



## Perspective

# Silent domestication of wildlife in the Anthropocene: The mallard as a case study

Jocelyn Champagnon<sup>a,\*</sup>, Johan Elmberg<sup>b</sup>, Matthieu Guillemain<sup>c</sup>, Philip Lavretsky<sup>d</sup>, Robert G. Clark<sup>e</sup>, Pär Söderquist<sup>b</sup>

<sup>a</sup> Tour du Valat, Research Institute for conservation of Mediterranean wetlands, Arles, France

<sup>b</sup> Department of Environmental Science, Faculty of Natural Sciences, Kristianstad University, SE-291 88 Kristianstad, Sweden

<sup>c</sup> Office Français de la Biodiversité, Service Conservation et Gestion Durable des Espèces Exploitées, Arles, France

<sup>d</sup> Department of Biological Sciences, University of Texas El Paso, El Paso, TX, USA

<sup>e</sup> Pacific Wildlife Research Centre, Environment and Climate Change Canada, 5421 Robertson Road, Delta V4K 3Y3, British Columbia, Canada

## ARTICLE INFO

## Keywords:

Adaptation  
Evolution  
Hybridization  
Selection  
Speciation

## ABSTRACT

In the Anthropocene, human activities have been a dominant force affecting wildlife, natural habitats, and climate worldwide. Over time, increasing incidences of wildlife-human interactions may have positive outcomes for some generalist species, but studies continue to uncover that most predictably these generalist wild species also suffer from such interactions. In particular, the line between domestic and wild continues to blur as gene flow between these groups intensifies in the Anthropocene. We explore the meaning of wildness, focusing on the mallard, currently the most abundant duck species in the world. Mallard has been connected to humans for tens of thousands of years. Considered an exemplary generalist species with the capacity to adapt to rapidly changing environments, evidence gathered from a variety of disciplines suggests that some management efforts over the last centuries have resulted in the deterioration of the mallard's prolific nature, and that the apparent success in terms of current population size and wide distribution could mask a genetic collapse. Highlighting warning signs from the mallard system, in this *Perspectives* paper we discuss how active management of habitats and populations runs the risk of compromising species' wildness, and we suggest precautionary and counter-measures in the context of species management and conservation.

## 1. Introduction

Although 'the Anthropocene' as a scientific concept remains debated in geology and environmental science (e.g. [Wuerthner et al., 2014](#)), it is unquestionable that human activities for some time have been a dominant force affecting wildlife, natural habitats, and climate worldwide. The first articles in conservation biology and biodiversity research adopting the Anthropocene as a concept appeared in the early 2000s ([Meybeck, 2003](#); [Smol et al., 2005](#)). These have been followed by a large number of studies highlighting grave concerns about the profound changes to the world's natural ecosystems due to human impacts ([Dirzo et al., 2014](#); [Ceballos et al., 2015](#); [IPBES, 2019](#)).

Measures to mitigate negative human footprint have mainly focused on protection of habitats and species, recently also on ecosystem services and socio-ecological issues ([Leclère et al., 2020](#)). However, one important aspect of change in the Anthropocene has received much less

attention, namely the distinction between wild and non-wild. By definition, truly wild plants and animals are unaffected by human impact, while genuinely non-wild forms are typically domesticated via deliberate processes of artificial selection. Such processes can span active management of wild species such as large herbivores through feeding, predator control or fencing, to the return of some domesticated forms to the wild (e.g. feral horses). This makes it increasingly difficult to distinguish between wild and non-wild species today ([Mysterud, 2010](#)). The nature and strength of the relationship between wildlife (especially birds) and humans has long received scientific attention (e.g. [Nicholson, 1951](#)). A gradient exists from purely wild to purely domestic, with intermediate and overlapping situations such as synanthropic or feral (e.g. [Tomiałojć, 1970](#); [Nuorteva, 1971](#); [Johnston, 2001](#); [Table 1](#)). Here, we argue that incremental slow changes along the wild-non-wild continuum can have severe ecological, evolutionary, zoonotic, social, and economic consequences.

\* Corresponding author.

E-mail address: [champagnon@tourduvalat.org](mailto:champagnon@tourduvalat.org) (J. Champagnon).

**Table 1**  
Status of relationships between animals and humans (based on Tomialojć, 1970; Nuorteva, 1971; Johnston, 2001), ranked by decreasing affinity with humans. Note that the different categories are not fully independent and may overlap.

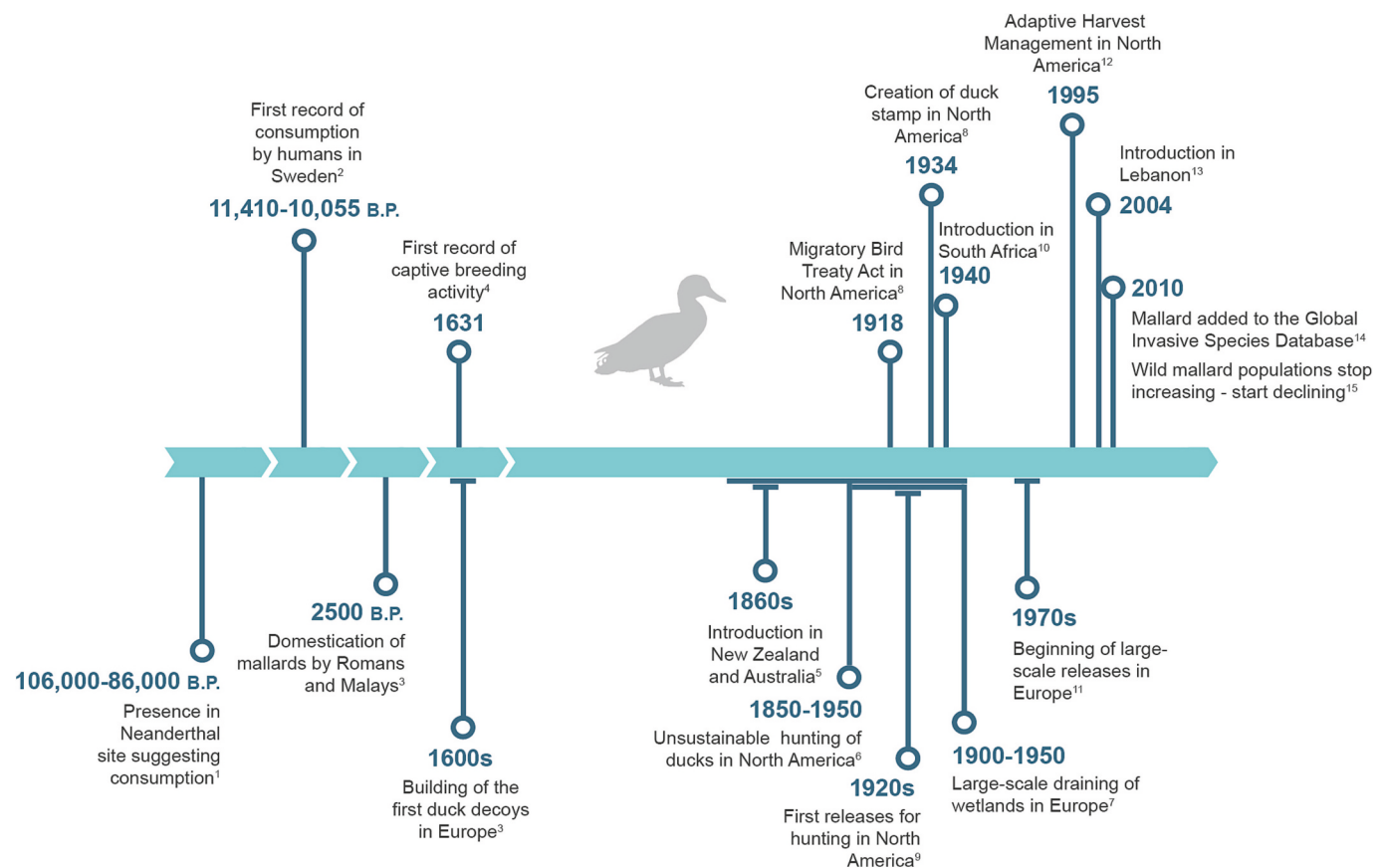
Status	Definition
Domestic	Raised entirely by humans. Can rarely persist in natural settings for extensive periods.
Feral	Escaped or released from captivity to natural settings while retaining domestic traits.
Commensal or Anthropophilic	Benefiting from the use of human environments (a particular case of synanthropy).
Synanthropic	Using human-influenced areas without deliberate human actions (e.g., no feeding) nor benefit to the animal (which could as equally use natural settings).
Wild	Living in natural settings without any need for interactions with humans.

Interactions between wildlife and anthropogenic environments have increased in intensity and geographic extent over time. Additionally, many parts of the world have seen a change from a patchwork of areas that are either wild or anthropogenic, to a situation where truly wild patches are lost entirely or remain only as small, isolated islands in human-modified landscapes. This begs the questions of what wildness means today (cf. Leopold, 1944) and how changes to landscapes with few or no truly wild areas affect the species living in them (Fricke et al., 2022). For some species already living or prone to living close to humans (anthropophilic) this development may represent an opportunity in terms of population growth and subsequent spread of their genes, but beyond some threshold, or for other species, it may compromise their wild status.

