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► **To cite this version:**

Jocelyn Champagnon, Johan Elmberg, Matthieu Guillemain, Philip Lavretsky, Robert G Clark, et al.. Silent domestication of wildlife in the Anthropocene: The mallard as a case study. *Biological Conservation*, 2023, 288, pp.110354. 10.1016/j.biocon.2023.110354 . hal-04299537

HAL Id: hal-04299537

<https://hal.science/hal-04299537v1>

Submitted on 22 Nov 2023

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1 **Silent domestication of wildlife in the Anthropocene: the mallard**
2 **as a case study**

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14 **Short title:** Mallard and the Anthropocene

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16 **Key-words:** adaptation, evolution, hybridization, selection, speciation

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19 **Type of paper:** Perspectives

20
21 **ABSTRACT**

22 In the Anthropocene, human activities have been a dominant force affecting wildlife, natural
23 habitats, and climate worldwide. Over time, increasing incidences of wildlife-human

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

38

39 **INTRODUCTION**

40 Although 'the Anthropocene' as a scientific concept remains debated in geology and
41 environmental science (e.g. Wuerthner et al., 2014), it is unquestionable that human activities
42 for some time have been a dominant force affecting wildlife, natural habitats, and climate
43 worldwide. The first articles in conservation biology and biodiversity research adopting the
44 Anthropocene as a concept appeared in the early 2000s (Meybeck, 2003; Smol et al., 2005).
45 These have been followed by a large number of studies highlighting grave concerns about the
46 profound changes to the world's natural ecosystems due to human impacts (Dirzo et al.,
47 2014; Ceballos et al., 2015; IPBES, 2019).

48 Measures to mitigate negative human footprint have mainly focused on protection of
 49 habitats and species, recently also on ecosystem services and socio-ecological issues (Leclère
 50 et al., 2020). However, one important aspect of change in the Anthropocene has received
 51 much less attention, namely the distinction between wild and non-wild. By definition, truly
 52 wild plants and animals are unaffected by human impact, while genuinely non-wild forms are
 53 typically domesticated via deliberate processes of artificial selection. Such processes can span
 54 active management of wild species such as large herbivores through feeding, predator control
 55 or fencing, to the return of some domesticated forms to the wild (e.g. feral horses). This
 56 makes it increasingly difficult to distinguish between wild and non-wild species today
 57 (Mysterud, 2010). The nature and strength of the relationship between wildlife (especially
 58 birds) and humans has long received scientific attention (e.g. Nicholson, 1951). A gradient
 59 exists from purely wild to purely domestic, with intermediate and overlapping situations such
 60 as synanthropic or feral (e.g. Tomiałojć, 1970; Nuorteva, 1971; Johnston, 2001; Table 1).
 61 Here, we argue that incremental slow changes along the wild-non-wild continuum can have
 62 severe ecological, evolutionary, zoonotic, social, and economic consequences.

Table 1
 Status of relationships between animals and humans (based on Tomiałojć, 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 Synanthropic	Benefiting from the use of human environments (a particular case of synanthropy). 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.

