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Morphological differences between wild and game-farm Mallards (*Anas platyrhynchos*) in North America

SUSANNAH L. HALLIGAN,[1] MICHAEL L. SCHUMMER,*[1] AURIEL M. V. FOURNIER,[2] PHILIP LAVRETSKY,[3] J. BRIAN DAVIS,[4] CYNTHIA J. DOWNS[1] & VERGIE MUSNI[3]

[1]*Department of Environmental Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York, USA*

[2]*Forbes Biological Station–Bellrose Waterfowl Research Center, Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana Champaign, Havana, Illinois, USA*

[3]*Department of Biological Sciences, University of Texas at El Paso, El Paso, Texas, USA*

[4]*Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi State, Mississippi, USA*

Large-scale releases of domesticated, game-farm Mallards *Anas platyrhynchos* to supplement wild populations have resulted in widespread introgressive hybridization that changed the genetic constitution of wild populations in eastern North America. The resulting gene flow is well documented between game-farm and wild Mallards, but the mechanistic consequences from such interactions remain unknown in North America. We provide the first study to characterize and investigate potential differences in morphology between genetically known, wild and game-farm Mallards in North America. We used nine morphological measurements to discriminate between wild and game-farm Mallards with 96% accuracy. Compared with their wild counterparts, game-farm Mallards had longer bodies and tarsi, shorter heads and wings, and shorter, wider and taller bills. The nail on the end of the bill of game-farm Mallards was longer, and game-farm Mallard bills had a greater lamellae:bill length ratio than wild Mallards. Differences in body morphologies between wild and game-farm Mallards are consistent with an artificial, terrestrial life whereby game-farm Mallards are fed pelleted foods, resulting in artificial selection for a more 'goose-like' bill. We posit that: (1) game-farm Mallards have diverged from their wild ancestral traits of flying and filter feeding towards becoming optimized to run and peck for food; (2) game-farm morphological traits optimized over the last 400 years in domestic environments are likely to be maladaptive in the wild; and (3) the introgression of such traits into wild populations is likely to reduce fitness. Understanding the effects of game-farm Mallard introgression requires analysis of various game-farm × wild hybrid generations to determine how domestically derived traits persist or diminish with each generation.

Keywords: *Anas platyrhynchos*, artificial, genetics, hybrid, introgression.

Species evolve morphological traits that match life-history strategies to maximize the survival and reproductive potential of an individual (Darwin 1860, Lack 1947, Ricklefs & Travis 1980). Survival is influenced by an individual's ability to acquire food (Gurd 2006, 2007), avoid predation (Martin 2015), move or migrate to more seasonally favourable climes in some species (Dingle 1996, Zink 2011), and successfully complete other daily and seasonal events. Natural selection involves non-random difference in replicating units, often influenced by differential survival in a particular environment that continuously enhances the proportion of beneficial, heritable traits passed generationally in populations (Darwin 1860, Gregory 2009).

Species are distinguished by morphological and physiological adaptations to optimize survival and

*Corresponding author.
Email: mlschumm@esf.edu

fecundity in their niche space (Schoener 1974). In birds, variability in beak morphology is directly associated with prey types, resulting in strong directional selection among species on these traits (Schoener 1974, Gurd 2006, 2007, Hughes *et al.* 2022). Additional morphological traits are often associated with specific avian life-history characteristics, such as leg position, which influences aquatic, terrestrial and aerial mobility (Abourachid & Höfling 2012), and wing shape and size, which affect flight dynamics (Brown 1963, Kokshaysky 1973).

Although once considered inconsequential for wild populations, landscape genomics studies continue to uncover widespread introgressive hybridization of domesticated lineages into wild populations across various taxa (Araki *et al.* 2007, Lavretsky *et al.* 2023). Artificial selection imposed in domestic settings often results in relatively rapid changes in morphology, physiology and behaviours that are predictably maladaptive in the wild (Araki *et al.* 2007, Ellison & Burton 2008, Morin *et al.* 2023). Consequently, determining how gene flow from domestic into wild populations translates into phenotypic changes, and whether such effects are positive, neutral or negative, is now at the forefront of wildlife conservation (Kidd *et al.* 2009, Bolstad *et al.* 2017, Söderquist *et al.* 2017, Lavretsky *et al.* 2023). For example, the release of millions of domestically raised game-farm Mallards *Anas platyrhynchos* to supplement wild populations and increase harvest opportunity has resulted in widespread introgressive hybridization that has transformed the genetic composition of wild Mallard populations across much of Europe and eastern North America (Champagnon *et al.* 2016, Söderquist *et al.* 2017, Lavretsky *et al.* 2023, Schummer *et al.* 2023). All domestic, game-farm Mallards released in Europe and North America are descendants of wild, Eurasian Mallards (Lavretsky *et al.* 2023). The fitness and population-level consequences from introductions of these game-farm Mallards into wild Mallard populations remain largely unknown.

Approximately 500 000 game-farm Mallards were released annually in the eastern USA from 1920 to ~1950 (Heusmann 1991, Osborne *et al.* 2010, Schummer *et al.* 2023). However, these releases, which were primarily ducklings, failed to meet the goals of individual states to supplement their wild Mallard populations because survival of released birds was generally low (Lincoln 1934). More recently, an estimated 270 000 flighted game-farm Mallards (i.e. not ducklings) continue to be released annually from about 300 licensed shooting preserves, although these numbers are not well documented and not all states collect these data or require permits to release birds (Smith 1999, USFWS 2013, Lavretsky *et al.* 2020). Several techniques exist in the USA for release of game-farm Mallards: (1) release from towers with the intent of an immediate shooting opportunity as the Mallards fly away from the tower; (2) free-flying release whereby Mallards are released at a hunted area at different time intervals before hunting; (3) a hybrid method whereby Mallards are kept on a home pond, captured before the shoot, released and allowed to fly back to their home pond (USFWS 2013); and (4) a less common technique is selling ducklings to individuals who then raise them locally until they can fly and are released into the huntable population (M. Schummer pers. obs.). The release of game-farm Mallards was once considered benign for wild populations as the former group was not expected to survive or reproduce in the wild. However, recent landscape genomic studies have confirmed that game-farm Mallards survive in sufficient numbers to breed with wild counterparts (Brown *et al.* 2019, Lavretsky *et al.* 2020, 2023, Davis *et al.* 2022). Many central European and eastern North American Mallard populations are considered game-farm × wild Mallard hybrid swarms (Brown *et al.* 2019, Lavretsky *et al.* 2020, 2023, Schummer *et al.* 2023), and regions where Mallards have declined in the wild overlap geographically with locations where game-farm × wild Mallard hybrids comprise most of the population (e.g. >90%; Lavretsky *et al.* 2023).