Apart from climate change and loss of natural habitats, living close to humans can affect wildlife in several ways. Some populations are exploited so that age structure and genetic diversity are altered (Allendorf et al., 2008; Milner et al., 2007). Other species face alien invasive species that may increase competition and introduce new diseases (Crowl et al., 2008). Another threat to genuine wildness is domestication (e.g., Diamond, 2002; Wiener and Wilkinson, 2011; Larson and Fuller, 2014). Domestication becomes a serious problem for wild conspecifics when they are removed from their environment to the point of becoming rare or where they interact increasingly with domestic individuals or their descendants. The latter process erodes local adaptations and genetic integrity of wild populations, which can have strong evolutionary consequences (Laikre et al., 2010; Olden et al., 2004; Rhymer and Simberloff, 1996). For instance, a case of releasing wild rabbits *Oryctolagus cuniculus* for hunting led to mixing of two distinct evolutionary lineages in the wild (Delibes-Mateos et al., 2008).

Many species of the order Anseriformes (e.g., swans, geese, and ducks) provide illustrative examples of the issues mentioned above. Humans have affected them by over-exploitation, habitat loss, domestication, translocation to new areas, and supplementing wild populations with farmed birds to increase hunting opportunities (Kear, 1990). Among Anseriform birds, the mallard duck *Anas platyrhynchos* is a prime example of a species that has been tightly interlinked and managed by humans. Being domesticated at very large scales while still being one of the most abundant and widespread waterfowl species globally, it also remains a valuable model species for management of wild populations (e.g., Anderson and Burnham, 1976) and for the study of zoonotic diseases (e.g., Jourdain et al., 2010).

Indeed, there are few other species for which so much management



**Fig. 1.** Chronological timeline on a log scale illustrating key events in the relationship between humans and mallard. B.P.: before present; <sup>1</sup>Zilhão et al. (2020); <sup>2</sup>Ericson and Tyrberg (2004); <sup>3</sup>Kear (1990); <sup>4</sup>Leopold (1933); <sup>5</sup>Thomson (2011); <sup>6</sup>Smalley and Reeves (2022); <sup>7</sup>Fluet-Chouinard et al. (2023); <sup>8</sup>Anderson et al. (2017); <sup>9</sup>Forbush (1925); <sup>10</sup>Stafford (2010); <sup>11</sup>Tamisier and Dehorter (1999); <sup>12</sup>Nichols et al. (2007); <sup>13</sup>Banks et al. (2008); <sup>14</sup>Global Invasive Species Database (2023); <sup>15</sup>Wetlands International (2023). Silhouette of mallard by Maija Karala from PhyloPic (<http://phylopic.org/>) under a Creative Commons licence (CC BY-NC-SA 3.0).

effort has been made to secure a favourable conservation status in combination with high harvest levels; the mallard was the model species for major advances in research on the consequences of harvest levels (e.g. Anderson and Burnham, 1976), including being the primary species for which the North American waterfowl adaptive harvest management plan was developed (e.g. Chapter 25 in Williams et al., 2002). Given the wealth of background information and the long history of interaction with humans (Fig. 1), the mallard provides an excellent case for exploring compromised wildness in the Anthropocene. We explore this issue by addressing the intertwined history of humans and mallards, and discuss implications for less well-studied species. In particular, we ask whether the mallard's present status is a success story considering its traits, genetics and dynamics; or if we are rather witnessing a thought-provoking example of demise through cryptic domestication and high vulnerability to future global changes. We address this question by presenting empirical evidence from the literature in the fields of ecology, evolution, zoonotics, sociology, economics, genetics, and population dynamics. However, as a *Perspectives* paper, we provide opinions based on selected references from a variety of scientific fields.

## 2. The mallard example and model

### 2.1. Traits of the wild mallard

The mallard is a classic example of a generalist species that has evolved many plastic and successful physiological and life history traits. First, it is among the largest duck species worldwide, with a mean body mass of males and females being ca. 1200 and ca. 1000 g, respectively (Cramp and Simmons, 1977, page 518). For a migratory species venturing into remote northern areas during the breeding season, its size provides benefits in terms of capacity to endure cold temperatures (Fig. 2). Large body size also permits spending the winter at higher latitudes close to and even beyond the zero-degree isotherm, thus a

position closer to nesting areas. This saves long and costly migration journeys such as those undertaken by related smaller species (Schummer et al., 2010; Dalby, 2013).

In French etymology the name “mallard” is actually considered to be related to the boldness of these birds (Kear, 1990, p 225). Their physiological advantages translate to generally higher annual survival rates than in smaller *Anas* species, i.e., adult male mallard versus green-winged teal *Anas carolinensis* have survival rates of 62–68 % and 55 %, respectively (Devineau et al., 2010; Baldassarre, 2014, pages 403–409; note that these rates include hunting mortality). Although generation time is about 2.5 years, the longevity records for wild mallards are 27.5 and 17.5 years for males and females, respectively (Baldassarre, 2014). In addition to being large, hardy birds with potentially high longevity, mallards also have traits that are typical of an r-selected species, including the capacity to breed in the first year of life, high fecundity (i.e., average clutch of ca. 9 eggs), and even producing multiple clutches in a single breeding season (review in Baldassarre, 2014). Coupling these flexible annual life-history traits with their migratory capacity (Scott and Rose, 1996; Li et al., 2009; Baldassarre, 2014) explains the mallard's Holarctic distribution and occurrence across wetland types up to 2000 m a.s.l. (Cramp and Simmons, 1977, page 508). Moreover, such traits potentially allow for considerable mixing of individuals over a wide geographic range, explaining why molecular work generally finds weak to no genetic structure geographically among wild mallards (Kraus et al., 2013, 2016; Lavretsky et al., 2023). The widespread occurrence of mallard remains in excavations or as fossils across Europe (e.g., Sweden in the Pleistocene, Late Glacial and Holocene periods: Ericson and Tyrberg, 2004, pages 32–42; Bulgaria in the Middle Holocene in Boev, 2018) and North America (e.g., Yukon in the Pleistocene: Fitzgerald, 1991; Idaho in the upper Pliocene: Brodkorb, 1958 and California in the late Holocene: Broughton, 2004) supports that the current Holarctic distribution was already established in pre-historic times. In evolutionary terms the mallard has successfully



**Fig. 2.** Wild and domesticated mallards in contrasting environments. A) A pair of wild mallards in the snow in northern Europe. Photo credit: Josef Chaib; B) A flying wild mallard in a Mediterranean environment. Photo credit: Pierre-Lou Chapot; C) Captive-bred mallards released for hunting in a managed fishpond. Photo credit: Maurice Benmergui; D) Mallards in a city park. Photo credit: Josef Chaib.

colonized a huge geographic area, where it is often abundant, exemplifying an outstanding evolutionary success story.

## 2.2. Win-win situation from the human-mallard interaction

Humans and mallards have long been closely associated, as these birds were apparently an important food source to ancient peoples (Jensen et al., 2019); indeed a large number of archaeological studies recurrently list mallard among the wild bird species consumed by ancient and modern humans over the last 100,000 years, while hundreds of other species were also available to them (Broughton, 2004; Ericson and Tyrberg, 2004, page 32; Table 1.1 and Chapter 5 in Shrubb, 2013; Boev, 2018; Zilhão et al., 2020; Fig. 1). In particular, human societies over time took advantage of the large numbers of flightless juveniles and molting adults that gathered in restricted areas in summer, which made them an easy catch and a valuable source of protein (Chapter 3 in Kear, 1990). More elaborate trapping systems (“duck decoys”) were built by people in the United Kingdom and other countries along the North and Baltic Seas starting in the seventeenth century (Fig. 1). Such practices continued into modern times, with hundreds of thousands of wild mallards being caught annually in the Netherlands until the 1950s (Chapter 3 in Kear, 1990), as well as in Britain, where they continued to fetch much higher prices than the other dabbling duck species (e.g., Eurasian wigeon *Mareca penelope* and northern pintail *Anas acuta*; Heaton, 2001, page 27).

Besides wild individuals, humans and mallards developed a tight relationship as civilizations began to domesticate the species ca. 2000 years ago somewhere in Eurasia (Kear, 1990; see also Boessneck, 1979 in Larson and Fuller, 2014; Fig. 1). Generally, the mallard's demonstrated capacity to readily tolerate captive conditions explains the success of its domestication (e.g. Rose et al., 2022), permitting people to further select favourable life-history traits resulting in larger body size, longer egg-laying seasons, and larger clutches (i.e., some breeds being able to produce one egg daily over periods of several months; Chapter 2 in Kear, 1990). As a result, apart from the domestication of the muscovy duck *Cairina moschata* in South America, farmed ducks today largely originate from the mallard (Reeber, 2015, page 364), with tens of breeds selected for meat and/or egg-production qualities. These long-standing interactions have even resulted in an integrated farming system in Asia that is developed around such domestic mallards (e.g., Pekin ducks), combining rice, duck, and fish farming (e.g. Furuno, 2001). In addition to being farmed as poultry, many ornamental mallard breeds exist, in which specific phenotypes of conspicuous male plumage have been exaggerated through selective breeding (e.g., crested duck in Fig. 19 of Lack, 1974). Moreover, the tameness of the species, and the ease with which it can settle into new environments have long made it very popular in zoos, parks, and gardens (reviews in Young, 2005; Guillemain et al., 2020). The mallard's success story as a domestic bird is also exemplified by their importance to the farming industry, as over half a billion farmed mallards are sold worldwide annually for human food consumption (Tanabe, 1995). Taken together, it can be argued that domestication has benefited the mallard in the sense that there are so many copies of its genes spread over the world in duck farms.