63

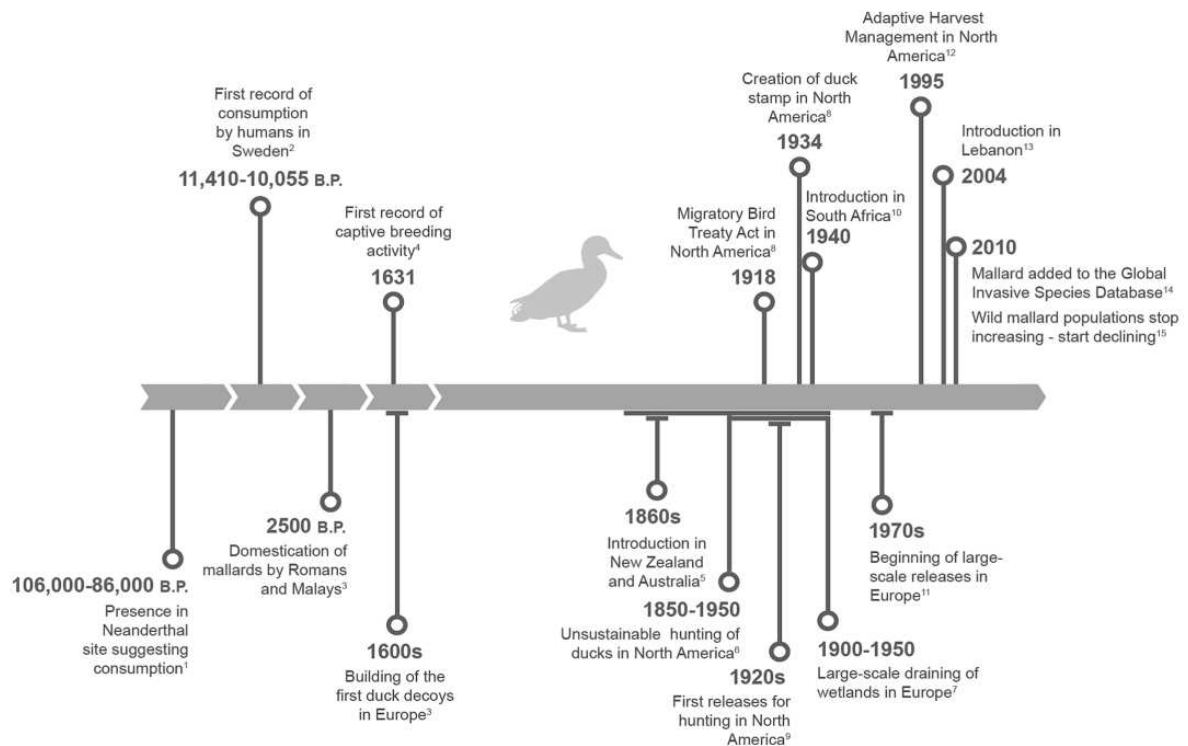
64 Interactions between wildlife and anthropogenic environments have increased in intensity
 65 and geographic extent over time. Additionally, many parts of the world have seen a change
 66 from a patchwork of areas that are either wild or anthropogenic, to a situation where truly

67 wild patches are lost entirely or remain only as small, isolated islands in human-modified
68 landscapes. This begs the questions of what wildness means today (cf. Leopold, 1944) and
69 how changes to landscapes with few or no truly wild areas affect the species living in them
70 (Fricke et al., 2022). For some species already living or prone to living close to humans
71 (anthropophilic) this development may represent an opportunity in terms of population
72 growth and subsequent spread of their genes, but beyond some threshold, or for other species,
73 it may compromise their wild status.

74 Apart from climate change and loss of natural habitats, living close to humans can affect
75 wildlife in several ways. Some populations are exploited so that age structure and genetic
76 diversity are altered (Allendorf et al., 2008; Milner et al., 2007). Other species face alien
77 invasive species that may increase competition and introduce new diseases (Crowl et al.,
78 2008). Another threat to genuine wildness is domestication (e.g., Diamond, 2002; Wiener and
79 Wilkinson, 2011; Larson and Fuller, 2014). Domestication becomes a serious problem for
80 wild conspecifics when they are removed from their environment to the point of becoming
81 rare or where they interact increasingly with domestic individuals or their descendants. The
82 latter process erodes local adaptations and genetic integrity of wild populations, which can
83 have strong evolutionary consequences (Laikre et al., 2010; Olden et al., 2004; Rhymer and
84 Simberloff, 1996). For instance, a case of releasing wild rabbits *Oryctolagus cuniculus* for
85 hunting led to mixing of two distinct evolutionary lineages in the wild (Delibes-Mateos et al.,
86 2008).

87 Many species of the order Anseriformes (e.g., swans, geese, and ducks) provide
88 illustrative examples of the issues mentioned above. Humans have affected them by over-
89 exploitation, habitat loss, domestication, translocation to new areas, and supplementing wild
90 populations with farmed birds to increase hunting opportunities (Kear, 1990). Among

91 Anseriform birds, the mallard duck *Anas platyrhynchos* is a prime example of a species that
 92 has been tightly interlinked and managed by humans. Being domesticated at very large scales
 93 while still being one of the most abundant and widespread waterfowl species globally, it also
 94 remains a valuable model species for management of wild populations (e.g., Anderson and
 95 Burnham, 1976) and for the study of zoonotic diseases (e.g., Jourdain et al., 2010).