Game-farm Mallard releases in Europe can number up to 6 million annually (Champagnon *et al.* 2013, Madden 2021). In the UK alone, 2.6 million game-farm Mallards are estimated to be released annually (Madden 2021). By the 1990s, Denmark was releasing ≤500 000 birds annually, and Sweden and France released 250 000 and 1.4 million birds annually, respectively, while the wild Mallard population wintering in France numbered ~300 000 (Söderquist *et al.* 2013, 2017). In the Netherlands, the wild Mallard population declined by approximately 30% between 1990 and 2019 (Wiegers *et al.* 2022). Similarly, regions in North America where game-farm Mallards are traditionally released have also experienced the largest

population declines (USFWS 2019, Lavretsky *et al.* 2023). This includes the Mallard populations in eastern North America and the Great Lakes Regions, which declined by 50% and 28% during the 1990s to 2010s, respectively (USFWS 2019, Schummer *et al.* 2023). In contrast, where game-farm × wild Mallard hybrids are less common, Mallard populations were typically stable or increasing in numbers across the mid-continent of North America during the same period (USFWS 2019, Lavretsky *et al.* 2023). Consistency among regions with substantial game-farm Mallard introgression and wild Mallard population decline has led many to hypothesize about morphological and functional consequences of such hybridization (Lavretsky *et al.* 2023, Roberts *et al.* 2023, Schummer *et al.* 2023). Releasing game-farm Mallards may increase harvest opportunities in the near-term because more ducks are available for shooting, but there may be negative effects on wild population size because of introgression of domestically derived traits and their associated genetic variation that make birds maladapted to their local environment (Champagnon *et al.* 2012b, Norwegian Scientific Committee for Food Safety 2017).

Studies of game-farm and wild Mallard interactions in Europe have revealed concerns over how artificial selection in captivity may have resulted in differences in body and bill morphology of game-farm Mallards compared with their wild ancestor (Champagnon *et al.* 2010, Söderquist *et al.* 2014). Similar concerns have been expressed for Mallards of game-farm stock in North America (Byers & Cary 1991). Release of these game-farm Mallards in France between 1950 and 2008 appears to have resulted in bills shaped more like those of geese (*Anser* spp.) (Guillemain *et al.* 2002, 2010, Söderquist *et al.* 2014). Consequently, deviations in morphology in game-farm Mallards relative to wild Mallards may affect their ability to obtain nutrient reserves for survival and reproduction, which could be contributing to declining wild Mallard populations in Europe and North America (Champagnon *et al.* 2012b, 2016, Söderquist *et al.* 2013, 2021b, Schummer *et al.* 2023). Low intake rate of food by game-farm Mallards could be disadvantageous and contribute to poorer body condition commonly found in migrating female game-farm Mallards in Europe (Champagnon *et al.* 2012a, 2012b).

Concerns about the potential consequences of game-farm Mallard introgression into wild Mallard populations in North America prompted our current study. We investigated potential differences in key morphological characteristics between contemporary wild and game-farm Mallards that occur in North America to provide information about differences that could affect fitness. Further, understanding differences in morphology could be used to develop techniques to differentiate between wild and game-farm raised Mallards based on morphological traits in the field, especially when marking birds with bands or telemetry units to test for differences in survival, reproduction and migration patterns.

METHODS

Morphological measurements

We conducted our study at two captive waterfowl facilities: (1) the Forbes Biological Station (hereafter Forbes) in Havana, Illinois, and (2) Pinola Conservancy (hereafter Pinola), in Shreveport, Louisiana. For the first year at Forbes, we obtained 12 female and 12 male game-farm Mallards from a commercial breeder in Hanover, Illinois, that were hatched in June 2020. Ducks were housed at Forbes from 15 February to 3 December 2021, when they were euthanized. Using traps baited with corn in Illinois and Tennessee, biologists aimed to capture a similar number of apparent wild Mallards in February 2021, which resulted in 11 males and nine females captured and subsequently housed at Forbes during the same period as the game-farm cohort. All Mallards were later confirmed as pure-game-farm, pure wild or game-farm × wild hybrid. During the second year at Forbes, we obtained 21 female and 20 male game-farm Mallards that had hatched in June 2021 from the same breeder. These Mallards were housed at Forbes from 31 January 2022 to 1 July 2022, when they were euthanized. In February 2022, we captured an additional 20 male and 13 female wild Mallards in Tennessee and housed them at Forbes during the same period as the game-farm Mallards. For Pinola, we obtained and hatched 20 fresh eggs of presumably wild Mallards, seven males and 13 females, that were collected from Colusa, Sutter and Yolo Counties, California, from 8 to 16 June 2021 as part of the California Waterfowl Association's egg salvage programme. We also obtained 12 male and eight female full-grown, presumably game-farm Mallards from a commercial breeder in

Willison, Tennessee, and housed these ducks at Pinola from 8 October 2021 until they were euthanized on 23 May 2022. Mallards were banded to distinguish individual birds and housed in outdoor pens. All Mallards were provided with water and similar commercial, pelleted duck feed *ad libitum*.

