Large-Scale Releases of Native Species: the Mallard as a Predictive Model System

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Abstract

Human alteration of natural systems, and its consequences are of great concern and the impact on global ecosystems is one of the biggest threats that biodiversity stands before. Translocations of invasive species, as well as intraspecific contingents with non-native genotypes, whether they are deliberate or unintentional, are one such alteration and its consequences are continuously being assessed.

The mallard (*Anas platyrhynchos*) is the most numerous and widespread duck in the world and a flagship in wetland conservation. It is also an important game species which is heavily restocked for hunting purposes, especially in Europe where over three million ducklings are released every year. Because of its hunted status, its abundance, and the number of released individuals, it can serve as a model species to study effects of releases, both for conservation and restocking for hunting, on wild populations.

In this thesis the status of the mallard was assessed in the Nordic countries and the effects of releases on the wild populations were studied by mining historical ringing data, comparing morphology of present-day wild, farmed, and historical mallards, and analyzing phylogeography of wild and farmed mallards in Europe. The status of the mallard population in the Nordic countries are generally good, however, a joint effort of European countries is needed to monitor and manage the population. A significant difference between wild and farmed mallards concerning longevity, migration, bill morphology and genetic structure was also found, together with signs of cryptic introgression of farmed genotypes in the wild population with potential fitness reduction as a result. The effect is however limited by that only a fraction of released farmed mallards reach the breeding season due to low survival.

A natural captive environment is crucial to keep individuals wild-like with high survival rates after release. However, with an introgression of potentially maladapted farmed genotypes leading to a reduction in fitness, a low survival of released mallards would favor the wild population. A legislative change regarding obligation to report numbers, provenance, and release sites of farmed mallard should be considered, together with practical solutions of ringing and genetic monitoring of released mallards.

Keywords: Anas platyrhynchos, Farmed, Hunting, Introgression, Longevity, Mallard, Migration, Morphology, Population genetic, Restocking, SNPs, Sweden

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Dedication

To my family

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I Dalby L, Söderquist P, Kjær Christensen T, Clausen P, Einarsson A, Elmberg J, Fox A D, Holmqvist N, Langendoen T, Lehikoinen A, Lindström Å, Lorentsen S-H, Nilsson L, Pöysä H, Rintala J, Þórir Sigfússon A, Svenning J-C (2013) Status of the Nordic mallard in a changing world. *Ornis Fennica* 90: 2-15.

II Söderquist P, Elmberg J, Gunnarsson G (2013) Longevity and migration distance differ between wild and hand-reared mallards *Anas platyrhynchos* in Northern Europe. *European Journal of Wildlife Research* 59: 159-166.

III Söderquist P, Norrström J, Elmberg J, Gunnarsson G (2014) Wild mallards have more ”goose-like” bills than their ancestors: a case of anthropogenic influence? *PLoS ONE* 9(12): e115143.

IV Söderquist P, Elmberg J, Gunnarsson G, Thulin C-G, Champagnon J, Guillemain M, Kreisinger J, Prins H, Crooijmans R, Kraus R. (manuscript) Released game birds cause continent-wide introgression: a changing genetic landscape in European mallard (*Anas platyrhynchos*).

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The contribution of PS to the papers included in this thesis was as follows:

I PS formulated parts of the idea and research questions, and wrote parts of the manuscript.

II PS formulated parts of the idea and research questions, analyzed most of the data and wrote parts of the manuscript. PS was the corresponding author with the journal.

III PS formulated parts of the idea and research questions, collected most of the data, analyzed a majority of the data and wrote most of the manuscript. PS was the corresponding author with the journal.

IV PS formulated parts of the idea and research questions, collected and prepared a majority of the samples, analyzed most of the data and wrote a major part of the manuscript. PS is the corresponding and coordinating author of the manuscript.