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

97 Indeed, there are few other species for which so much management effort has been made
 98 to secure a favourable conservation status in combination with high harvest levels; the
 99 mallard was the model species for major advances in research on the consequences of harvest
 100 levels (e.g. Anderson & Burnham 1976), including being the primary species for which the
 101 North American waterfowl adaptive harvest management plan was developed (e.g. Chapter
 102 25 in Williams et al. 2001). Given the wealth of background information and the long history
 103 of interaction with humans (Figure 1), the mallard provides an excellent case for exploring

104 compromised wildness in the Anthropocene. We explore this issue by addressing the
105 intertwined history of humans and mallards, and discuss implications for less well-studied
106 species. In particular, we ask whether the mallard's present status is a success story
107 considering its traits, genetics and dynamics; or if we are rather witnessing a thought-
108 provoking example of demise through cryptic domestication and high vulnerability to future
109 global changes. We address this question by presenting empirical evidence from the literature
110 in the fields of ecology, evolution, zoonotic, sociology, economics, genetics, and population
111 dynamics. However, as a *Perspectives* paper, we provide opinions based on selected
112 references from a variety of scientific fields.

113

114 **The mallard example and model**

115 **Traits of the wild mallard**

116 The mallard is a classic example of a generalist species that has evolved many plastic and
117 successful physiological and life history traits. First, it is among the largest duck species
118 worldwide, with a mean body mass of males and females being ca. 1,200 and ca. 1,000
119 grams, respectively (Cramp and Simmons, 1977, page 518). For a migratory species
120 venturing into remote northern areas during the breeding season, its size provides benefits in
121 terms of capacity to endure cold temperatures (Figure 2). Large body size also permits
122 spending the winter at higher latitudes close to and even beyond the zero-degree isotherm,
123 thus a position closer to nesting areas. This saves long and costly migration journeys such as
124 those undertaken by related smaller species (Schummer et al., 2010; Dalby, 2013).

125 In French etymology the name "mallard" is actually considered to be related to the
126 boldness of these birds (Kear, 1990, p 225). Their physiological advantages translate to

127 generally higher annual survival rates than in smaller *Anas* species, i.e., adult male mallard
128 *versus* green-winged teal *Anas carolinensis* have survival rates of 62-68% and 55%,
129 respectively (Devineau et al., 2010; Baldassarre, 2014, pages 403-409; note that these rates
130 include hunting mortality). Although generation time is about 2.5 years, the longevity records
131 for wild mallards are 27.5 and 17.5 years for males and females, respectively (Baldassarre,
132 2014). In addition to being large, hardy birds with potentially high longevity, mallards also
133 have traits that are typical of an r-selected species, including the capacity to breed in the first
134 year of life, high fecundity (i.e., average clutch of ca. 9 eggs), and even producing multiple
135 clutches in a single breeding season (review in Baldassarre, 2014). Coupling these flexible
136 annual life-history traits with their migratory capacity (Scott and Rose, 1996; Li, 2009;
137 Baldassarre, 2014) explains the mallard's Holarctic distribution and occurrence across
138 wetland types up to 2,000 meters a.s.l. (Cramp and Simmons, 1977, page 508). Moreover,
139 such traits potentially allow for considerable mixing of individuals over a wide geographic
140 range, explaining why molecular work generally finds weak to no genetic structure
141 geographically among wild mallards (Kraus et al., 2013; 2016; Lavretsky et al. 2023). The
142 widespread occurrence of mallard remains in excavations or as fossils across Europe (e.g.,
143 Sweden in the Pleistocene, Late Glacial and Holocene periods: Ericson and Tyrberg, 2004,
144 pages 32-42; Bulgaria in the Middle Holocene in Boev 2018) and North America (e.g.,
145 Yukon in the Pleistocene: Fitzgerald, 1991; Idaho in the upper Pliocene: Brodkorb 1958 and
146 California in the late Holocene: Broughton 2004) supports that the current Holarctic
147 distribution was already established in prehistoric times. In evolutionary terms the mallard
148 has successfully colonized a huge geographic area, where it is often abundant, exemplifying
149 an outstanding evolutionary success story.

