly between time points. For Pārera, culmen length was the sole measurement to change significantly for both sexes (Table 1).

Nest fate and clutch

The final binomial generalised linear model explained a significant portion of the variation in daily nest survival (residual deviance = 2205.0, *df* = 127, AIC = 2219). Female age, study area, nesting attempt, body size, body condition and genotype all had significant effects on survival probability. Juvenile females exhibited lower daily nest survival (DSR) than adults (Estimate = 0.78, $p < 0.01$), and nests located in the Waikato region had higher survival than those in the South Island (Estimate = 0.55, $p < 0.01$). Subsequent nesting attempts were associated with reduced DSR (Estimate = –0.32, $p < 0.01$), whereas both larger body size (Estimate = 0.19, $p < 0.01$) and better body condition (Estimate = 2.301, $p = 0.01$) significantly increased the likelihood of daily nest survival. Genotype also had a strong influence on nest outcome, with Mallard females exhibiting substantially lower DSR than hybrids (Estimate = –0.87, $p < 0.01$) (Tables 3 and 5; Figure 2).

Using the predicted DSR values and nest-specific exposure days, cumulative nest survival over the observed periods indicated that NZ Mallards had lower DSR than Pārera until approximately day 25, at which point survival trajectories began to converge. Hybrids reached their lowest cumulative survival 7on day 16 (41.88% ± 0.05), while NZ Mallards reached their lowest on day 19 (26.82% ± 0.07). The highest cumulative survival was observed on day 41 for hybrids (96.13%) and on day 34 for NZ Mallards (87.88%). These final days correspond to the maximum duration

Table 5. Mean cumulative survival per day (and standard error) for NZ Mallards (MALL) (Day 1, n = 93) and hybrid (HYBRID) (Day 1, n = 41) nests. Standard errors were calculated only for exposure days with more than one nest contributing observations. By day 36, only a single hybrid nest remained under observation, and by day 34 only a single Mallard nest remained; consequently, standard errors could not be estimated beyond these points.

Species	Day	Mean Survival	Standard Error Survival	Species	Day	Mean Survival	Standard Error Survival
HYBRID	1	57.24%	0.04	MALL	1	47.35%	0.06
HYBRID	2	64.93%	0.04	MALL	2	46.65%	0.07
HYBRID	3	60.80%	0.04	MALL	3	41.57%	0.07
HYBRID	4	56.27%	0.04	MALL	4	38.23%	0.07
HYBRID	5	53.74%	0.04	MALL	5	37.18%	0.07
HYBRID	6	50.91%	0.04	MALL	6	35.65%	0.07
HYBRID	7	48.45%	0.04	MALL	7	33.44%	0.07
HYBRID	8	47.67%	0.05	MALL	8	31.67%	0.07
HYBRID	9	47.82%	0.05	MALL	9	33.68%	0.07
HYBRID	10	45.99%	0.05	MALL	10	32.30%	0.07
HYBRID	11	46.49%	0.05	MALL	11	31.09%	0.07
HYBRID	12	44.92%	0.05	MALL	12	31.24%	0.07
HYBRID	13	43.49%	0.05	MALL	13	30.25%	0.07
HYBRID	14	43.59%	0.05	MALL	14	29.35%	0.07
HYBRID	15	42.34%	0.05	MALL	15	28.53%	0.07
HYBRID	16	41.88%	0.05	MALL	16	27.77%	0.07
HYBRID	17	43.75%	0.05	MALL	17	28.18%	0.07
HYBRID	18	43.44%	0.05	MALL	18	27.48%	0.07
HYBRID	19	44.84%	0.05	MALL	19	26.82%	0.07
HYBRID	20	44.66%	0.05	MALL	20	31.42%	0.08
HYBRID	21	45.21%	0.05	MALL	21	34.10%	0.08
HYBRID	22	44.29%	0.05	MALL	22	37.51%	0.09
HYBRID	23	45.66%	0.05	MALL	23	45.16%	0.09
HYBRID	24	47.49%	0.05	MALL	24	46.25%	0.09
HYBRID	25	51.92%	0.06	MALL	25	46.46%	0.10
HYBRID	26	54.90%	0.06	MALL	26	52.30%	0.11
HYBRID	27	60.45%	0.06	MALL	27	51.35%	0.12
HYBRID	28	62.86%	0.06	MALL	28	51.43%	0.14
HYBRID	29	68.90%	0.06	MALL	29	71.21%	0.07
HYBRID	30	64.86%	0.07	MALL	30	70.44%	0.07
HYBRID	31	67.50%	0.09	MALL	31	74.27%	0.11
HYBRID	32	78.67%	0.06	MALL	32	84.43%	0.04
HYBRID	33	80.96%	0.06	MALL	33	83.99%	0.04
HYBRID	34	86.86%	0.09	MALL	34	87.88%	
HYBRID	35	96.20%	0.00				
HYBRID	36	96.60%					
HYBRID	37	96.50%					
HYBRID	38	96.41%					
HYBRID	39	96.32%					
HYBRID	40	96.22%					
HYBRID	41	96.13%					