Apart from mallard strains being targeted for consumption or ornamental purposes, traits favourable for hunting have also resulted in specific mallard breeds. The extensive use of live decoys in some areas has resulted in selective breeding of highly vocal females to call and attract wild conspecifics in countries where this is permitted (e.g., Bortolotti et al., 2012). In addition, there is a long and rich history of using a specific mallard breed (e.g., game-farm mallard) for releases and restocking for hunting in Europe and North America (Section 7.9 in Owen and Black, 1990; Chapter 4 in Kear, 1990; Fig. 1). Imprecise estimates indicate that ca. 5,000,000 and 270,000 farmed mallards are released annually in Europe and North America, respectively (Champagnon et al., 2013; U.S. Fish and Wildlife Service, 2013; Madden, 2021). Despite their generally low survival, and that some birds are

intended to be hunted very shortly after release (*put-and-take*), these released birds do contribute substantially to the free-flying population, especially in Europe and during the beginning of the hunting season (Champagnon et al., 2016a, 2016b; Söderquist et al., 2021). Such efforts continue today as mallards are prized by hunters on both sides of the North Atlantic, with an annual harvest estimated at ca. 4 million in Europe (including Russia) and ca. 3 million in North America (Guillemain et al., 2016; Solokha and Gorokhovskiy, 2017; Raftovich et al., 2021). In some countries the mallard is the only hunted duck or comprises nearly the entire duck harvest (e.g., Hungary, Netherlands). Consequently, it can be considered a proximate driver of the hunting economy in many countries, explaining the mallard's present socio-economic importance (Green and Elmerberg, 2014).

In addition to economic benefits, interest in mallard hunting promotes conservation and restoration of its habitats over large areas. Revenues from targeted federal programs (e.g., the U.S. Federal Duck Stamp program) and the coalition of various non-profit organizations have resulted in the direct purchase, restoration, and/or management of millions of hectares of wetlands in North America (Miller and Ahlers, 2017). In this context, the mallard can be considered an umbrella species for many other animals and plants living in such wetlands. Today, the mallard remains the most abundant and widely distributed duck worldwide, with a total population estimated at ca. 20 million individuals (Wetlands International, 2023). However, population fluctuations, including long-term lows, are being observed across geographical strongholds in North America (Fig. 4 in U.S. Fish and Wildlife Service, 2022a) and Europe (e.g., North-West Europe, Nagy and Langendoen, 2020), raising concerns about the species' future.

## 2.3. The mallard today - success or cryptic demise?

Where has the relationship with humans taken the mallard today? Can it serve as a model for the issue of success versus demise of wild species in the Anthropocene? With the change towards a globe more profoundly affected by humans, mallards have coped by readily using human-managed habitats such as agricultural landscapes (Thomas, 1981; Fleskes et al., 2012; Pernollet et al., 2015) and constructed wetlands (Čehovská et al., 2022). The mallard is a synanthropic bird that can also thrive in purely artificial habitats, such as parks and cities (Luniak, 2004). Indeed Johnston (2001) considered the mallard as a tangential synanthrope due to substantial portions of its population's close relationship with artificial or highly managed habitats.

By constantly releasing farmed mallards, many genomic combinations have been ‘tested’, and eventually some likely flourished in the Anthropocene. Over the last 50 years, wild-living mallards have increased by 5–10 % in body mass in Europe (Guillemain et al., 2010; Gunnarsson et al., 2012) and North America (Veon, 2021). This can partly be explained by a growing reliance on artificial habitats with food such as spilled agricultural grains (Owen and Cook, 1977; Bengtsson et al., 2014), and supplemental food intended to support released mallards for hunting (Guillemain et al., 2010). Present-day mallards have more goose-like bills with a lower density of lamellae (comb-like structures on the edges of the bill) than their wild European ancestors (Champagnon et al., 2010; Söderquist et al., 2014), reflecting such changes in foraging habits. Decreased lamellar density likely results from greater reliance on human-provided larger food items (e.g., poultry pellets), but in-turn leading to a reduced capacity to extract small natural food items such as seeds and micro-invertebrates (Halligan, 2023). Additionally, mallard migratory habits have changed over the last 50 years, with some populations becoming increasingly short-distance migrants, while others are already completely sedentary (Sauter et al., 2010; Gunnarsson et al., 2012; Guillemain et al., 2015). Changes in migratory behaviour can potentially result in reduced gene flow in what has long been considered a panmictic species, and may explain recently identified substructuring among wild mallards from Eurasia and North America (Lavretsky et al., 2023).

Although climate change is likely a contributing factor explaining some behavioural changes, other factors (i.e., improved feeding conditions in some areas) are likely to be involved as well, including hybridization with released farmed mallards. The latter are less prone to migrate compared to wild, even when releases occur at or close to northern breeding areas (Lincoln, 1934; Boyd and Harrison, 1962; Fog, 1964; Söderquist, 2015). An important aspect of large-scale releases of farmed mallards is the subsequent introgression of 'farm genes' into the wild population by two main mechanisms leading to hybridization: a) wild mallards encounter domesticated stock in anthropogenic environments, and b) released farmed birds survive the hunting season and mix with resident or migratory wild mallards (Čížková et al., 2012; Champagnon et al., 2013; Baratti et al., 2015; Söderquist et al., 2017; Lavretsky et al., 2020). Of the many domesticated breeds, recent molecular analyses have determined that interbreeding with game-farm mallard strains is the greatest genetic threat to wild mallard populations. Indeed data suggest that interbreeding between an artificially-selected and inbred game-farm lineage is not only resulting in reduced genetic variation (i.e., inbreeding), but is replacing important genetic variation born from millennia of natural selection with ones established in captivity (i.e., outbreeding depression; Söderquist et al., 2017; Lavretsky et al., 2020, 2023). Unlike most domestic strains bred for consumption or ornaments (Chapter 2 in Kear, 1990), the game-farm mallard was specifically bred to supplement wild populations. The first record of such breeding activity can be dated to 1631 in England, by orders of King Charles II to begin propagation for hunting, and eggs from wild mallards were brought into captivity (Leopold, 1933; Fig. 1). Moreover, the first use of game-farm mallard can be attributed to the establishment of formal breeding and ringing operations in the 1890s in England (Sellers and Greenwood, 2018). Thus, the game-farm mallard breed has developed over the last 400 years. The success of this captive-breeding process is the source of today's self-sustaining feral mallard populations in Hawaii and New Zealand (Lavretsky et al., 2023). Consequently, Hawaiian ducks *Anas wyvilliana* and grey ducks *Anas superciliosa* are nowadays relegated to a specific island (Wells et al., 2019) or limited locations (Williams, 2017), respectively.

Hybridization between game-farm and wild mallards has evolutionary consequences for the species by transforming the genetic landscape of the wild populations, homogenising genetic variation and potentially leading to loss of local adaptations (Olden et al., 2004; Laikre et al., 2010). Most studies show that farmed mallards have a much lower survival after release than wild conspecifics (Lincoln, 1934; Brakhage, 1953; Yerkes and Bluhm, 1998; Champagnon et al., 2016a, 2016b; Söderquist et al., 2021). While a decline in mallard survival rates from pre-release times (1950–1970) to the present was not recorded in Camargue, southern France, a recent study demonstrated greater survival heterogeneity in the modern population, comprising more polarized groups of individuals with either higher or lower survival rates than in the past (Grzegorzczuk, 2023). One hypothesis is that an increasing difference exists between few pure wild mallards capable of benefiting from improved environmental conditions (e.g. warmer climate, less need to migrate). Moreover, large portions of wild mallard populations now consist of released farmed birds, or hybrids between wild and farmed ancestry that suffer from 'a burden of captivity,' preventing them from using their environment efficiently (reduced effectiveness when foraging (Champagnon et al., 2012) or effectively detecting and evading predators) and resulting in very low survival rates.

The blurred distinction between wild and captive mallards may reduce interest among some managers and the public in the conservation of this species, and consequently, valuable wetland habitats. The perceived value of the species may be reflected by the observation that mallard tarsal rings are less frequently reported when found by hunters or the general public than are the rings of another purely wild migratory species (Eurasian Teal *Anas crecca*; Guillemain et al., 2011). These releases lack much-needed follow-up programs (Laikre et al., 2006), which raises doubts about the origin of mallards (are they all pure, mixed or all

captive?). However, a landscape genetic study of North American mallards found that higher levels of introgressive hybridization occur in the eastern parts of the continent, and decrease westward (Lavretsky et al., 2019). Importantly, the proportion of populations consisting of game-farm or hybrid ducks corresponded geographically to where most game-farm mallard releases occur today. We note that the genetic contributions of captive-bred mallards could have significant impacts on survival and fecundity parameters of wild mallard populations, as shown in red-legged partridges *Alectoris rufa* and Atlantic salmon *Salmo salar* (Casas et al., 2012; McGinnity et al., 2003). Finally, the mixing of mallards with captive and wild genes violates any one-population assumptions made in current wildlife management models (e.g., mallard adaptive harvest management in North America; U.S. Fish and Wildlife Service, 2022b), which for instance do not account for the possible coexistence of categories of individuals with different survival rates (i.e., the demographic heterogeneity demonstrated in Grzegorzczuk, 2023).

Whether mallard populations will eventually succumb to the fate of being sustained by continued stocking practices is unknown, but when supplementation of captive-bred individuals in the wild is initiated, it rarely ends (e.g., Araki et al., 2009; Fraser, 2008). This is unfortunate because population declines are occurring where farmed mallards are being released in large numbers annually (Dalby et al., 2013; Moussy et al., 2022). In Europe, recent waterbird population estimates show a moderate decrease in the short term (10-year period of 2008–2017) for the two flyways with good quality data (Northwest Europe and Northern Europe/West Mediterranean; Nagy and Langendoen, 2020; Nagy et al., 2020). Similarly, the estimated breeding population size for North American mallards in the Eastern flyway, where >90 % of farmed mallard releases occur, has experienced substantial declines since the mid-1990s (U.S. Fish and Wildlife Service, 2013; Fig. 5 in U.S. Fish and Wildlife Service, 2022a, 2022b). Such declines have so far tended to be short term, and more research is needed to prove a causal effect of hybridisation on population decline.