150

151 **Win-win situation from the human-mallard interaction**

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

167 Besides wild individuals, humans and mallards developed a tight relationship as
168 civilizations began to domesticate the species ca. 2,000 years ago somewhere in Eurasia
169 (Kear, 1990; see also Boessneck, 1979 in Larson and Fuller, 2014; Figure 1). Generally, the
170 mallard’s demonstrated capacity to readily tolerate captive conditions explains the success of
171 its domestication (e.g. Rose et al., 2022), permitting people to further select favourable life-
172 history traits resulting in larger body size, longer egg-laying seasons, and larger clutches (i.e.,
173 some breeds being able to produce one egg daily over periods of several months; Chapter 2 in
174 Kear, 1990). As a result, apart from the domestication of the muscovy duck *Cairina*

175 *moschata* in South America, farmed ducks today largely originate from the mallard (Reeber,
176 2015, page 364), with tens of breeds selected for meat and/or egg-production qualities. These
177 long-standing interactions have even resulted in an integrated farming system in Asia that is
178 developed around such domestic mallards (e.g., Pekin ducks), combining rice, duck, and fish
179 farming (e.g. Furuno, 2001). In addition to being farmed as poultry, many ornamental mallard
180 breeds exist, in which specific phenotypes of conspicuous male plumage have been
181 exaggerated through selective breeding (e.g., crested duck in Figure 19 of Lack, 1974).
182 Moreover, the tameness of the species, and the ease with which it can settle into new
183 environments have long made it very popular in zoos, parks, and gardens (reviews in Young,
184 2005; Guillemain et al., 2020). The mallard's success story as a domestic bird is also
185 exemplified by their importance to the farming industry, as over half a billion farmed
186 mallards are sold worldwide annually for human food consumption (Tanabe, 1995). Taken
187 together, it can be argued that domestication has benefited the mallard in the sense that there
188 are so many copies of its genes spread over the world in duck farms.

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

200 substantially to the free-flying population, especially in Europe and during the beginning of
201 the hunting season (Champagnon et al., 2016a, 2016b; Söderquist et al., 2021). Such efforts
202 continue today as mallards are prized by hunters on both sides of the North Atlantic, with an
203 annual harvest estimated at ca. 4 million in Europe (including Russia) and ca. 3 million in
204 North America (Guillemain et al., 2016; Solokha and Gorokhovskiy, 2017; Raftovich et al.,
205 2021). In some countries the mallard is the only hunted duck or comprises nearly the entire
206 duck harvest (e.g., Hungary, Netherlands). Consequently, it can be considered a proximate
207 driver of the hunting economy in many countries, explaining the mallard's present socio-
208 economic importance (Green and Elmberg, 2014).

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

221

222 **The mallard today - success or cryptic demise?**

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

232 By constantly releasing farmed mallards, many genomic combinations have been 'tested',
233 and eventually some likely flourished in the Anthropocene. Over the last 50 years, wild-
234 living mallards have increased by 5-10% in body mass in Europe (Guillemain et al., 2010,
235 Gunnarsson et al. 2012) and North America (Veon, 2021). This can partly be explained by a
236 growing reliance on artificial habitats with food such as spilled agricultural grains (Owen and
237 Cook, 1977; Bengtsson et al., 2014), and supplemental food intended to support released
238 mallards for hunting (Guillemain et al., 2010). Present-day mallards have more goose-like
239 bills with a lower density of lamellae (comb-like structures on the edges of the bill) than their
240 wild European ancestors (Champagnon et al., 2010; Söderquist et al., 2014), reflecting such
241 changes in foraging habits. Decreased lamellar density likely results from greater reliance on
242 human-provided larger food items (e.g., poultry pellets), but in-turn leading to a reduced
243 capacity to extract small natural food items such as seeds and micro-invertebrates (Halligans
244 2023). Additionally, mallard migratory habits have changed over the last 50 years, with some
245 populations becoming increasingly short-distance migrants, while others are already
246 completely sedentary (Sauter et al., 2010; Gunnarsson et al., 2012; Guillemain et al., 2015).
247 Changes in migratory behaviour can potentially result in reduced gene flow in what has long

248 been considered a panmictic species, and may explain recently identified substructuring
249 among wild mallards from Eurasia and North America (Lavretsky et al., 2023).