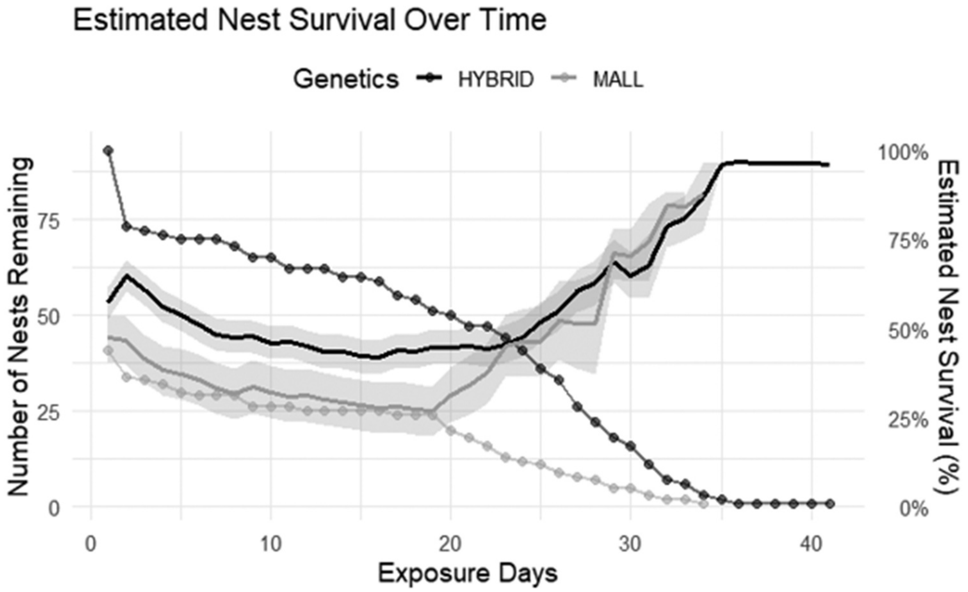

Figure 2. Estimated daily nest survival over time for NZ Mallards (MALL) and Pārera x NZ Mallard hybrids (HYBRID), based on a binomial GLM weighted by exposure days. Shaded ribbons show 95% confidence intervals, with dotted lines indicating the number of nests contributing to each day of observation.

that nests were observed in the dataset. Due to the diminishing number of nests remaining under observation at the end of the period, standard errors for cumulative survival at these points were not calculated and instead are based on the variability among all nests contributing data for each day (Figure 2; Table 5). The chi-square test of the nest fate categories (successful, abandoned, destroyed and non-viable) indicated no significant differences between hybrid and parental females ($p = 0.71$).

Clutch size differed slightly between genotypes, with hybrids averaging 9.90 ± 2.27 eggs per nest and Mallards averaging 10.46 ± 1.95. Distributions were roughly symmetrical (hybrid skewness = 0.21; Mallard skewness = 0.36), and Shapiro–Wilk tests indicated a slight deviation from normality (hybrid: $W = 0.97$, $p = 0.08$; Mallard: $W = 0.95$, $p = 0.16$). The interquartile range was 8.25–11 for hybrids and 9.00–12 for Mallards (Figures 1 and 4).

Discussion

We provide the first analysis of morphometrics and viability rates among genotyped Pārera, NZ Mallards and their hybrids in New Zealand. Pārera and NZ Mallards were morphometrically distinct, with NZ Mallards generally being heavier and larger (Tables 2 and 4). This trend has continued over the past 60 years since sampling began (Table 1). Morphometrically transformed z-scores revealed significantly lower scores among Pārera compared to NZ Mallards and showed generally distinct clustering when plotting raw values of morphometric measurements (Figures 1 and 3). Interestingly, we observed that morphometrics of hybrids became increasingly similar to the parental species to which they backcrossed, suggesting a genetic underpinning to these traits (Figure 5). Considering only hybrids, NZ Mallard-backcrossed hybrids tended to be heavier and, along with F1 hybrids, had longer wings than Pārera-backcrossed hybrids. While it may be possible to distinguish between Pārera and NZ Mallards based on putative morphological differences, field identification remains extremely difficult. However, when combined with other reliable phenotypic variations, this represents a potential future approach (see Brown *et al.* 2022).