Massive releases of mallards may also produce negative consequences in terms of habitat management. For example, to accommodate released birds, landowners sometimes engage in actively hunting-oriented management of wetlands, which may provide basic habitat that is attractive to mallard, but at the same time be detrimental to other components of biodiversity such as plants (Tamisier and Grillas, 1994). In addition, providing food ad libitum after releases is likely to affect water quality, nutrient level, and predation pressure locally (Söderquist et al., 2021). In southern France, marshes are sometimes managed specifically to harbour released mallards instead of making such habitats attractive to wild conspecifics and biodiversity in general (e.g., through artificial flooding disconnected from the natural rainfall regime; Champagnon, 2011). Such artificial management of hunted wetlands may also prevent waterbirds from adapting to climate change by shifting their geographic distribution, and by promoting residency instead (Gaget et al., 2023). Finally, the mallard is considered an invasive species in many countries where it has been widely introduced outside its natural range, and can outcompete local waterbird species (Fox, 2009; Guillemain et al., 2020; GISD, 2023; Fig. 1).

Given the long history of mallard domestication, and large numbers of farmed birds still being released in the wild, one may question whether 'pure' ancestral mallards continue to exist, and if the species is still wild at all. Recent genetic analyses provide contrasting results. While free-living populations have been fundamentally changed by intensive releases of farm-raised, game-farm mallards over the last century in North America and Eurasia, genetic wild-type mallards still occur across the Holarctic (Champagnon et al., 2013; Söderquist et al., 2017; Lavretsky et al., 2023), suggesting that at least for now some populations genetically resist anthropogenic pressures.

### 3. Discussion

The mallard exemplifies how a species can adapt to rapidly changing

environments in the Anthropocene, although there are signs that the situation is nearing its limits and that the mallard may be less able to cope with rapidly changing human-modified habitats. Here, we highlight a wide range of processes by which a formerly distinctly wild species can be affected via altered habitats, climate change, and direct human activities. The mallard example shows how the delineation between captive populations (over which humans have total control) and purely wild conspecifics may vanish in the Anthropocene. The situation may not be equally alarming in species that remain further away from human influences (see wolf *Canis lupus* in [Randi, 2008](#)). However, domestication or captive conditions often lead to loss of some wild physiological and ecological traits (e.g., wild wheat *Triticum* spp. and barley *Hordeum vulgare* ([Diamond, 2002](#)); honeybee *Apis mellifera* ([Herrera, 2020](#)); Atlantic salmon ([McGinnity et al., 2009](#)); red-legged partridge ([Barbanera et al., 2010](#)); reindeer *Rangifer tarandus* ([Baskin, 2000](#)); wild ass *Equus africanus* ([Kimura et al., 2011](#)); various ungulates in [Mysterud \(2010\)](#)). Earth currently hosts a greater biomass of farmed animals than wild ones (from which they originated), with an estimated 60 million tonnes of wild terrestrial and marine mammals vs. 630 million tonnes of mammalian livestock ([Greenspoon et al., 2023](#)). Depending on species, formerly clear distinctions between captive and purely wild individuals have become progressively blurred.

Then, is it a problem if the distinction between wild and non-wild conspecifics vanishes? Examples abound of species showing a flourishing demography (population increase and/or range expansion) in regions under strong human influence: hunted ungulates benefit from modern farming and forestry practices, as well as from declines of their natural predators, all caused by humans ([Mysterud, 2010](#)). Snow geese *Chen caerulescens* (and many other goose species in general) benefit from modern agriculture at the same time as climate change reduces their energy needs, so that the population has increased enormously and become difficult to control even with highly liberalized hunting regulations (e.g. [Alisauskas et al., 2011](#)). Glossy ibis *Plegadis falcinellus* expanded in Southern France in response to climate change and human introduction of formerly exotic food sources (crayfish) ([Champagnon et al., 2019](#)), and cattle egret *Bubulcus ibis* thrives by associating with livestock ([Telfair II, 2006](#)). Species with such ecology are able to remain largely wild even in present-day human-modified ecosystems.

In many conservation programs, reintroduction of captive-bred conspecifics is the only solution to save populations in the wild, although in these cases great care is often taken to ensure captive-bred individuals remain as wild and shy of humans as possible (e.g., sandhill crane *Grus canadensis*; [Horwich, 1989](#)). But there are species that humans have used and affected even more profoundly, in which the separation between wild and non-wild indeed may be difficult to draw. Illustrative examples are common in the context of harvest such as wild boar *Sus scrofa* ([Scandura et al., 2011](#)), Atlantic salmon ([Ciborowski et al., 2007](#); [McDowell, 2002](#)), Norway spruce *Picea abies* ([Björkman and Bradshaw, 1996](#)), brown hare *Lepus europaeus* ([Mamuris et al., 2001](#); [Fickel et al., 2005](#)), and European rabbit ([Delibes-Mateos et al., 2008](#)). Many of these species have increased in abundance and/or range enormously, but such apparent demographic success may conceal unwanted evolutionary change. For instance, [McGinnity et al. \(2009\)](#) showed that massive restocking of Atlantic salmon into a river with captive-bred individuals disrupted the capacity of natural populations to adapt to higher winter temperatures. Similarly, the pathogen loads of wild individuals may be higher in areas of extensive overlap with captive-reared, released animals (e.g., red-legged partridges; [Díaz-Sánchez et al., 2012](#); wild boar; [Ruiz-Fons et al., 2006](#); or mallard; [Vitecoq et al., 2012](#)).

The issue whether or not humans should actively manage wildlife populations ('rewilding') or let natural equilibria occur is a lively scientific and ethical debate for the Anthropocene, one that also questions the way we can and should conserve biodiversity ([Sarrazin and Lecomte, 2016](#); [Otto, 2018](#)). In general, economic interests such as hunting or fishing drive intensive management. The consequence is a potential

decrease in the value of the species: in the case of hunted species, for instance, the value of the game animal for hunters is directly related to its perceived wildness ([Leopold, 1933](#)).

The value of wildness in itself is central to conservation science, so that gradual loss of such a condition through a creeping domestication process may in itself raise ethical and philosophical questions (e.g., Nash in [Wuerthner et al., 2014](#)). Furthermore, some may consider that any alteration of the pristine wild nature of a species makes it lose most conservation interest, so that it is not worth any further attention. The example of the rock dove *Columba livia* is highly illustrative in this context as it was domesticated long ago to be bred in farms and backyard gardens, but some individuals escaped and interbred with wild rock doves. Genetic introgression from such marooned city and village birds is considered one of the main threats to wild rock doves today ([Johnston et al., 1988](#)). Purely wild rock dove populations have now disappeared from most places except in a few remote cliffs and islands (e.g. [Thibault et al., 1990](#); [Smith et al., 2022](#)), but this has occurred in a general indifference, as most people do not even realize that this is also a wild species. Thankfully, the mallard has not yet suffered the same fate, as wild mallards still exist, and they are attracting the attention of a range of stakeholders, including conservationists and hunters alike.

As shown by the mallard example, we should not be naïve towards apparent successes based on current large population sizes alone, as they may mask behavioural, demographic and/or genetic degradation. Such degradation may be an unenviable fate, in so far that the species may not be able to survive in the future without human interventions. If such negative changes are occurring in a species as adaptable and resistant as the mallard ([Bellrose, 1985](#)), it is likely that significant processes remain overlooked in less common or more poorly studied species. This would have important implications for conservation and management in general. In particular, the extent of active management versus natural rewilding of habitats and populations remains an important question when attempting to decrease the risk of anthropomorphising systems. Will systems return to 'normal' by themselves in a world we have changed so much? These issues are difficult to resolve, and they involve ethical, sociological, and ecological aspects. However, the mallard case and lessons learned from other species collectively offer a range of precautionary actions that may be taken:

- 1) Avoid loss of wild habitat (e.g., owing to urbanisation or agriculture) that would increase contact between wild and domesticated/farmed populations. Habitat loss forces species to depend on human-modified habitat (e.g., cranes *Grus* spp., geese *Anser* spp., *Branta* spp., and *Chen* spp.);
- 2) Emulate natural cycles and disturbance patterns when managing natural habitats (e.g., adhere to natural precipitation regimes in the case of artificial flooding), to favour local wild species instead of accustoming exotics or promoting local adaptation to artificial conditions;
- 3) Perform rewilding through habitat restoration rather than by population reintroduction or reinforcement. The recovery of some species leads to improvement of habitats and helps ecosystems emulate their 'wild' state, e.g., the return of the American bison *Bison bison* and the Great Plains vegetation in areas formerly degraded by decades of continuous cattle grazing;
- 4) Refrain as much as possible from releasing or introducing individuals of captive origin, as a fraction of these will eventually interbreed with wild conspecifics, with unpredictable demographic, behavioural, and genetic consequences;
- 5) When it is necessary to release/relocate wild individuals, do so away from captive counterparts to avoid mixing and future loss of wild characteristics. What 'away' means will depend on the mobility of the focal species;
- 6) For the same reason as in 5), do not start farming a species within the geographic range of the same wild species. This is especially true for

plants and insects where confinement within a farmed area may be difficult (e.g., wind dispersal of pollen);

- 7) Put-and-take procedures for hunting and fishing should be avoided. Local wild populations should instead be enhanced through habitat management. If unavoidable, then aim to release individuals with low survival prospects (ideally dying naturally before the next breeding season), or release sterile individuals to avoid crosses between wild and farmed;
- 8) When (re)introduction is essential for conservation purposes, avoid contact with humans during the captive phase in order to retain wild characteristics of released individuals as much as possible. When releasing for future exploitation, do not try to 'improve' released strains for the reasons explained in 7); and,
- 9) Always mark released individuals to permit the study of their future fate in nature and better assess the consequences of releases for the wild segment of the population.