1 Introduction

Consequences of human alteration of nature are of great concern, and the anthropogenic impact on global ecosystems is considered as one of the biggest threats that biodiversity stands before (Vitousek *et al.*, 1997). Invasive species and releases of non-native species have been recognized as one of the major ways in which biodiversity is threatened (Clavero & García-Berthou, 2005; Chapin *et al.*, 2000). Both deliberate and unintentional relocations of non-native species have occurred for many reasons and for a long time. Native species have also been subjected to such relocations, and the consequences thereof have only recently begun to draw increased attention (Champagnon *et al.*, 2012; Hodder & Bullock, 1997). These relocations may involve intraspecific contingents with a non-native genome (Laikre *et al.*, 2006).

1.1 Translocation of organisms

Human induced relocations of organisms, also known as translocations, either unintentional or deliberate, have occurred for several thousands of years (Grayson, 2001). Such translocations include *introductions* of species to areas outside their native ranges, *reintroduction* of species to areas from where they have disappeared, and *restocking* of species to increase the size of present populations size (Armstrong & Seddon, 2008). Exotic organisms may be introduced in order to control pests, e.g. in biological control (Mack *et al.*, 2000), or for aesthetic and religious reasons (Fox, 2009; Agoramoorthy & Hsu, 2007). In conservation, reintroductions are used to re-establish a species within its historical range, preferably without disturbing the present ecosystem (Armstrong & Seddon, 2008). Restocking is also used within conservation to support threatened or declining populations by e.g. improving genetic diversity, or by increasing actual numbers to reduce the risk of genetic or demographic collapse (Ewen *et al.*, 2012). The terminology of translocations has changed a lot over the years (IUCN/SSC, 2013; IUCN/SSC, 1998), here I use *restocking* and *augmentation* synonymously to *reinforcement*, all according to the guidelines of IUCN/SSC (2013).

Within forestry, fishery management, and wildlife management restocking is a common practice to increase populations and thereby also the possibility to exploit them. In Northern Europe, indigenous species such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) have been cultivated for a long time, and for well over 100 years, non-native provenances have been used for reforestation (Almäng, 1996). Releases of fish, especially salmon and trout (*Salmo* spp.), have also been practiced for a long time with the purpose of augmenting populations for harvest (Ryman, 1981). Most of the birds and mammals across the world that are restocked are actually game species released primarily for hunting purposes (Champagnon *et al.*, 2012).

1.2 The mallard – a commonly farmed, released, and hunted species

The mallard (*Anas platyrhynchos*) is a model species in ecology, genetics, and epidemiology as well as a flagship species in wetland management and conservation. In North America alone, it generates hundreds of millions of US dollars each year in different ecosystem services together with other duck species (Green & Elmberg, 2014). It is also one of the world's most important game species and in the European Union alone there are nine million hunters that regard the mallard as a game species (Elmberg, 2009). The annual harvests are estimated at 4.5 million each in Europe and North America (Raftovich *et al.*, 2011; Hirschfeld & Heyd, 2005). The species is subject to massive management efforts, such as wetland restorations and restocking of wild populations with farmed individuals.

Restocking mallard populations with farmed birds to increase the population for hunting purposes is a practice that became common in the United States in the early 1900s (Lincoln, 1934), although, the first records of released reared mallards are from 1631 in England (Leopold, 1933). The early practice of releasing mallards was intended to compensate for overharvest or cold winters and to increase the breeding population. However, the survival of released ducks was low and releases were deemed unpractical and expensive in North America (Brakhage, 1953; Lincoln, 1934). Later, adaptive harvest management was used to optimize the harvest of ducks in the United States (Nichols *et al.*, 2007). Still today, more than 270000 farmed mallards are released in the United States (U.S. Fish and Wildlife Service, 2013).