250 Although climate change is likely a contributing factor explaining some behavioural
251 changes, other factors (i.e., improved feeding conditions in some areas) are likely to be
252 involved as well, including hybridization with released farmed mallards. The latter are less
253 prone to migrate compared to wild, even when releases occur at or close to northern breeding
254 areas (Lincoln, 1934; Boyd and Harrison, 1962; Fog, 1964; Söderquist, 2015). An important
255 aspect of large-scale releases of farmed mallards is the subsequent introgression of ‘farm
256 genes’ into the wild population by two main mechanisms leading to hybridization: a) wild
257 mallards encounter domesticated stock in anthropogenic environments, and b) released
258 farmed birds survive the hunting season and mix with resident or migratory wild mallards
259 (Čížková et al., 2012; Champagnon et al., 2013; Baratti et al., 2015; Söderquist et al., 2017;
260 Lavretsky et al., 2020). Of the many domesticated breeds, recent molecular analyses have
261 determined that interbreeding with game-farm mallard strains is the greatest genetic threat to
262 wild mallard populations. Indeed data suggest that interbreeding between an artificially-
263 selected and inbred game-farm lineage is not only resulting in reduced genetic variation (i.e.,
264 inbreeding), but is replacing important genetic variation born from millenia of natural
265 selection with ones established in captivity (i.e., outbreeding depression; Söderquist et al.
266 2017; Lavretsky et al., 2020; 2023). Unlike most domestic strains bred for consumption or
267 ornaments (Chapter 2 in Kear, 1990), the game-farm mallard was specifically bred to
268 supplement wild populations. The first record of such breeding activity can be dated to 1631
269 in England, by orders of King Charles II to begin propagation for hunting, and eggs from
270 wild mallards were brought into captivity (Leopold, 1933; Figure 1). Moreover, the first use
271 of game-farm mallard can be attributed to the establishment of formal breeding and ringing
272 operations in the 1890s in England (Sellers and Greenwood, 2018). Thus, the game-farm

273 mallard breed has developed over the last 400 years. The success of this captive-breeding
274 process is the source of today's self-sustaining feral mallard populations in Hawaii and New
275 Zealand (Lavretsky et al., 2023). Consequently, Hawaiian ducks *Anas wyvilliana* and grey
276 ducks *Anas superciliosa* are nowadays relegated to a specific island (Wells et al. 2019) or
277 limited locations (Williams, 2017), respectively.

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

295 The blurred distinction between wild and captive mallards may reduce interest among
296 some managers and the public in the conservation of this species, and consequently, valuable

297 wetland habitats. The perceived value of the species may be reflected by the observation that
298 mallard tarsal rings are less frequently reported when found by hunters or the general public
299 than are the rings of another purely wild migratory species (Eurasian Teal *Anas crecca*;
300 Guillemain et al. 2011). These releases lack much-needed follow-up programs (Laikre et al.,
301 2006), which raises doubts about the origin of mallards (are they all pure, mixed or all
302 captive?). However, a landscape genetic study of North American mallards found that higher
303 levels of introgressive hybridization occur in the eastern parts of the continent, and decrease
304 westward (Lavretsky et al. 2019). Importantly, the proportion of populations consisting of
305 game-farm or hybrid ducks corresponded geographically to where most game-farm mallard
306 releases occur today. We note that the genetic contributions of captive-bred mallards could
307 have significant impacts on survival and fecundity parameters of wild mallard populations, as
308 shown in red-legged partridges *Alectoris rufa* and Atlantic salmon *Salmo salar* (Casas et al.,
309 2012; McGinnity et al., 2003). Finally, the mixing of mallards with captive and wild genes
310 violates any one-population assumptions made in current wildlife management models (e.g.,
311 mallard adaptive harvest management in North America; U.S. Fish and Wildlife Service,
312 2022b), which for instance do not account for the possible coexistence of categories of
313 individuals with different survival rates (i.e., the demographic heterogeneity demonstrated in
314 Grzegorzcyk, 2023).