We must appreciate that wildness develops over evolutionary time scales, but can be eroded or extinguished by just years or decades of poor population management. Selective exploitation of some phenotypes in a population can cause a 'Darwinian debt' by which depressed genotypic variability requires extremely long periods to recover (e.g., Pandolfi, 2009). Similarly, losing the wild nature of plants and animals by undesirable habitat alteration, inappropriate farming, and thoughtless releases may cause a similar Darwinian debt left to future generations, preventing wild species from providing either beneficial ecosystem services or the simple enjoyment of experiencing them unexpectedly in natural environments.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

No data were used for the research described in the article.

#### Acknowledgements

We would like to thank Vincent Devictor, two anonymous reviewers, and Alain Caizergues for their valuable comments on an earlier version of the manuscript. We thank Nathalie Chokier for the design of Fig. 1, and Roberta Fausti, Aude Caizergues, Alain Caizergues and Hervé Lormée for their help with the literature. We are grateful to Josef Chaib, Pierre-Loup Chapot and Maurice Benmergui for providing the images in Fig. 2.

#### References

- Alisauskas, R.T., Rockwell, R.F., Dufour, K.W., Cooch, E.G., Zimmerman, G., Drake, K.L., Leafloor, J.O., Moser, T.J., Reed, E.T., 2011. Harvest, survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. *Wildl. Monogr.* 179, 1–42.
- Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A., Ryman, N., 2008. Genetic effects of harvest on wild animal populations. *TREE* 23, 327–337.
- Anderson, D.R., Burnham, K.P., 1976. Population Ecology of the Mallard: VI. The Effect of Exploitation on Survival. US Fish and Wildlife Service.
- Anderson, M.G., Alisauskas, R.T., Batt, B.D.J., Blohm, R.J., Higgins, K.F., Perry, M.C., Ringelman, J.K., Seder, J.S., Serie, J.R., Sharp, D.E., Trauger, D.L., Williams, C.K., 2017. The migratory bird treaty and a century of waterfowl conservation. *J. Wildl. Manage.* 82 (2), 247–259. <https://doi.org/10.1002/jwmg.21326>.
- Araki, H., Cooper, B., Blouin, M.S., 2009. Carry-over effect of captive breeding reduces reproductive fitness of wild-born descendants in the wild. *Biol. Lett.* 5, 621–624.
- Baldassarre, G., 2014. Ducks, Geese, and Swans of North America. JHU Press.
- Banks, A.N., Wright, L.J., Maclean, I.M.D., Hann, C., Rehfish, M.M., 2008. Review of the status of introduced non-native waterbird species in the area of the African-Eurasian Waterbird Agreement. In: 2007 Update. BTO Research Report No. 489, Thetford, UK.
- Baratti, M., Baccetti, N., Cordaro, M., Mori, A., Dessi-Fulgheri, F., 2015. Investigating the puzzling genetic structure of mallard populations (*Anas platyrhynchos* L.) in Italy. *Eur. J. Wildl. Res.* 61, 81–89. <https://doi.org/10.1007/s10344-014-0876-2>.
- Barbanera, F., Pergams, O.R.W., Guerrini, M., Forcina, G., Panayides, P., Dini, F., 2010. Genetic consequences of intensive management in game birds. *Biol. Conserv.* 143, 1259–1268. <https://doi.org/10.1016/j.biocon.2010.02.035>.
- Baskin, L.M., 2000. Reindeer husbandry/hunting in Russia in the past, present and future. *Pol. Res.* 19, 23–29.
- Bellorose, F.C., 1985. The adaptability of the Mallard leads to its future. In: Proc. Mallard Symp., August 19–22, 1985, Bismarck, North Dakota.
- Bengtsson, D., Avril, A., Gunnarsson, G., Elmberg, J., Söderquist, P., Norevik, G., Tolf, C., Safi, K., Fiedler, W., Wikelski, M., Olsen, B., Waldenström, J., 2014. Movements, home-range size and habitat selection of mallards during autumn migration. *PLoS One* 9 (6), e100764.
- Björkman, L., Bradshaw, R., 1996. The immigration of *Fagus sylvatica* L. and *Picea abies* (L.) Karst. into a natural forest stand in southern Sweden during the last 2000 years. *J. Biogeogr.* 23, 235–244.
- Boev, Z., 2018. Fossil and subfossil record of vertebrate animals (Vertebrata J.-B. Lamarck, 1801) along the Western Black Sea Coast (Bulgaria). *Acta Zool. Bulg. (Suppl.)*, 105–110.
- Bortolotti, L., Rizzo, S., Favero, L., Bonfanti, L., Comin, A., Marangon, S., 2012. Implementation of an information system for the traceability of live decoy birds. *Avian Dis.* 46 (4s1), 1021–1024.
- Boyd, H., Harrison, J., 1962. First-autumn dispersal of hand-reared mallard. *Wildfowl* 13, 4.
- Brakhage, G.K., 1953. Migration and mortality of ducks hand-reared and wild-trapped at Delta, Manitoba. *J. Wildl. Manag.* 17 (4), 465–477.
- Brodkorb, P., 1958. Fossil birds from Idaho. *Wilson Bull.* 70, 237–242.
- Broughton, J., 2004. Prehistoric human impacts on California birds: evidence from the Emeryville Shellmound avifauna. *Ornithol. Monogr.* 78, 1–90. <https://doi.org/10.2307/40166805>.
- Casas, F., Mougeot, F., Sánchez-Barbudo, I., Dávila, J.A., Viñuela, J., 2012. Fitness consequences of anthropogenic hybridization in wild red-legged partridge (*Alectoris rufa*, Phasianidae) populations. *Biol. Invasions* 14, 295–305. <https://doi.org/10.1007/s10530-011-0062-3>.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1, e1400253.
- Čehovská, M., Kattainen, S., Väänänen, V.M., Putaala, A., Nummi, P., 2022. Compensating freshwater habitat loss—duck productivity and food resources in man-made wetlands. *Eur. J. Wildl. Res.* 68, 35. <https://doi.org/10.1007/s10344-022-01577-8>.
- Champagnon, J., 2011. Conséquences des introductions d'individus dans les populations d'oiseaux d'eau exploitées: l'exemple du canard colvert *Anas platyrhynchos* (PhD thesis). University of Montpellier 2, France.
- Champagnon, J., Guillemain, M., Elmberg, J., Folkesson, K., Gauthier-Clerc, M., 2010. Changes in mallard *Anas platyrhynchos* bill morphology after 30 years of supplemental stocking. *Bird Study* 57 (3), 344–351.
- Champagnon, J., Guillemain, M., Elmberg, J., Masseur, G., Cavallo, F., Gauthier-Clerc, M., 2012. Low survival after release into the wild: assessing "the burden of captivity" on mallard physiology and behaviour. *Eur. J. Wildl. Res.* 58 (1), 255–267.
- Champagnon, J., Crochet, P.A., Kreisinger, J., Čížková, D., Gauthier-Clerc, M., Masseur, G., Söderquist, P., Albrecht, T., Guillemain, M., 2013. Assessing the genetic impact of massive restocking on wild mallard. *Anim. Conserv.* 16 (3), 295–305.
- Champagnon, J., Guillemain, M., Mondain-Monval, J.-Y., Souchay, G., Legagneux, P., Bretagnolle, V., Van Ingen, L., Bourguemestre, F., Lebreton, J.-D., 2016a. Contribution of released captive-bred mallards to the dynamics of the natural population. *Orn. Fenn.* 93, 3–11.
- Champagnon, J., Legagneux, P., Souchay, G., Inchausti, P., Bretagnolle, V., Bourguemestre, F., Van Ingen, L., Guillemain, M., 2016b. Robust estimation of survival and contribution of captive-bred mallards *Anas platyrhynchos* to a wild population in a large-scale release programme. *Ibis* 158, 343–352. <https://doi.org/10.1111/ibi.12341>.
- Champagnon, J., Kayser, Y., Petit, J., Marion, L., Reeber, S., Blanchon, T., Hilaire, S., Badone, I., Crouzier, P., Purenne, R., Gauthier-Clerc, M., 2019. The settlement of glossy Ibis in France. *SIS Conserv.* 1, 50–55.
- Ciborowski, K.L., Consuegra, S., García de Leániz, C., Wang, J., Beaumont, M.A., Jordan, W.C., 2007. Stocking may increase mitochondrial DNA diversity but fails to halt the decline of endangered Atlantic salmon populations. *Conserv. Genet.* 8, 1355–1367. <https://doi.org/10.1007/s10592-007-9286-2>.
- Čížková, D., Javůrková, V., Champagnon, J., Kreisinger, J., 2012. Duck's not dead: does restocking with captive bred individuals affect the genetic integrity of wild mallard (*Anas platyrhynchos*) population? *Biol. Conserv.* 152, 231–240.
- Cramp, S., Simmons, K.E.L., 1977. Birds of the Western Palearctic. Oxford University Press.
- Crowl, T.A., Crist, T.O., Parmenter, R.R., Belovsky, G., Lugo, A.E., 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. *Front. Ecol. Environ.* 6, 238–246. <https://doi.org/10.1890/070151>.
- Dalby, L., 2013. Waterfowl, Duck Distributions and a Changing Climate (PhD thesis). Department of Bioscience, Aarhus University, Denmark.
- Dalby, L., Söderquist, P., Christensen, T.K., Clausen, P., Einarsson, Å., Elmberg, J., Fox, A.D., Holmqvist, N., Langendoen, A., Lehtikoinen, A., Lindström, Å., Lorentsen, S.-H., Nilsson, L., Pöysä, H., Rintala, J., Sigfússon, A.P., Svenning, J.-C., 2013. The status of the Nordic populations of the mallard (*Anas platyrhynchos*) in a changing world. *Orn. Fenn.* 90, 2–15.