Examining body mass and size through time, we found that male and female NZ Mallards have decreased in mass by 6% and 2%, respectively. Both male and female NZ Mallards also experienced a 2% shortening of the wing and a 1% decrease in culmen length (Table 1). Pārera males similarly decreased in mass by approximately 7%, and culmen length was reduced by 4%. While body mass and morphometrics in both species remain different, contemporary female NZ Mallards and female Pārera now have similar culmen lengths (Table 1). Overall, we conclude that Pārera and NZ Mallards have changed in mass and size. Although the ultimate causes require further analysis, we propose that these changes may reflect adaptation of the feral population to New Zealand local through the feralization process (Gering *et al.* 2019). Continued monitoring of Pārera and NZ

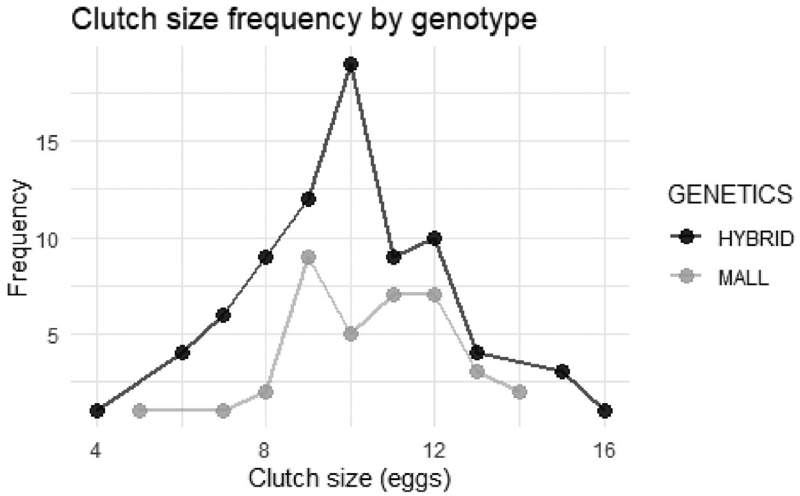

Figure 3. Percent frequency vs. clutch size between NZ Mallards (black) and Pārera x NZ Mallard hybrids in New Zealand during 2014–2015 (grey).