315 Whether mallard populations will eventually succumb to the fate of being sustained by
316 continued stocking practices is unknown, but when supplementation of captive-bred
317 individuals in the wild is initiated, it rarely ends (e.g., Araki et al. 2009; Fraser 2008). This is
318 unfortunate because population declines are occurring where farmed mallards are being
319 released in large numbers annually (Dalby et al., 2013; Moussy et al., 2022). In Europe,
320 recent waterbird population estimates show a moderate decrease in the short term (10-year
321 period of 2008 – 2017) for the two flyways with good quality data (Northwest Europe and

322 Northern Europe/West Mediterranean; Nagy and Langendoen, 2020; Nagy et al., 2020).
323 Similarly, the estimated breeding population size for North American mallards in the Eastern
324 flyway, where >90% of farmed mallard releases occur, has experienced substantial declines
325 since the mid-1990s (U.S. Fish and Wildlife Service, 2013; Figure 5 in U.S. Fish and Wildlife
326 Service, 2022). Such declines have so far tended to be short term, and more research is
327 needed to prove a causal effect of hybridisation on population decline.

328 Massive releases of mallards may also produce negative consequences in terms of habitat
329 management. For example, to accommodate released birds, landowners sometimes engage in
330 actively hunting-oriented management of wetlands, which may provide basic habitat that is
331 attractive to mallard, but at the same time be detrimental to other components of biodiversity
332 such as plants (Tamisier & Grillas 1994). In addition, providing food *ad libitum* after releases
333 is likely to affect water quality, nutrient level, and predation pressure locally (Söderquist et
334 al., 2021). In southern France, marshes are sometimes managed specifically to harbour
335 released mallards instead of making such habitats attractive to wild conspecifics and
336 biodiversity in general (e.g., through artificial flooding disconnected from the natural rainfall
337 regime; Champagnon, 2011). Such artificial management of hunted wetlands may also
338 prevent waterbirds from adapting to climate change by shifting their geographic distribution,
339 and by promoting residency instead (Gaget et al., 2023). Finally, the mallard is considered an
340 invasive species in many countries where it has been widely introduced outside its natural
341 range, and can outcompete local waterbird species (Fox, 2009; Guillemain et al., 2020; GISD,
342 2023; Figure 1).

343 Given the long history of mallard domestication, and large numbers of farmed birds still
344 being released in the wild, one may question whether ‘pure’ ancestral mallards continue to
345 exist, and if the species is still wild at all. Recent genetic analyses provide contrasting results.

346 While free-living populations have been fundamentally changed by intensive releases of
347 farm-raised, game-farm mallards over the last century in North America and Eurasia, genetic
348 wild-type mallards still occur across the Holarctic (Champagnon et al., 2013; Söderquist et
349 al., 2017; Lavretsky et al. 2023), suggesting that at least for now some populations
350 genetically resist anthropogenic pressures.

351

352 **Discussion**

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

369 Depending on species, formerly clear distinctions between captive and purely wild
370 individuals have become progressively blurred.

371 Then, is it a problem if the distinction between wild and non-wild conspecifics vanishes?
372 Examples abound of species showing a flourishing demography (population increase and/or
373 range expansion) in regions under strong human influence: hunted ungulates benefit from
374 modern farming and forestry practices, as well as from declines of their natural predators, all
375 caused by humans (Mysterud, 2010). Snow geese *Chen caerulescens* (and many other goose
376 species in general) benefit from modern agriculture at the same time as climate change
377 reduces their energy needs, so that the population has increased enormously and become
378 difficult to control even with highly liberalized hunting regulations (e.g. Alisauskas et al.
379 2011). Glossy ibis *Plegadis falcinellus* expanded in Southern France in response to climate
380 change and human introduction of formerly exotic food sources (crayfish) (Champagnon et
381 al., 2019), and cattle egret *Bubulcus ibis* thrives by associating with livestock (Telfair, 2006).
382 Species with such ecology are able to remain largely wild even in present-day human-
383 modified ecosystems.

384 In many conservation programs, reintroduction of captive-bred conspecifics is the only
385 solution to save populations in the wild, although in these cases great care is often taken to
386 ensure captive-bred individuals remain as wild and shy of humans as possible (e.g., sandhill
387 crane *Grus canadensis*; Horwich 1989). But there are species that humans have used and
388 affected even more profoundly, in which the separation between wild and non-wild indeed
389 may be difficult to draw. Illustrative examples are common in the context of harvest such as
390 wild boar *Sus scrofa* (Scandura et al., 2011), Atlantic salmon (Ciborowski et al., 2007;
391 McDowell, 2002), Norway spruce *Picea abies* (Björkman and Bradshaw, 1996), brown hare
392 *Lepus europaeus* (Mamuris et al., 2001; Fickel et al., 2005), and European rabbit (Delibes-