- Delibes-Mateos, M., Ramírez, E., Ferreras, P., Villafuerte, R., 2008. Translocations as a risk for the conservation of European wild rabbit *Oryctolagus cuniculus* lineages. *Oryx* 42 (2), 259–264.
- Devineau, O., Guillemain, M., Johnson, A.R., Lebreton, J.-D., 2010. A comparison of green-winged teal *Anas crecca* survival and harvest between Europe and North America. *Wildl. Biol.* 16, 12–24. <https://doi.org/10.2981/08-071>.
- Diamond, J., 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418, 700–707.
- Díaz-Sánchez, S., Moriones, A.M., Casas, F., Höfle, U., 2012. Prevalence of *Escherichia coli*, *Salmonella* sp. and *Campylobacter* sp. in the intestinal flora of farm-reared, restocked and wild red-legged partridges (*Alectoris rufa*): is restocking using farm-reared birds a risk? *Eur. J. Wildl. Res.* 58, 99–105. <https://doi.org/10.1007/s10344-011-0547-5>.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.
- Ericson, P.G.P., Tyrberg, T., 2004. The early history of the Swedish avifauna. A review of the subfossil record and early written sources. In: *Kungl. Vitterhets Historie och Antikvitets Akademiska Handlingar*, Vol. 4.
- Fickel, J., Schmidt, A., Putze, M., Spittler, H., Ludwig, A., Streich, W.J., Pitra, C., 2005. Genetic structure of populations of European brown hare: implications for management. *J. Wildl. Manage.* 69 (2), 760–770.
- Fitzgerald, G.R., 1991. Pleistocene ducks of the Old Crow Basin, Yukon Territory, Canada. *Can. J. Earth Sc.* 28, 1561–1571.
- Fleskes, J.P., Skalos, D.A., Farinha, M.A., 2012. Bird use of fields treated postharvest with two types of flooding in Tulare Basin, California. *J. Fish Wildl. Manag.* 3 (1), 164–174 e1944-687X. <https://doi.org/10.3996/092011-JFWM-056>.
- Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelme, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. *Nature* 614, 281–286. <https://doi.org/10.1038/s41586-022-05572-6>.
- Fog, J., 1964. Dispersal and survival of released mallards (*Anas platyrhynchos* L.). *Dan. Rev. Game Biol.* 4 (3), 1–57.
- Forbush, E.H., 1925. *Birds of Massachusetts and Other New England States: Land Birds from Bob Whites to Grackles*. Berwick and Smith Company.
- Fox, A.D., 2009. What makes a good alien? Dealing with the problems of non-native wildfowl. *Brit. Birds* 102, 660–679.
- Fraser, D.J., 2008. How well can captive breeding programs conserve biodiversity? A review of salmonids. *Evol. Appl.* 1, 535–586.
- Fricke, E.C., Ordóñez, A., Rogers, H.S., Svenning, J.-C., 2022. The effects of defaunation on plants' capacity to track climate change. *Science* 375, 210–214. <https://doi.org/10.1126/science.abk3510>.
- Furuno, T., 2001. *The Power of Duck: Integrated Rice and Duck Farming*. Tagari Publications, Sisters Creek.
- Gaget, E., Galewski, T., Brommer, J.E., Le Viol, I., Jiguet, F., Baccetti, N., Langendoen, T., Molina, B., Moniz, C., Zenatello, M., Guillemain, M., 2023. Habitat management favouring hunted waterbird species prevents distribution changes in response to climate warming. *An. Conserv.* <https://doi.org/10.1111/acv.12872>.
- Global Invasive Species Database (GISD), 2023. Species profile *Anas platyrhynchos*. <http://www.iucngisd.org/gisd/species.php?sc=1241>.
- Green, A.J., Elmer, J., 2014. Ecosystem services provided by waterbirds. *Biol. Rev.* 89, 105–122. <https://doi.org/10.1111/brv.12045>.
- Greenspoon, L., Krieger, E., Sender, R., Rosenberg, Y., Bar-On, Y.M., Moran, U., Antman, T., Meiri, S., Roll, U., Noor, E., Milo, R., 2023. The global biomass of wild mammals. *PNAS* 120 (10), e2204892120. <https://doi.org/10.1073/pnas.2204892120>.
- Grzegorzczak, E., 2023. *La chasse des oiseaux en Europe: quelles conséquences démographiques et évolutives?* (PhD. Thesis) University of Montpellier, France.
- Guillemain, M., Elmer, J., Gauthier-Clerc, M., Massez, G., Hearn, R., Champagnon, J., Simon, G., 2010. Wintering French mallard and teal are heavier and in better body condition than 30 years ago: effects of a changing environment? *Ambio* 39, 170–180.
- Guillemain, M., Devineau, O., Gauthier-Clerc, M., Hearn, R., King, R., Simon, G., Grantham, M., 2011. Changes in ring recovery rates over the last 50 years: shall we continue to ring ducks? *J. Ornithol.* 152, 55–61. <https://doi.org/10.1007/s10336-010-0546-4>.
- Guillemain, M., Champagnon, J., Massez, G., Pernollet, C.A., George, T., Momerency, A., Simon, G., 2015. Becoming more sedentary? Changes in recovery positions of mallard *Anas platyrhynchos* ringed in the Camargue, France, over the last 50 years. *Wildfowl* 65, 51–63.
- Guillemain, M., Aubry, P., Folliot, B., Caizergues, A., 2016. Duck hunting bag estimates for the 2013/14 season in France. *Wildfowl* 66, 126–141.
- Guillemain, M., Söderquist, P., Champagnon, J., Elmer, J., 2020. Mallard (*Anas platyrhynchos* Linnaeus, 1758). In: *Downs, C.T., Hart, L.A. (Eds.), Invasive Birds: Global Trends and Impacts*. CABI, Wallingford, Oxfordshire; Boston.
- Gunnarsson, G., Waldenström, J., Fransson, T., 2012. Direct and indirect effects of winter harshness on the survival of mallards *Anas platyrhynchos* in northwest Europe. *Ibis* 154 (2), 307–317.
- Halligan, S.L., 2023. *Comparisons of Morphology and Food Intake Rate between Wild-caught and Game-farm Mallards*. Master of Science Degree State University of New York College of Environmental Science and Forestry Syracuse, New York.
- Heaton, A., 2001. *Duck decoys*. Shire Publications Ltd., Princes Risborough, UK.
- Herrera, C.M., 2020. Gradual replacement of wild bees by honeybees in flowers of the Mediterranean Basin over the last 50 years. *Proc. R. Soc. B* 287, 20192657. <https://doi.org/10.1098/rspb.2019.2657>.
- Horwich, R.H., 1989. Use of surrogate parental models and age periods in a successful release of hand-reared sandhill cranes. *Zoo Biol.* 8, 379–390.
- IPBES, 2019. *Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services*. Zenodo. <https://doi.org/10.5281/zenodo.6417333>.
- Jensen, T.Z.T., Niemann, J., Iversen, K.H., Fotakis, A.K., Gopalakrishnan, S., Vågene, Å. J., Pedersen, M.W., Sinding, M.-H.S., Ellegaard, M.R., Allentoft, M.E., Lanigan, L.T., Taurozzi, A.J., Nielsen, S.H., Dee, M.W., Mortensen, M.N., Christensen, M.C., Sørensen, S.A., Collins, M.J., Gilbert, M.T.P., Sikora, M., Rasmussen, S., Schroeder, H., 2019. A 5700 year-old human genome and oral microbiome from chewed birch pitch. *Nat. Commun.* 10, 5520. <https://doi.org/10.1038/s41467-019-13549-9>.
- Johnston, R.F., 2001. *Synanthropic birds of North America*. In: *Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World*. Springer, New-York.
- Johnston, R.F., Siegel-Causey, D., Johnson, S.G., 1988. European populations of the Rock Dove *Columba livia* and genotypic extinction. *Am. Midl. Nat.* 120, 1–10.
- Jourdain, E., Gunnarsson, G., Wahlgren, J., Latorre-Margalef, N., Bröjer, C., Sahlin, S., Svensson, L., Waldenström, J., Lundkvist, Å., Olsen, B., 2010. Influenza virus in a natural host, the mallard: experimental infection data. *PLoS ONE* 5, e8935. <https://doi.org/10.1371/journal.pone.0008935>.
- Kear, J., 1990. *Man and Wildfowl*. T. & A.D. Poyser, London.
- Kimura, B., Marshall, F.B., Chen, S., Rosenbom, S., Moehlan, P.D., Tuross, N., Sabin, R. C., Peters, J., Barich, B., Yohannes, H., Kebede, F., Teclai, R., Beja-Pereira, A., Mulligan, C.J., 2011. Ancient DNA from Nubian and Somali wild ass provides insights into donkey ancestry and domestication. *Proc. R. Soc. B* 278, 50–57. <https://doi.org/10.1098/rspb.2010.0708>.
- Kraus, R.H.S., van Hooft, P., Megens, H.-J., Tsvey, A., Fokin, S.Y., Ydenberg, R.C., Prins, H.H.T., 2013. Global lack of flyway structure in a cosmopolitan bird revealed by a genome wide survey of single nucleotide polymorphisms. *Mol. Ecol.* 22, 41–55. <https://doi.org/10.1111/mec.12098>.
- Kraus, R.H.S., Figuerola, J., Klug, K., 2016. No genetic structure in a mixed flock of migratory and non-migratory mallards. *J. Orn.* 157, 919–922. <https://doi.org/10.1007/s10336-016-1354-2>.
- Lack, D., 1974. *Evolution Illustrated by Waterfowl*. Blackwell Scientific Publications, Oxford.
- Laike, L., Palmé, A., Josefsson, M., Utter, F., Ryman, N., 2006. Release of alien populations in Sweden. *Ambio* 35 (5), 255–261. <https://doi.org/10.1579/05-A-060R.1>.
- Laike, L., Schwartz, M.K., Waples, R.S., Ryman, N., 2010. Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *TREE* 25, 520–529.
- Larson, G., Fuller, D.Q., 2014. The evolution of animal domestication. *Ann. Rev. Ecol. Evol. Syst.* 45, 115–136.
- Lavretsky, P., Janzen, T., McCracken, K.G., 2019. Identifying hybrids & the genomics of hybridization: Mallards & American black ducks of Eastern North America. *Ecol. Evol.* 9 (6), 3470–3490. <https://doi.org/10.1002/ece3.4981>.
- Lavretsky, P., McInerney, N.R., Mohl, J.E., Brown, J.I., James, H.F., McCracken, K.G., Fleischer, R.C., 2020. Assessing changes in genomic divergence following a century of human-mediated secondary contact among wild and captive-bred ducks. *Mol. Ecol.* 29 (3), 578–595.
- Lavretsky, P., Mohl, J., Söderquist, P., Kraus, R.H., Schummer, M.L., Brown, J.I., 2023. *Manhandling mallards: The conservation paradox of feral populations and the meaning of wild*. *Commun. Biol.* 6 (1), 819.
- Leclère, D., Obersteiner, M., Barrett, M., Butchart, S.H.M., Chaudhary, A., De Palma, A., DeClerck, F.A.J., Di Marco, M., Doelman, J.C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J.P., Hill, S.L.L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G.M., Ohashi, H., Popp, A., Purvis, A., Schipper, A. M., Tabeau, A., Valin, H., van Meijl, H., van Zeist, W.-J., Visconti, P., Alkemade, R., Almond, R., Bunting, G., Burgess, N.D., Cornell, S.E., Di Fulvio, F., Ferrier, S., Fritz, S., Fujimori, S., Grooten, M., Harwood, T., Havlík, P., Herrero, M., Hoskins, A. J., Jung, M., Kram, T., Lotze-Campen, H., Matsui, T., Meyer, C., Nel, D., Newbold, T., Schmidt-Traub, G., Stehfest, E., Strassburg, B.B.N., van Vuuren, D.P., Ware, C., Watson, J.E.M., Wu, W., Young, L., 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* 585, 551–556. <https://doi.org/10.1038/s41586-020-2705-y>.
- Leopold, A., 1933. *Game Management*. University of Wisconsin Press, Madison.
- Leopold, A.S., 1944. The nature of heritable wildness in turkeys. *Condor* 46, 133–197. <https://doi.org/10.2307/1364213>.
- Li, Z.W.D., Bloem, A., Delany, S., Martakis, G., Quintero, J.O., 2009. *Status of Waterbirds in Asia - Results of the Asian Waterbird Census: 1987–2007*. Wetlands International, Kuala Lumpur, Malaysia.
- Lincoln, F.C., 1934. Restocking of marshes with hand-reared mallards not proved practicable. *Yearb. Agric.* 310–313.
- Luniak, M., 2004. *Synurbization—adaptation of animal wildlife to urban development*. In: *Proceedings 4th International Urban Wildlife Symposium*. University of Arizona, Tucson, pp. 50–55.
- Madden, J.R., 2021. How many gamebirds are released in the UK each year? *Eur. J. Wildl. Res.* 67, 72. <https://doi.org/10.1007/s10344-021-01508-z>.
- Mamuris, S., Sfougaris, A.I., Stamatis, C., 2001. Genetic structure of Greek brown hare (*Lepus europaeus*) populations as revealed by mtDNA RFLP-PCR analysis: implications for conserving genetic diversity. *Biol. Conserv.* 101 (2), 187–196.
- McDowell, N., 2002. Stream of escaped farm fish raises fears for wild salmon. *Nature* 416, 571.
- McGinnity, P., Prodöhl, P., Ferguson, A., Hynes, R., O'Maoiléidigh, N., Baker, N., Cotter, D., O'Hea, B., Cooke, D., Rogan, G., et al., 2003. Fitness reduction and