Before obtaining measurements from individual birds, all Mallards were dispatched by cervical puncture as described by AMVA guidelines and referenced by the American Ornithologists' Union and following SUNY ESF Animal Protocol #200604. All Mallards were fully grown (≥ 11 months old) when measured. Following euthanasia, we measured various bill and head components including: (1) culmen 1 (length of the tip of the bill to the bottom of the V-point where ligaments meet the bill); (2) length of the culmen from the tip of the bill to the start of the nares; (3) bill height and width at the middle of the nares; and (4) bill nail length and head length. We also measured: (5) flattened wing chord length, (6) total tarsus length (the length of the most medial condyle of the tarsus where it articulates with the mid-toe to the rounded exterior portion of the distal condyles of the tibia) and (7) body length (from the tip of the bill to the end of the rump, not including the rectrices) (± 1 mm; Dzubin & Cooch 1992, Champagnon *et al.* 2010, Söderquist *et al.* 2014). We also counted: (8) the number of maxillar lamellae in positions 1–4 (Fig. 1) following Söderquist *et al.* (2014) and then calculated the ratio of lamellae to culmen 1 to understand the density of lamellae per bill length because this ratio is important in foraging ecology (Nudds & Bowlby 1984, Nudds *et al.* 2000). Lastly, we calculated (9) the ratio of wing to body length because of its importance in migration efficiency (Newton 2010).

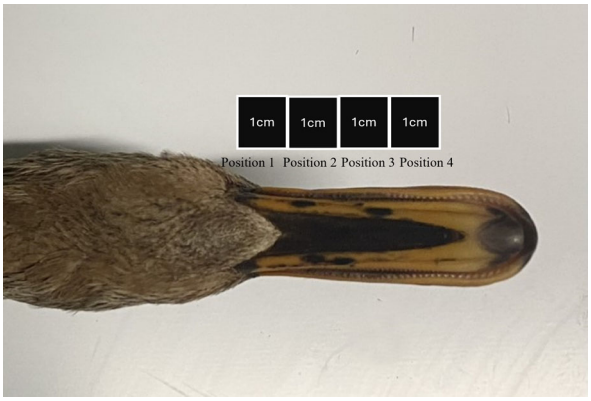

Figure 1. Measurement of bill lamellar density. Scaled photography of the ventral view of a Mallard bill used to count maxillar lamellae per centimetre. Positions 1–4 correspond to the first (i.e. proximate, here to the left) 4 cm of the bill.

Genetic ancestry analyses

We genetically assessed all ducks in our study to ensure that game-farm and wild Mallards were used in analyses, and that wild × game-farm Mallard hybrids were excluded. From live Mallards, we obtained a maximum volume of ~0.01 mL of blood from the vessels in the tibio-tarsi with a 23-gauge needle (Fair *et al.* 2023). From this blood, we extracted DNA using the protocol of a DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, USA). We used gel electrophoresis with a 1% agarose gel to assess DNA quality via the presence of a high-molecular-weight band. We used a Qubit 3 Fluorometer (Invitrogen, Carlsbad, CA, USA) to ensure a minimum of 20 ng/μL. Subsequently, double-digest restriction-site-associated DNA sequence (ddRAD-seq) libraries were constructed following DaCosta and Sorenson (2014) except for size selection (mean size = 350 base pairs; range 100–500 base pairs) following a double-sided magnetic-bead-based protocol as described in Hernández *et al.* (2021). All samples were then pooled in equimolar volume, and the multiplexed library was sequenced on an Illumina HiSeq X using single-end 150-base-pair chemistry at NovoGene (Novogene Co., Ltd, Sacramento, CA, USA). Raw Illumina reads were deposited in the NCBI SRA repository (SRA project ID PRJNA1151683 and accession numbers SAMN43321743–SAMN43321880).

Raw Illumina reads were de-multiplexed and aligned to the wild Mallard genome (Lavretsky *et al.* 2023) using custom in-house Python scripts (Python scripts available at https://github.com/jonmohl/PopGen; see Lavretsky *et al.* 2020) to automate sequence filtering, alignment and genotyping using a combination of TRIMMOMATIC (Bolger *et al.* 2014), BWAv. 07.15 (Li & Durbin 2011) and SAMTOOLS v. 1.7 (Bolger *et al.* 2014). The VCF files were then further filtered for any base-pair missing >5% of samples that also included a minimum base-pair depth of 5× (i.e. 10× per genotype) and quality per base PHRED scores of ≥30 using VCFTOOLS v. 0.1.15

(Danecek *et al.* 2011). We included comparable sequences and alignments for previously published game-farm and wild Mallards that served as references for these types (Lavretsky *et al.* 2019, 2020, 2023).

Individual ancestry assignments were based on independent bi-allelic ddRAD-seq single nucleotide polymorphisms (SNPs) without using *a priori* assignment of individuals to populations or species. The final dataset was obtained by using VCFTOOLS v. 0.1.15 (Danecek *et al.* 2011) to first extract bi-allelic SNPs, and then PLINK v. 1.9 (Purcell *et al.* 2007) to filter for singletons, or any SNP missing ≥10% of data across samples or in linkage disequilibrium. Independent bi-allelic SNPs were then analysed in ADMIXTURE v. 1.3 (Alexander *et al.* 2009, Alexander & Lange 2011, Shringarpure *et al.* 2016) to obtain individual assignment probabilities (Q values).

We considered birds with ≥90% wild genetics as wild, whereas hybrids were 0.1–89% wild genetics and game-farm Mallards were ≤0.09% wild genetics (Lavretsky *et al.* 2023). We only retained wild and game-farm Mallards in our analyses because hybrids may express varying morphological traits of the parent populations that are currently unknown and require additional investigation (Lavretsky *et al.* 2020, Schummer *et al.* 2023).