393 Mateos et al., 2008). Many of these species have increased in abundance and/or range
394 enormously, but such apparent demographic success may conceal unwanted evolutionary
395 change. For instance, McGinnity et al. (2009) showed that massive restocking of Atlantic
396 salmon into a river with captive-bred individuals disrupted the capacity of natural populations
397 to adapt to higher winter temperatures. Similarly, the pathogen loads of wild individuals may
398 be higher in areas of extensive overlap with captive-reared, released animals (e.g., red-legged
399 partridges; Díaz-Sánchez et al., 2012; wild boar; Ruiz-Fons et al., 2006; or mallard; Vittecoq
400 et al., 2012).

401 The issue whether or not humans should actively manage wildlife populations
402 ('rewilding') or let natural equilibria occur is a lively scientific and ethical debate for the
403 Anthropocene, one that also questions the way we can and should conserve biodiversity
404 (Sarrazin and Lecomte, 2016; Otto, 2018). In general, economic interests such as hunting or
405 fishing drive intensive management. The consequence is a potential decrease in the value of
406 the species: in the case of hunted species, for instance, the value of the game animal for
407 hunters is directly related to its perceived wildness (Leopold 1933).

408 The value of wildness in itself is central to conservation science, so that gradual loss of
409 such a condition through a creeping domestication process may in itself raise ethical and
410 philosophical questions (e.g., Nash in Wuerthner et al., 2014). Furthermore, some may
411 consider that any alteration of the pristine wild nature of a species makes it lose most
412 conservation interest, so that it is not worth any further attention. The example of the rock
413 dove *Columba livia* is highly illustrative in this context as it was domesticated long ago to be
414 bred in farms and backyard gardens, but some individuals escaped and interbred with wild
415 rock doves. Genetic introgression from such marooned city and village birds is considered
416 one of the main threats to wild rock doves today (Johnston et al., 1988). Purely wild rock

417 dove populations have now disappeared from most places except in a few remote cliffs and
418 islands (e.g. Thibault et al., 1990; Smith et al., 2022), but this has occurred in a general
419 indifference, as most people do not even realize that this is also a wild species. Thankfully,
420 the mallard has not yet suffered the same fate, as wild mallards still exist, and they are
421 attracting the attention of a range of stakeholders, including conservationists and hunters
422 alike.

423 As shown by the mallard example, we should not be naïve towards apparent successes
424 based on current large population sizes alone, as they may mask behavioural, demographic
425 and/or genetic degradation. Such degradation may be an unenviable fate, in so far that the
426 species may not be able to survive in the future without human interventions. If such negative
427 changes are occurring in a species as adaptable and resistant as the mallard (Bellrose, 1995),
428 it is likely that significant processes remain overlooked in less common or more poorly
429 studied species. This would have important implications for conservation and management in
430 general. In particular, the extent of active management versus natural rewilding of habitats
431 and populations remains an important question when attempting to decrease the risk of
432 anthropomorphising systems. Will systems return to ‘normal’ by themselves in a world we
433 have changed so much? These issues are difficult to resolve, and they involve ethical,
434 sociological, and ecological aspects. However, the mallard case and lessons learned from
435 other species collectively offer a range of precautionary actions that may be taken:

436 1) Avoid loss of wild habitat (e.g., owing to urbanisation or agriculture) that would
437 increase contact between wild and domesticated/farmed populations. Habitat loss forces
438 species to depend on human-modified habitat (e.g., cranes *Grus* spp., geese *Anser* spp.,
439 *Branta* spp., and *Chen* spp.);