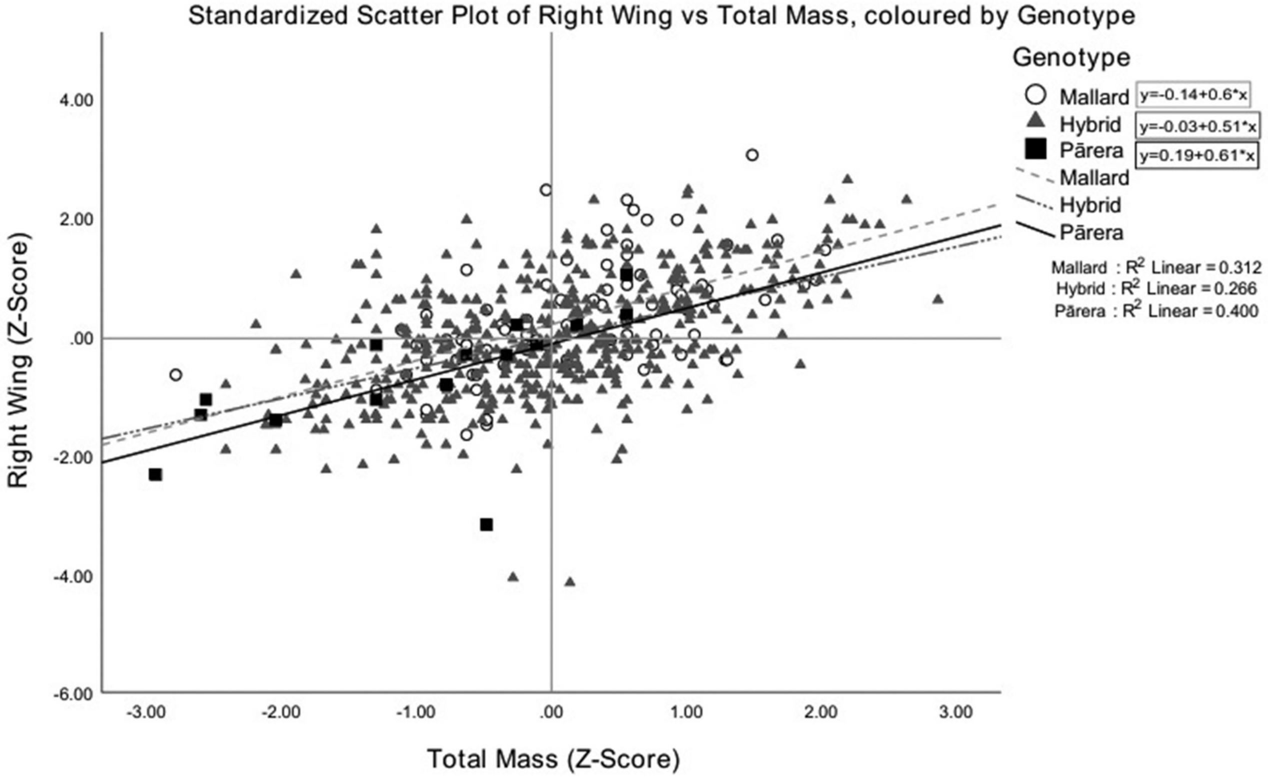

Figure 4. Total mass (g) and standardized Z–scores of right–wing chord of NZ Pārera (black), NZ Mallard (white), or Pārera x NZ Mallard hybrids (grey), collected during 2014–2018 in New Zealand. Linear regressions revealed significant interactions between mass and wing length among groups (p < 0.00).

Mallard populations would help to understand how morphometrics and genetics change over time.

We hypothesised that contemporary hybrids would have reduced productivity, and our analysis revealed that genotype significantly influences daily nest survival, with Mallard females showing lower survival than hybrids (Estimate = −0.87, $p < 0.001$) (Table 3). However, general NZ Mallard nest success was comparable to that estimated for wild Mallard populations (e.g. 71% in North American wetlands; Kaminski *et al.* 2013), as both Mallards and hybrids showed daily survival of 74% and 82%, respectively. Feral NZ Mallard

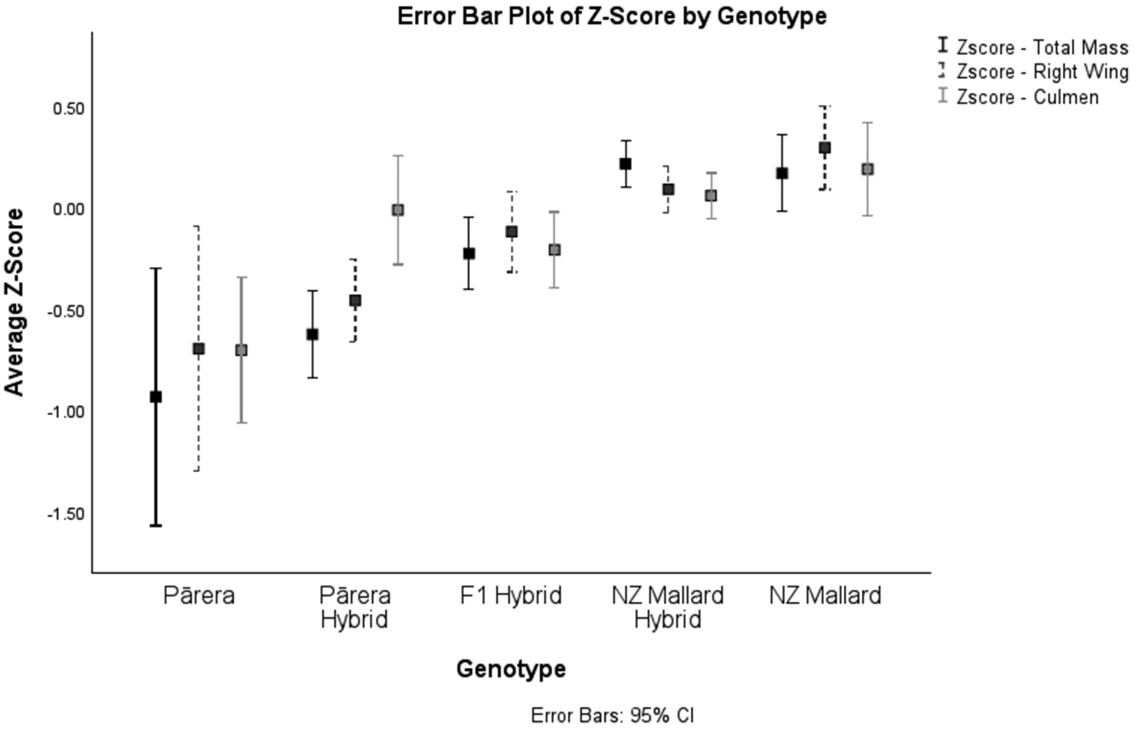

Figure 5. Standardized morphometric traits (Z-scores) for total mass (g), right wing chord length (mm), and culmen length (mm) across genotypes: Pārera, Pārera-backcrossed hybrids, F1 Hybrids, NZ Mallard-backcrossed hybrids, and NZ Mallards. Error bars represent standard error (95% CI). Morphometric traits of hybrids increasingly resembled the parental type to which they backcrossed, suggesting a genetic basis for these.