Statistical analyses

We calculated Pearson correlation coefficients between morphological variables and used principal component analysis (PCA) to determine the amount of morphological variation explained by principal components PC1 and PC2. We then applied discriminant function analysis (DFA) with cross-validation to statistically categorize birds as wild or game-farm Mallards, determined the percentage error of these designations and reported linear DFA results, which were useful in differentiating between game-farm and wild Mallards. When DFA indicated capacity to discriminate between wild and game-farm Mallards, we conducted univariate linear regressions of body morphologies, number of lamellae in positions 1–4, total lamellae, lamellae:culmen 1 ratios and wing:body length ratio to determine if they were influenced by source (wild or game-farm), sex and source × sex interaction. We also included year by location categories (e.g. Forbes, year 1) as fixed covariates to control for differences in environmental conditions potentially influencing growth and structural size. We removed ducks with ongoing wing feather moult from PCA and DFA but included other measurements from these birds in univariate tests to maximize sample sizes. We visualized studentized residuals of model outputs, which approximated a normal distribution. All analyses were conducted in R (RStudio Team 2020). All tests were considered significant at $\alpha = 0.05$, but worthy of discussion at $\alpha = 0.10$.

RESULTS

Our sample of 158 Mallards included 53 wild, 20 hybrid and 85 game-farm Mallards (Fig. 2). We did not include hybrids in our analyses, so our final sample size was 138 ducks, which included 40 game-farm females, 24 wild females, 45 game-farm males and 29 wild males (Table 1). Game-farm Mallards in our study were assigned to the same genetic cluster as the reference set of game-farm Mallards (also see Lavretsky *et al.* 2020, 2023). Ducks with ongoing wing moult that could not be included in PCA and DFA ($n = 17$) included three and two game-farm females and males, respectively, and five and seven wild females and males, respectively (Table 2 & Table S1).

Measurements used in the DFA were correlated for wild ($r = 0.23$ to $r = 0.89$) and game-farm ($r = 0.18$ to $r = 0.92$) Mallards (Table S2) and explained 96.7% of the variation in structural size (PC1 = 79.7% and PC2 = 17.0%) (Table S3). By applying a DFA to the nine morphological measurements we were able to correctly classify 95.1% of wild and 97.5% of game-farm Mallards used in the study (weighted average 3.3% error; Table 3; Fig. 3).

On average, game-farm Mallards had shorter and wider culmens, greater bill height and longer bill nails than wild Mallards (Tables 2, 4 & 5). The number of lamellae were greater at positions 3 and 4 in game-farm than wild Mallards but did not differ at positions 1 and 2 at the proximate part of the bill. Game-farm Mallards also had longer bodies, shorter wings, shorter heads and longer tarsi than wild Mallards (Tables 2, 4 & 5). The wing:body length ratio was less in game-farm than in wild Mallards, whereas game-farm Mallards had greater density of lamellae:culmen 1 than wild Mallards (Tables 2, 4 & 5).