- potential extinction of wild populations of Atlantic salmon, *Salmo salar*, as a result of interactions with escaped farm salmon. *Proc. R. Soc. Lond. Series B: Biol. Sci.* 270, 2443–2450.
- McGinnity, P., Jennings, E., deEyo, E., Allott, N., Samuelsson, P., Rogan, G., Whelan, K., Cross, T., 2009. Impact of naturally spawning captive-bred Atlantic salmon on wild populations: depressed recruitment and increased risk of climate-mediated extinction. *Proc. R. Soc. B: Biol. Sci.* 276, 3601–3610. <https://doi.org/10.1098/rspb.2009.0799>.
- Meybeck, M., 2003. Global analysis of river systems: from earth system controls to Anthropocene syndromes. *Phil. Trans. R. Soc. London. Series B: Biol. Sc.* 358, 1935–1955.
- Miller, C.A., Ahlers, A.A., 2017. Where does the money go? Awareness of federal duck stamp fund expenditures among Illinois waterfowl hunters. *Human Dim. Wildl.* 22, 291–294.
- Milner, J.M., Nilsen, E.B., Andreassen, H.P., 2007. Demographic side effects of selective hunting in ungulates and carnivores. *Cons. Biol.* 21, 36–47.
- Moussy, C., Quaintenne, G., Gaudard, C., 2022. Comptage des Oiseaux d'eau à la mi-janvier en France. Résultats 2022 du comptage Wetlands International. In: LPO BirdLife France - Service Connaissance, Wetlands International, Ministère de la Transition écologique et de la Cohésion des territoires (30 pp. & annexes 101 pp., Rochefort).
- Mysterud, A., 2010. Still walking on the wild side? Management actions as steps towards 'semi-domestication' of hunted ungulates. *J. Appl. Ecol.* 47, 920–925. <https://doi.org/10.1111/j.1365-2664.2010.01836.x>.
- Nagy, S., Langendoen, T., 2020. Flyway Trend Analyses Based on Data from the African-Eurasian Waterbird Census from the Period of 1967–2018. Online publication. Wetlands International, Wageningen, The Netherlands. <http://iwc.test.wetlands.org/index.php/aewatrends8>.
- Nagy, S., Silarova, E., Skorpilová, J., Teufelbauer, N., Seaman, B., Derouaux, A., Hristov, I., Ieronymidou, C., Reif, J., Eskildsen, D.P., Lehikoinen, A., Fontaine, B., Jiguet, F., Trautmann, S., Portolou, D., Lewis, L., Aunins, A., Kurlavičius, P., Redel, C., van Turnhout, C., Jostein Øien, I., Källås, J.A., Chodkiewicz, T., Alonso, H., Benkó, Z., Ridzón, J., Kmecl, P., Molina, B., Lindström, Å., Schmid, H., Strebler, N., Noble, D., 2020. Trends of Breeding Waterbird Populations in Europe Based on the Pan-European Common Bird Monitoring Scheme Data. Pan-European Common Bird Monitoring Scheme and Wetlands International, Wageningen, The Netherlands.
- Nichols, J.D., Runge, M.C., Johnson, F.A., Williams, B.K., 2007. Adaptive harvest management of North American waterfowl populations: a brief history and future prospects. *J. Orn.* 148, 343–349. <https://doi.org/10.1007/s10336-007-0256-8>.
- Nicholson, E.M., 1951. *Birds and Men*. Collins New Naturalist Library, London.
- Nuorteva, P., 1971. The synanthropy of birds as an expression of the ecological cycle disorder caused by urbanization. *Ann. Zool. Fenn.* 8, 547–553.
- Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. *TREE* 19 (1), 18–24. <https://doi.org/10.1016/j.tree.2003.09.010>.
- Otto, S.P., 2018. Adaptation, speciation and extinction in the Anthropocene. *Proc. R. Soc. B* 285, 20182047. <https://doi.org/10.1098/rspb.2018.2047>.
- Owen, M., Black, J.M., 1990. *Waterfowl Ecology*. Blackie, Glasgow & London.
- Owen, M., Cook, W.A., 1977. Variations in body weight, wing length and condition of mallard *Anas platyrhynchos* and their relationship to environmental changes. *J. Zool.* 183 (3), 377–395.
- Pandolfi, J.M., 2009. Evolutionary impacts of fishing: overfishing's 'Darwinian debt'. *F1000 Biol. Rep.* 1, 43 (doi:10.3410).
- Pernollet, C.A., Guelmami, A., Green, A.J., Curcò Masip, A., Dies, B., Bogliani, G., Tesio, F., Brogi, A., Gauthier-Clerc, M., Guillemain, M., 2015. A comparison of wintering duck numbers among European rice production areas with contrasting flooding regimes. *Biol. Conserv.* 186, 214–224.
- Raftovich, R.V., Fleming, K.K., Chandler, S.C., Cain, C.M., 2021. Migratory Bird Hunting Activity and Harvest During the 2019–20 and 2020–21 Hunting Seasons. US Fish and Wildlife Service, Laurel, Maryland, USA.
- Randi, E., 2008. Detecting hybridization between wild species and their domesticated relatives. *Mol. Ecol.* 17, 285–293. <https://doi.org/10.1111/j.1365-294X.2007.03417.x>.
- Reeber, S., 2015. *Wildfowl of Europe. Asia and North America*, Christopher Helm, London.
- Rhymer, J.M., Simberloff, D., 1996. Extinction by hybridization and introgression. *Ann. Rev. Ecol. Syst.* 27, 83–109.
- Rose, P., Roper, A., Banks, S., Giorgio, C., Timms, M., Vaughan, P., Hatch, S., Halpin, S., Thomas, J., O'Brien, M., 2022. Evaluation of the time-activity budgets of captive ducks (Anatidae) compared to wild counterparts. *Appl. Anim. Behav. Sci.* 251, 105626. <https://doi.org/10.1016/j.applanim.2022.105626>.
- Ruiz-Fons, F., Vicente, J., Vidal, D., Höfle, U., Villanúa, D., Gauss, C., Segalés, J., Almería, S., Montoro, V., Gortázar, C., 2006. Seroprevalence of six reproductive pathogens in European wild boar (*Sus scrofa*) from Spain: the effect on wild boar female reproductive performance. *Theriogenology* 65, 731–743. <https://doi.org/10.1016/j.theriogenology.2005.07.001>.
- Sarrazin, F., Lecomte, J., 2016. Evolution in the Anthropocene. *Science* 351 (6276), 922–923. <https://doi.org/10.1126/science.aad6756>.
- Sauter, A., Korner-Nievergelt, F., Jenni, L., 2010. Evidence of climate change effects on within-winter movements of European mallards *Anas platyrhynchos*. *Ibis* 152 (3), 600–609.
- Scandura, M., Iacolina, L., Apollonio, M., 2011. Genetic diversity in the European wild boar *Sus scrofa*: phylogeography, population structure and wild x domestic hybridization: genetic variation in European wild boar. *Mammal Rev.* 41, 125–137. <https://doi.org/10.1111/j.1365-2907.2010.00182.x>.
- Schummer, M.L., Kaminski, R.M., Raedeke, A.H., Graber, D.A., 2010. Weather-related indices of autumn–winter dabbling duck abundance in Middle North America. *J. Wildl. Manag.* 74, 94–101. <https://doi.org/10.2193/2008-524>.
- Scott, D.A., Rose, P.M., 1996. *Atlas of Anatidae Populations in Africa and Western Eurasia*. Wetlands International Publication 41, Wageningen, The Netherlands.