- 440 2) Emulate natural cycles and disturbance patterns when managing natural habitats (e.g.,
441 adhere to natural precipitation regimes in the case of artificial flooding), so as to favour
442 local wild species instead of accustoming exotics or promoting local adaptation to
443 artificial conditions;
- 444 3) Perform rewilding through habitat restoration rather than by population reintroduction
445 or reinforcement. The recovery of some species leads to improvement of habitats and
446 helps ecosystems emulate their ‘wild’ state, e.g., the return of the American bison *Bison*
447 *bison* and the Great Plains vegetation in areas formerly degraded by decades of
448 continuous cattle grazing;
- 449 4) Refrain as much as possible from releasing or introducing individuals of captive origin,
450 as a fraction of these will eventually interbreed with wild conspecifics, with
451 unpredictable demographic, behavioural, and genetic consequences;
- 452 5) When it is necessary to release/relocate wild individuals, do so away from captive
453 counterparts to avoid mixing and future loss of wild characteristics. What ‘away’ means
454 will depend on the mobility of the focal species;
- 455 6) For the same reason as in 5), do not start farming a species within the geographic range
456 of the same wild species. This is especially true for plants and insects where
457 confinement within a farmed area may be difficult (e.g., wind dispersal of pollen);
- 458 7) Put-and-take procedures for hunting and fishing should be avoided. Local wild
459 populations should instead be enhanced through habitat management. If unavoidable,
460 then aim to release individuals with low survival prospects (ideally dying naturally
461 before the next breeding season), or release sterile individuals to avoid crosses between
462 wild and farmed;

463 8) When (re)introduction is essential for conservation purposes, avoid contact with humans
464 during the captive phase in order to retain wild characteristics of released individuals as
465 much as possible. When releasing for future exploitation, do not try to ‘improve’
466 released strains for the reasons explained in 7); and,

467 9) Always mark released individuals to permit the study of their future fate in nature and
468 better assess the consequences of releases for the wild segment of the population.

469

470 We must appreciate that wildness develops over evolutionary time scales, but can be
471 eroded or extinguished by just years or decades of poor population management. Selective
472 exploitation of some phenotypes in a population can cause a ‘Darwinian debt’ by which
473 depressed genotypic variability requires extremely long periods to recover (e.g., Pandolfi,
474 2009). Similarly, losing the wild nature of plants and animals by undesirable habitat
475 alteration, inappropriate farming, and thoughtless releases may cause a similar Darwinian
476 debt left to future generations, preventing wild species from providing either beneficial
477 ecosystem services or the simple enjoyment of experiencing them unexpectedly in natural
478 environments.

479

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- 928

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

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944 **FIGURE 1:** Chronological timeline on a log scale illustrating key events in the relationship
945 between humans and mallard. B.P.: before present; ¹ Zilhão et al. (2020); ² Ericson and
946 Tyrberg (2004); ³ Kear (1990); ⁴ Leopold (1933); ⁵ Thomson (1922); ⁶ Smalley and Reeves
947 (2022); ⁷ Fluet-Chouinard et al. (2023); ⁸ Anderson et al. (2017); ⁹ Forbush (1925); ¹⁰ Stafford
948 (2010); ¹¹ Tamisier and Dehorter (1999); ¹² Nichols et al. (2007); ¹³ Banks et al. (2008);
949 ¹⁴ Global Invasive Species Database (2023); ¹⁵ Wetlands International (2023). Silhouette of
950 mallard by Maija Karala from PhyloPic (<http://phylopic.org/>) under a Creative Commons
951 licence (CC BY-NC-SA 3.0).
952

953 **Content (below)**

954 Presence in Neanderthal site suggesting consumption – 106,000-86,000 B.P. ¹

955 First record of consumption by humans in Sweden – 11,410-10,055 B.P. ²

956 Domestication of mallards by Romans and Malays – 2 500 B.P. ³

957 Building of the first duck decoys in Europe – 1600s ³

958 First record of captive breeding activity – 1631 ⁴

959 Introduction in New Zealand and Australia – 1860s ⁵

960 Unsustainable hunting of ducks in North America – 1850-1950 ⁶

961 Large-scale draining of wetlands in Europe – 1900-1950 ⁷

962 Migratory Bird Treaty Act in North America – 1918 ⁸

963 First releases for hunting in North America – 1920s ⁹

964 Creation of duck stamp in North America – 1934 ⁸

965 Introduction in South Africa – 1940 ¹⁰

966 Beginning of large-scale releases in Europe – 1970s ¹¹

967 Adaptive Harvest Management in North America – 1995 ¹²

968 Introduction in Lebanon – 2004 ¹³

969 Mallard added to the Global Invasive Species Database – 2010 ¹⁴

970 Wild mallard populations stop increasing – 2010 ¹⁵

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

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