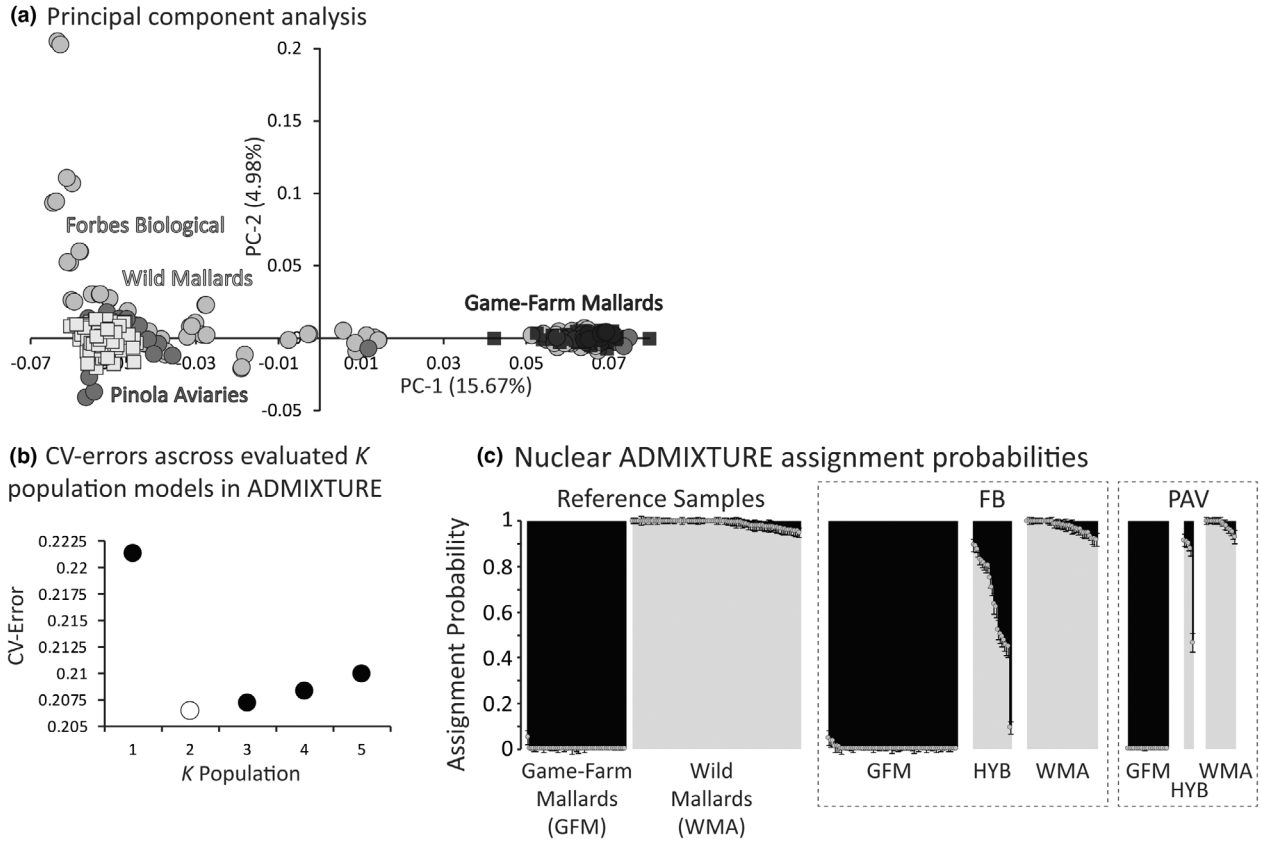

Figure 2. Population structure analyses based on 19 314 independent bi-allelic double-digest restriction-site-associated DNA sequence single nucleotide polymorphisms assayed across individuals housed in Forbes Biological (FB; light grey circle) or Pinola Aviaries (PAV; dark grey circle), as well as reference wild (WMA; light grey square) and game-farm (GFM; black square) Mallards. Population structure was visualized by (a) plotting of the first two principal components. Additionally, we recovered an optimum *K* population value of 2 based on (b) CV errors and (c) plot per sample ADMIXTURE assignment probabilities under the optimum *K* value, along with standard errors obtained from 100 bootstrap values.

DISCUSSION

Domestication can create or relax selective pressures resulting in relatively fast and substantial changes in the morphology of captive populations relative to their wild ancestors (Araki *et al.* 2007, Ellison & Burton 2008). Our study of Mallard ducks in North America supports evidence from Europe that game-farm Mallards differ morphologically from wild Mallards (Champagnon *et al.* 2010, Söderquist *et al.* 2014). We demonstrated that nine morphological measurements could be used to distinguish between wild and game-farm Mallards with 96% accuracy. Effects on fitness in the wild resulting from these differences and how hybrid forms affect survival and reproduction are unknown, but here we describe foundational differences between pure wild North American Mallards and game-farm Mallards of European descent.

Among traits, we found the strongest differences for bill, body length:wing ratios and tarsus morphology between wild and game-farm Mallards. Duck bills are morphologically adaptive because they have been shaped through millennia of evolution, enabling acquisition of nutrients necessary for survival and reproduction (Byers & Cary 1991, Guillemain *et al.* 2002). Our results corroborated those from Europe whereby game-farm Mallards had shorter, wider and taller bills than wild Mallards (Champagnon *et al.* 2010, 2012b, Söderquist *et al.* 2014). Moreover, we detected that mean bill nail length and density of lamellae:culmen length of game-farm Mallards

Table 1. Sample demographics of wild (n = 53) and game-farm (n = 85) Mallards *Anas platyrhynchos* used in morphological analyses and housed at Forbes Biological Station, Illinois (June–December 2021; April–June 2022), and at Pinola Conservancy, Louisiana (February–May 2022).

Study site and year	Source	Sex	Final sample
Forbes year 1	Wild	Male	8
		Female	5
	Game-farm	Male	12
		Female	12
Forbes year 2	Wild	Male	15
		Female	7
	Game-farm	Male	21
		Female	20
Pinola year 2	Wild	Male	6
		Female	12
	Game-farm	Male	12
		Female	8

were greater than in wild Mallards and most of the increase in lamellae occurred towards the front of the bill. Overall, game-farm Mallard bill morphology in our study resembled the morphology of waterfowl that peck or pick food items, i.e. goose-like, rather than strain food. Over the past 30 years, Mallards in Europe have experienced a 1.6% decrease in culmen length as game-farm Mallards have introgressed into wild Mallard populations (Champagnon *et al.* 2012a, Söderquist *et al.* 2014). Our results could signify a similar trend in North America, as the game-farm Mallards in our sample had a reduction in culmen length of 2.5% compared with wild Mallards. Variations in bill morphology may have fitness consequences if distinctly smaller and differently shaped bills lead to decreased foraging efficiency or other

Table 2. Descriptive statistics of various morphometric measurements of captive wild (n = 41) and game-farm (n = 80) Mallards in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022). SE, standard error.

Source	Morphometric	Mean ± SE	Minimum	Maximum
Wild female	Body length	438.92 ± 4.65	411.00	516.00
	Head length	107.98 ± 0.75	101.33	116.04
	Wing chord	251.21 ± 4.31	220.00	281.00
	Tarsus length	54.02 ± 0.48	50.60	60.82
	Culmen 1 length	52.57 ± 0.51	46.88	56.75
	Culmen width	21.01 ± 0.19	19.70	24.05
	Culmen nares	39.48 ± 0.37	34.36	42.33
	Bill height	17.10 ± 0.21	15.72	20.64
	Nail length	11.01 ± 0.12	10.29	12.14
Wild male	Body length	477.48 ± 2.59	454.00	505.00
	Head length	115.99 ± 0.68	109.15	122.02
	Wing chord	271.32 ± 3.68	240.00	290.00
	Tarsus length	55.92 ± 0.37	50.99	61.30
	Culmen 1 length	55.13 ± 0.54	48.45	60.84
	Culmen width	22.28 ± 0.11	21.27	23.28
	Culmen nares	42.57 ± 0.37	38.55	46.22
	Bill height	18.65 ± 0.18	16.76	21.23
	Nail length	11.32 ± 0.12	9.66	12.62
Game-farm female	Body length	446.3 ± 2.63	411.00	475.00
	Head length	106.50 ± 0.47	100.70	112.60
	Wing chord	250.90 ± 1.83	235.00	275.00
	Tarsus length	58.54 ± 0.24	55.01	61.74
	Culmen 1 length	50.68 ± 0.26	48.00	54.42
	Culmen width	22.37 ± 0.12	20.93	24.40
	Culmen nares	38.23 ± 0.19	35.87	41.02
	Bill height	17.95 ± 0.14	16.34	19.82
	Nail length	11.19 ± 0.09	10.05	12.73
Game-farm male	Body length	483.30 ± 2.68	431.00	512.00
	Head length	113.0 ± 0.42	108.00	118.62
	Wing chord	264.30 ± 1.42	240.00	280.00
	Tarsus length	61.09 ± 0.28	54.17	65.01
	Culmen 1 length	54.20 ± 0.33	49.86	58.56
	Culmen width	23.55 ± 0.12	20.68	25.43
	Culmen nares	41.02 ± 0.24	37.29	44.33
	Bill height	18.75 ± 0.11	16.27	20.32
	Nail length	11.65 ± 0.10	10.05	12.87

Table 3. Linear discriminant function for classification as captive wild ($n = 41$) and game-farm ($n = 80$) Mallards in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022). A Mallard of unknown genetics is assigned to the group that produces the greatest classification score.