- Sellers, R.M., Greenwood, J.J.D., 2018. Sir Richard Graham and the marking of ducks at Netherby, Cumberland, 1908–1933 – an early bird-ringing project. *Ring. Mig.* 33 (2), 86–93. <https://doi.org/10.1080/03078698.2018.1629151>.
- Shrubb, M., 2013. Feasting, fowling and feathers. In: *A History of the Exploitation of Wild Birds*. T. & A.D. Poyser, London.
- Smalley, A.L., Reeves, H.M., 2022. *The Market in Birds: Commercial Hunting, Conservation, and the Origins of Wildlife Consumerism, 1850–1920*. John Hopkins University Press, Baltimore.
- Smith, W.J., Sendell-Price, A.T., Fayet, A.L., Schweizer, T.M., Jezierski, M.T., van de Kerkhof, C., Sheldon, B.C., Ruegg, K.C., Kelly, S., Turnbull, L.A., Clegg, S.M., 2022. Limited domestic introgression in a final refuge of the wild pigeon. *iScience* 25, 104620.
- Smol, J.P., Wolfe, A.P., Birks, H.J.B., Douglas, M.S., Jones, V.J., Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D., 2005. Climate-driven regime shifts in the biological communities of arctic lakes. *PNAS* 102, 4397–4402.
- Söderquist, P., 2015. *Large-Scale Releases of Native Species: The Mallard as a Predictive Model System* (PhD thesis). Swedish University of Agricultural Sciences, Umeå, Sweden.
- Söderquist, P., Norrström, J., Elmberg, J., Guillemain, M., Gunnarsson, G., 2014. Wild mallards have more “goose-like” bills than their ancestors: a case of anthropogenic influence? *PLoS One* 9 (12), e115143.
- Söderquist, P., Elmberg, J., Gunnarsson, G., Thulin, C.G., Champagnon, J., Guillemain, M., Kreisinger, J., Prins, H.H., Crooijmans, R.P., Kraus, R.H., 2017. Admixture between released and wild game birds: a changing genetic landscape in European mallards (*Anas platyrhynchos*). *Eur. J. Wildl. Res.* 63 (6), 1–13.
- Söderquist, P., Gunnarsson, G., Elmberg, J., Dessborn, L., 2021. Survival of wild and farmed-released mallards: the Swedish example. *Eur. J. Wildl. Res.* 67, 19. <https://doi.org/10.1007/s10344-021-01465-7>.
- Solokha, A., Gorokhovskiy, K., 2017. Estimating waterbird harvest in Russia. *Suomen Riista* 63, 43–52.
- Stafford, L., 2010. *Mallard Strategy for South Africa*. National Problem Bird Forum/CAPE Invasive Animal Working Group Report, South Africa.
- Tamisier, A., Dehorter, O., 1999. *Camargue, canards et foulques*. Centre Ornithologique du Gard, Nîmes.
- Tamisier, A., Grillas, P., 1994. A review of habitat changes in the Camargue: an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. *Biol. Conserv.* 70, 37–47.
- Tanabe, Y., 1995. History and phylogeny of Japanese native animals and strategies for their effective use. In: *The Third Ministry of Agriculture, Forestry and Fisheries, Japan (MAFF) International Workshop on Genetic Resources - Animal Genetic Resources: Efficient Conservation and Effective Use*. Agriculture, Forestry and Fisheries Research Council Secretariat, pp. 17–36.
- Telfair II, R.C., 2006. *Cattle egret (Bubulcus ibis)*, version 2.0. In: Poole, A.F. (Ed.), *The Birds of North America*. Cornell Lab of Ornithology, Ithaca, NY, USA, Ithaca, NY, USA.
- Thibault, J.-C., Daycard, L., Guyot, I., 1990. La reproduction du Pigeon biset *Columba livia* sur les îlots de Corse. *L'oiseau et R.F.O.* 60, 110–117.
- Thomas, G.J., 1981. Field feeding by dabbling ducks around the Ouse Washes, England. *Wildfowl* 32, 69–78.
- Thomson, G.M., 2011. *The Naturalisation of Animals and Plants in New Zealand*. Cambridge University Press, Cambridge, UK.
- Tomiałojć, L., 1970. Quantitative studies on the synanthropic avifauna of Legnica and its environs. *Acta Ornithol.* 21, 293–392.
- U.S. Fish and Wildlife Service, 2013. *Review of Captive-Reared Mallard Regulations on Shooting Preserves*. Division of Migratory Bird Management, Washington D.C., USA.
- U.S. Fish and Wildlife Service, 2022a. *Waterfowl Population Status, 2022*. U.S. Department of the Interior, Washington D.C., USA.
- U.S. Fish and Wildlife Service, 2022b. *Adaptive Harvest Management: 2023 Hunting Season*. U.S. Department of the Interior, Washington D.C., USA, p. 68.
- Veon, J., 2021. *Body Mass and Body Condition Variation of Mallards (Anas platyrhynchos) within and among Winters within the Lower Mississippi Alluvial Valley* (M.Sc. thesis). University of Arkansas, USA.
- Vittecoq, M., Grandhomme, V., Champagnon, J., Guillemain, M., Crescenzo-Chaigne, B., Renaud, F., Thomas, F., Gauthier-Clerc, M., van der Werf, S., 2012. High influenza A virus infection rates in mallards bred for hunting in the Camargue, South of France. *PLoS ONE* 7, e43974. <https://doi.org/10.1371/journal.pone.0043974>.
- Wells, C.P., Lavretsky, P., Sorenson, M.D., Peters, J.L., DaCosta, J.M., Turnbull, S., Ueyhara, K.J., Malachowski, C.P., Dugger, B.D., Eadie, J.M., Engilis, A.J., 2019. Persistence of an endangered island endemic, an introduced congener, and multiple hybrid swarms across the main Hawaiian islands. *Mol. Ecol.* 28, 5203–5216.
- Wetlands International, 2023. *Waterbird Populations Portal*. [wpp.wetlands.org](http://wpp.wetlands.org).
- Wiener, P., Wilkinson, S., 2011. Deciphering the genetic basis of animal domestication. *Proc. R. Soc. B* 278, 3161–3170. <https://doi.org/10.1098/rspb.2011.1376>.
- Williams, M., 2017. The changing relative abundance of grey duck (*Anas superciliosa*) and mallard (*A. platyrhynchos*) in New Zealand. *NOTORNIS* 64, 211–228.
- Williams, B.K., Nichols, J.D., Conroy, M.J., 2002. *Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making*. Academic Press, San Diego, USA.
- Wuerthner, G., Crist, E., Butler, T., 2014. *Keeping the Wild: Against the Domestication of Earth*. Island Press, Washington, USA.

- Yerkes, T., Bluhm, C., 1998. Return rates and reproductive output of captive-reared female mallards. *J. Wildl. Manage.* 62 (1), 192–198.
- Young, G., 2005. Northern mallard *Anas platyrhynchos*. In: Kear, J. (Ed.), *Ducks, Geese and Swans*. Oxford University Press, UK, pp. 513–517.
- Zilhão, J., Angelucci, D.E., Igreja, M.A., Arnold, L.J., Badal, E., Callapez, P., Cardoso, J. L., d'Errico, F., Daura, J., Demuro, M., Deschamps, M., Dupont, C., Gabriel, S.,

- Hoffmann, D.L., Legoinha, P., Matias, H., Monge Soares, A.M., Nabais, M., Portela, P., Queffelec, A., Rodrigues, F., Souto, P., 2020. Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science* 367, eaaz7943. <https://doi.org/10.1126/science.aaz7943>.