populations established from domestic game-farm lineages are known to suffer reduced survival and fecundity elsewhere (Champagnon *et al.* 2023), but in New Zealand these negative consequences are less pronounced, as hybrid females exhibit higher daily nest survival than Mallards. The absence of negative viability metrics among NZ Mallards and hybrids is consistent with the hypothesis that established NZ Mallard populations have been positively shaped by natural selection and/or adaptive introgression, leading to re-optimisation during the feralization process (Daehler and Carino 2001; Largiadèr 2007; Lavretsky *et al.* 2023). Although comparable viability data for pure Pārera are not available, the observed performance of hybrids remains consistent with potential hybrid vigour. Although the GLM focused on daily nest survival using a binary success/failure metric, the chi-square test revealed no significant differences between hybrid and parental females ($p = 0.71$), suggesting that hybrid and NZ Mallard females do not differ in their propensity to abandon nests or experience predation.

While our main results focus on morphology and fitness, diet represents a plausible mechanistic link between hybridisation and survivability. In dabbling ducks, bill morphology – including length, width and lamellae spacing – constrains the size and type of particles birds can efficiently handle (Gurd 2007; Lucy and Karthiayini 2022). Evolutionary pressures maintain lamellar density specific to the food particles a species targets (Nudds *et al.* 2000), shaping diet composition and foraging efficiency (Guillemain *et al.* 2002; Gurd 2007). Our GLM results further support the importance of intrinsic traits, showing that juveniles have lower daily nest survival rates than adults, larger females have higher survival, and better body condition strongly increases survival. Using predicted DSR values and nest-specific exposure days, cumulative nest survival revealed temporal patterns in nest fate: hybrids had their lowest cumulative survival on day 16, while NZ Mallards reached theirs on day 19. If NZ Mallard × Pārera hybrids inherit combinations of bill traits that broaden particle-size handling or improve filtering efficiency, they could exploit a wider range of foods across seasons and habitats, translating to higher body condition, fecundity and survivability. Future studies focusing on diet breadth in relation to bill morphometrics could test whether NZ Mallards and/or their hybrids are examples of adaptive introgression and hybrid vigour. Additionally, understanding clutch size and nest success of Pārera females compared to Pārera × NZ Mallard hybrids, as well as other population-based viability rates (e.g. duckling survival), would further explain the adaptive significance of hybrids in New Zealand. Although more difficult due to declining and increasingly isolated Pārera populations (Brown *et al.* 2025), such studies would inform conservation by elucidating manageable factors that promote Pārera survival and reproductive success.

The Anthropocene is marked by landscape-level ecological changes, including the introduction of invasive populations worldwide (Zalasiewicz *et al.* 2011; Wolkovich *et al.* 2014; Ålund *et al.* 2023; Ottenburghs 2021). These changes have led to increasing incidences of introgressive hybridisation, typically viewed as maladaptive (Pena Rodrigues and Lira 2019). Although NZ Mallard hybridisation has long been considered a threat to Pārera (Rhymer and Simberloff 1996; Brown *et al.* 2025), our results support a case of hybrid vigour in which hybrid populations are self-maintaining and thriving in nature. To fully understand how genetically admixed populations are viewed, case-by-case studies are required to balance their conservation threat to biodiversity against their potential to survive in increasingly urban environments (Jiang *et al.* 2008; Norra 2014). In addition to habitat loss, overharvest and predator introductions, hybridisation with NZ Mallards continues to be a primary existential threat to endemic Pārera. However, strong population trends of NZ Mallards and their hybrid populations, coupled with higher hybrid viability rates, may not only support a case for naturalisation (Brown *et al.* 2025), but could also serve as an effective ecological replacement if Pārera are lost. We argue that an important conservation effort for Pārera should focus on continuing to isolate them from NZ Mallards to prevent further genetic swamping (Todesco *et al.* 2016) and the potential loss of the distinct native Pārera lineage. Given that remnant populations of Pārera still exist primarily in the northwestern portion of the South Island (Brown *et al.* 2025), genotyping waterfowl during banding programmes, as well as potential translocation of remaining pure Pārera to offshore islands, may be necessary for their conservation.

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