Variable	Wild	Game-farm
Constant	−433.37	−465.92
Body length	0.19	0.16
Head length	3.09	2.53
Wing chord	0.29	0.21
Tarsus length	6.00	7.73
Culmen 1 length	2.0	1.70
Culmen width	2.44	3.90
Culmen nares	−5.46	−5.32
Bill height	2.89	2.77
Nail length	9.11	9.08

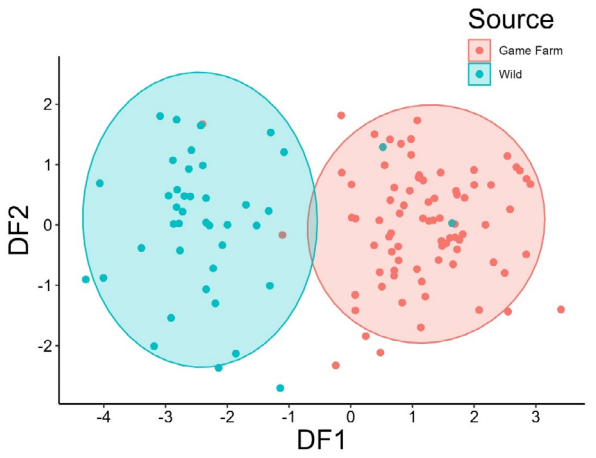

Figure 3. Results of discriminant functional analysis with discriminant functions DF 1 and 2 of captive wild ($n = 41$) and game-farm ($n = 80$) Mallards in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022). Includes 95% confidence ellipses, light ellipse = wild Mallards, dark ellipse = game-farm Mallards.

problems subsequently leading to decreased survival and reproduction in the wild (Söderquist *et al.* 2014).

Bill morphology can influence resource partitioning in various *Anas* and *Mareca* species (Gurd 2006, 2007), and the combination of distinct bills and behavioural differences (e.g. time spent feeding) may affect the food type and quality that can be consumed by game-farm Mallards (Kehoe & Thomas 1987, Gurd 2007, Söderquist *et al.* 2014). A longer bill and head that can reach

Table 4. Univariate linear models comparing body and bill morphometrics by source (wild or game-farm) and sex of Mallards, and by category (Forbes year 1, Forbes year 2 and Pinola) in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022).

Morphometric (n)	Predictor$_{df}$	F value	p value
Body length (138)	Source$_{1, 133}$	4.02	0.05
	Sex$_{1, 133}$	175.20	<0.01
	Category$_{2, 133}$	9.88	<0.01
Head length (138)	Source$_{1, 133}$	20.85	<0.01
	Sex$_{1, 133}$	180.68	<0.01
	Category$_{2, 133}$	7.31	<0.01
Wing chord (121)	Source$_{1, 116}$	3.46	0.07
	Sex$_{1, 116}$	62.93	<0.01
	Category$_{2, 116}$	31.48	<0.01
Tarsus length (138)	Source$_{1, 133}$	219.16	<0.01
	Sex$_{1, 133}$	53.52	<0.01
	Category$_{2, 133}$	3.11	0.05
Culmen 1 length (138)	Source$_{1, 133}$	13.07	<0.01
	Sex$_{1, 133}$	67.08	<0.01
	Category$_{2, 133}$	3.16	0.05
Culmen width (138)	Source$_{1, 133}$	103.52	<0.01
	Sex$_{1, 133}$	96.11	<0.01
	Category$_{2, 133}$	11.23	<0.01
Culmen nares (138)	Source$_{1, 133}$	27.83	<0.01
	Sex$_{1, 133}$	114.46	<0.01
	Category$_{2, 133}$	3.17	0.05
Nail length (138)	Source$_{1, 133}$	6.37	0.01
	Sex$_{1, 133}$	13.87	<0.01
	Category$_{2, 133}$	2.67	0.07
Bill height (138)	Source$_{1, 133}$	7.40	<0.01
	Sex$_{1, 133}$	50.64	<0.01
	Category$_{2, 133}$	1.19	0.31
Lamellae:culmen 1 ratio (138)	Source$_{1, 133}$	11.62	<0.01
	Sex$_{1, 133}$	41.89	<0.01
	Category$_{2, 133}$	0.50	0.63
Wing chord:body length ratio (121)	Source$_{1, 116}$	7.08	<0.01
	Sex$_{1, 116}$	3.72	0.06
	Category$_{2, 116}$	11.98	<0.01

food more deeply distributed in wetlands is not needed by Mallards raised domestically. Likewise, impaction of mud in the lamellae is no longer problematic in captive birds typically fed in bowls

Table 5. Generalized linear model for morphometrics of captive wild and game-farm Mallards in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022).

Morphometric (*n*)	Predictor	Mean ± SE	95% CI
Body length (138)	Intercept	486.58 ± 3.56	479.60 to 493.56
	Source (GF)	6.37 ± 2.92	0.63 to 12.11
	Sex (F)	−38.50 ± 2.88	−44.13 to −32.87
	Category (For2)	−15.45 ± 3.50	−22.32 to −8.58
	Category (Pin1)	−7.99 ± 3.77	15.38 to −0.60
Head length (138)	Intercept	116.79 ± 0.66	115.50 to 118.08
	Source (GF)	−2.50 ± 0.54	−3.56 to −1.44
	Sex (F)	−6.84 ± 0.53	−7.88 to −5.80
	Category (For2)	−1.04 ± 0.65	−2.31 to 0.23
	Category (Pin1)	−2.63 ± 0.70	−4.01 to −1.25
Wing chord (121)	Intercept	280.66 ± 2.43	275.89 to 285.43
	Source (GF)	−3.63 ± 2.09	−7.72 to 0.46
	Sex (F)	−15.36 ± 2.00	−19.26 to −11.46
	Category (For2)	−14.78 ± 2.41	−19.51 to −10.05
	Category (Pin1)	−19.01 ± 2.53	−24.00 to −14.02
Tarsus length (138)	Intercept	56.69 ± 0.40	55.91 to 57.47
	Source (GF)	4.82 ± 0.33	4.18 to 5.46
	Sex (F)	−2.24 ± 0.32	−2.87 to −1.61
	Category (For2)	−0.62 ± 0.39	−1.39 to 0.15
	Category (Pin1)	−1.05 ± 0.42	−1.87 to −0.23
Culmen 1 length (138)	Intercept	55.89 ± 0.48	54.95 to 56.83
	Source (GF)	−1.35 ± 0.40	−2.13 to −0.57
	Sex (F)	−3.27 ± 0.39	−4.03 to −2.51
	Category (For2)	−1.01 ± 0.47	−1.93 to −0.09
	Category (Pin1)	−0.06 ± 0.47	−0.98 to 0.86
Culmen width (138)	Intercept	22.74 ± 0.16	22.43 to 23.05
	Source (GF)	1.30 ± 0.13	1.04 to 1.56
	Sex (F)	−1.23 ± 0.13	−1.49 to −0.97
	Category (For2)	−0.71 ± 0.15	−1.01 to −0.41
	Category (Pin1)	−0.54 ± 0.16	−0.86 to 0.22
Culmen nares (138)	Intercept	42.84 ± 0.34	42.17 to 43.51
	Source (GF)	−1.40 ± 0.28	−1.95 to −0.85
	Sex (F)	−2.99 ± 0.27	−3.52 to −2.46
	Category (For2)	−0.73 ± 0.33	−1.38 to −0.08
	Category (Pin1)	−0.06 ± 0.36	−0.77 to 0.65
Bill height (138)	Intercept	18.62 ± 0.19	18.25 to 18.99
	Source (GF)	0.43 ± 0.16	0.11 to 0.75
	Sex (F)	−1.07 ± 0.15	−1.37 to −0.77
	Category (For2)	−0.21 ± 0.19	−0.58 to 0.16
	Category (Pin1)	−0.31 ± 0.20	−0.71 to 0.09
Nail length (138)	Intercept	11.44 ± 0.13	11.18 to 11.70
	Source (GF)	0.28 ± 0.11	0.07 to 0.49
	Sex (F)	−0.42 ± 0.11	−0.63 to −0.21
	Category (For2)	−0.22 ± 0.13	−0.48 to 0.04
	Category (Pin1)	0.05 ± 0.14	−0.23 to 0.33
Lamellae:culmen 1 (138)	Intercept	0.57 ± 0.01	0.55 to 0.59
	Source (GF)	0.03 ± 0.01	0.01 to 0.05
	Sex (F)	0.05 ± 0.01	0.03 to 0.07
	Category (For1)	<0.01 ± 0.01	−0.01 to 0.02
	Category (For2)	<0.01 ± 0.01	−0.01 to 0.02
Wing chord:body length (121)	Intercept	0.58 ± 0.01	0.56 to 0.60
	Source (GF)	−0.01 ± 0.01	−0.01 to 0.01
	Sex (F)	0.01 ± 0.01	−0.01 to 0.03
	Category (For2)	−0.01 ± 0.01	−0.03 to 0.01
	Category (Pin1)	−0.03 ± 0.01	−0.05 to −0.01

For2, Forbes Biological Station year 2; GF, birds of game-farm origin; *n*, sample size; Pin1, Pinola Conservancy year 1; SE, standard error; W, birds of wild origin.

or troughs filled with pellets or grain. Further, pen-raised birds lack selective pressure for narrow, long bills, with appropriate spacing of lamellae useful for wetland foraging on small seeds. Relaxation of such selective pressure would enable the expression of genetic variation that is typically removed through purifying selection in wild populations. We posit that this could be a mechanism behind the reduced food intake rate of game-farm compared with wild Mallards that was detected in an accompanying study (Halligan 2022).

Heads of game-farm Mallards in our study were 2.3% shorter than those of wild Mallards, which could affect absolute and relative brain volume of game-farm Mallards under artificial selection (Guay & Iwaniuk 2008). Head length was previously used to assess differences between wild and game-farm Mallard strains, and here we describe contemporary differences in North American Mallards of known genetic constitution (Byers & Cary 1991, Champagnon *et al.* 2010, Söderquist *et al.* 2021a, 2021b). Use of three-dimensional scans of skulls in future studies could improve understanding of how bill and brain-case morphology differ between wild and game-farm Mallards (Lattin *et al.* 2018).

Mean body length of game-farm Mallards was 7.0 mm (1.5%) longer than wild Mallards, whereas game-farm Mallard wings were 3.8 mm (1.4%) shorter than their wild counterparts. Overall, the ratio of body to wing lengths differed between wild and game-farm Mallards, presumably leading to changes in flight efficiency for the domestic cohort. Although these appear to be small differences, future research should estimate wing loading and include flight efficiency models of flight duration and other differences in migratory capacity between wild and game-farm Mallards. Indeed, several studies have shown that game-farm Mallards do not migrate as far as wild Mallards (Boyd & Harrison 1962, Fog 1964, Söderquist *et al.* 2013) and even at the local scale game-farm Mallards move less than wild Mallards (Söderquist *et al.* 2024). Such differences in movement patterns could partially be explained by a less adapted wing morphology in game-farm than wild Mallards.

Tarsus length of game-farm Mallards averaged 7.5% longer than their wild counterparts, which supports results from other European and North American studies on Mallard morphology (Byers & Cary 1991, Champagnon *et al.* 2012b). We attribute increasing tarsus length in game-farm Mallards to the artificial selective pressures of a domestic environment in breeding and rearing pens that are often more terrestrial than natural wetland and associated systems. Game-farm Mallards spend nearly all of their time on the ground running or walking extensively. Wild Mallards, alternatively, will also walk and forage amid mudflat or shallow wetlands or agricultural habitats. However, wild birds primarily swim and feed in physically diverse wetland systems (Byers & Cary 1991, Champagnon *et al.* 2012b).

Bill and body morphology of ducks can influence their foraging efficiencies and subsequent nutrient acquisition and lipid stores (Blem 1976, Gurd 2007). Functionally adaptive morphological traits to promote efficient foraging for a diversity of foods is paramount to Mallard survival and reproduction in the wild (Nudds *et al.* 2000). Further, the appropriate wing to body length ratio is necessary in migratory birds to sustain flight efficiency consistent with life-history migration strategies (Newton 2010). The difference in morphologies of game-farm Mallards that we detected in this study could affect their capacity to build and sustain absolute lipid reserves (Champagnon *et al.* 2010). Generally, the ratios of body, wing, head and tarsus length differed between game-farm Mallards compared with wild Mallards. Relative to wild Mallards, morphologies of game-farm Mallards appeared less conducive to efficient foraging in wetlands among silt and clay substrate for seeds and invertebrates, and wings and bodies of game-farm Mallards would seemingly be less capable of long-distance migration (Byers & Cary 1991, Champagnon *et al.* 2012b).

We posit that differences in morphology between wild and game-farm Mallards resulted from prolonged artificial selection in captivity that differs from natural selection pressures on wild Mallards. Such differences may limit the capacity of highly admixed Mallards to adapt to regional environmental conditions, such as dynamic wetland environments (Čížková *et al.* 2012). Moreover, domestically derived traits have been attributed to a low survival rate from release to breeding of approximately 3% of game-farm Mallards in the wild (Smith 1999, Champagnon *et al.* 2016, Söderquist *et al.* 2021a, 2021b). We suggest that differences in morphology could be

an agent influencing the recently detected declines in juvenile annual survival among Mallards in eastern North America (Roberts *et al.* 2023) where >90% of Mallards have been determined to be highly admixed (Lavretsky *et al.* 2023). Future research will require analysis of Mallards varying in wild × game-farm Mallard ancestry to determine persistence or loss of domestically derived morphological traits, thus providing a proxy to understand the selective pressures enacted on traits in the wild.

Studies of survival and reproduction of the various Mallard genotypes are still needed (Lavretsky *et al.* 2023, Roberts *et al.* 2023, Schummer *et al.* 2023). Nevertheless, a century of game-farm Mallard supplementation has not only transformed the genetic ancestry of wild populations, but this anthropogenic hybridization may be resulting in a less viable population in North America through morphological changes resulting from artificial pressures rather than natural selection (Araki *et al.* 2007).

Towards understanding population-level impacts of introgression, further research should focus on understanding the extent and frequency at which domestically derived traits occur among wild populations of Mallards in North America (e.g. Western, Mid-continent, Great Lake and Eastern Mallards as per USFWS 2019). Specifically, assessing prevalence of the aforementioned morphological traits of game-farm Mallards across game-farm × wild Mallard hybrids of various generational classes will be required to determine the strength of selection against (or for) game-farm Mallard traits in wild Mallard populations. Although all domestically derived game-farm Mallards in North America come from the same original European stock (Lavretsky *et al.* 2023), we also suggest determining if differences in morphology exist among breeders across North America; our game-farm sample originated from only two breeders. Lastly, once the utility of these morphological traits to differentiate between wild, game-farm and generation hybrids is determined, a suite of morphological traits could be used to assign ancestry to individuals in the field during tagging and banding without the constant need for molecular assessment, which is financially costly. Field identification of wild, game-farm and generational hybrids would present a powerful tool for Mallard population research and conservation efforts (Brown *et al.* 2022).

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AUTHOR CONTRIBUTIONS

Susannah L. Halligan: Conduct of the experiment, statistical analysis, writing. **Michael L. Schummer:** Conceptualization, funding, design of experiment, statistical analysis, writing. **Auriel M. V. Fournier:** Conceptualization, funding, design of experiment, writing. **Philip Lavretsky:** Conceptualization, funding, design of experiment, genetic analysis, writing. **J. Brian Davis:** Conceptualization, funding, design of experiment, writing. **Cynthia J. Downs:** Statistical analysis and writing. **Vergie Musni:** Genetic analysis.

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ETHICAL NOTE

All studies were conducted in accordance with approved Institutional Animal Care and Use Protocols and the American Ornithological Society Code of Conduct and Ethics. Eggs were collected under Scientific Collection ID # SC-13450. Ducks were used and cared for using Institutional Animal Use and Care Committee (IACUC) Protocols from the University of Illinois (IACUC protocol #18170), Mississippi State University (IACUC protocol #20–288) and SUNY ESF (IACUC #200604).

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data from this paper are available at https://data-bank.illinois.edu/datasets/IDB-3363781.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Data by source (wild or game-farm) and sex of Mallards *Anas platyrhynchos*, and by category (Forbes year 1, Forbes year 2 and Pinola) in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022).

Table S2. Pearson correlation coefficient matrices of body and bill morphologies of captive wild (n = 41) and game-farm (n = 80) Mallards *Anas platyrhynchos* in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022).

Table S3. Principal component loadings for analysis of body and bill morphology of captive wild (n = 41) and game-farm (n = 80) Mallards *Anas platyrhynchos* in Illinois (February–December 2021; January–July 2022) and Louisiana (June 2021–May 2022).