Although different to the early practice in North America, the general way of rearing and releasing mallards in Europe is probably similar in most countries, with minor differences. Here, I describe how it normally works in Sweden, and highlight differences to other countries when necessary. In Sweden there are seven registered breeding facilities that produce mallard eggs (Swedish Board of Agriculture, pers. comm.). Their breeding stock originates from wild trapped birds and are originally possibly also mixed with semi-domestic ducks, which is the case in Czech Republic (Čížková *et al.*, 2012). Breeding birds are sometimes exchanged between facilities and also renewed by new offspring. The eggs that are produced are gathered each day during the egg laying period (April-June) and put in incubators for about 28 days. Hatched ducklings stay at the breeding farms until they are ready to be released or are sold day-old to intermediators that rear them until sold to managers at release sites. Eggs can also be sold directly from breeding farms to intermediators that hatch and sell, or rear and release them themselves. In Sweden, ducklings are released at an age of about two to three weeks when they are still unfledged. In France however, they are released at seven to eight weeks´, at which age they start to learn to fly. Release age is a tradeoff between higher survival at higher age, and more release site fidelity and less habituation to humans and thereby more wild-like behavior when released at a younger age. The ducklings are released at ponds, lakes, wetlands, or by the sea coast between May and July and are continuously fed and often protected against predators by hunting, trapping, and fencing. The numbers of released ducklings varies greatly from site to site, all from 10 to several thousands have been observed. The hunting season for mallards in Europe varies from country to country but generally lasts from late August to mid-winter.

In Europe the releases of farmed mallards were limited in extent during the first half of the 20th century until e.g. Denmark and Great Britain started releases for hunting purposes at a larger scale during the 1950s (Boyd & Harrison, 1962; Fog, 1958). Since the 1970s, the practice has increased in other European countries as well, e.g. France (Champagnon *et al.*, 2009), Sweden (Wiberg & Gunnarsson, 2007), and the Czech Republic (Hůda, 2001). The present-day annual total number of released farmed mallards in Europe is hard to estimate, but most certainly exceeds 3 million (Champagnon *et al.*, 2013b) of which about 1.4 million in France (Mondain-Monval & Girard, 2000), 400000 in Denmark (Noer *et al.*, 2008), and 300000 in Czech Republic (Hůda, 2001). In Sweden, probably more than 250000 farmed mallards are released for hunting purposes each year (P. Söderquist unpublished data). The problem with accurately assessing the number of released individuals lies in the lack of obligation to register how many individuals that are released into the wild. Within Sweden, compulsory registration concerns birds in captivity, however, when the birds are released into the wild they are considered wild animals in legal terms. Import of fertilized eggs also occurs in Sweden; for example, during 2010, close to 40000 eggs were registered as imported from Denmark (Swedish Board of Agriculture, pers. comm.). The occurrence of sold eggs or ducklings without receipts, to avoid paying taxes, is another factor complicating tracking of numbers and provenance of released farmed mallards.

1.3 Captive breeding and its effects

To be able to restock exploited populations, captive breeding is needed to produce individuals for release. The terminology within this trade is not very consistent and many different terms can be found in the literature, e.g. hand-reared, captive-reared, captive-raised, captive-bred, farm-reared, and farmed. Also during the time I have been working with this thesis the terminology has changed from *'hand-reared'* in the first two papers to *'farmed'* in the two subsequent, *'farmed'* is also the term used in this thesis. Nevertheless, the definition is the same, namely, 'individuals that are bred in captivity for generations with the purpose of producing offspring that will restock exploited populations'.

When using a breeding stock to produce and rear individuals in a captive environment there is always a risk of alteration of genotypes and phenotypes, potentially making these individuals different compared to their conspecifics in the wild (Price, 1999). In captivity there are several mechanisms that may lead to genetic change in individuals, such as founder effects, inbreeding, genetic drift, and anthropogenic selection regimes (Price, 1999). Through this artificial selection, breeders may influence or maintain certain traits of individuals in captivity to prevent genetic drift from the wild phenotype or to make captive breeding populations as high producing as possible. Besides such deliberate selection of some traits, relaxation of natural selection in breeding facilities may occur. In captivity some behaviors are not as crucial as in the wild, e.g. predator avoidance, shelter-seeking, social interactions, and feeding (Price, 1999). Also the morphology of captive individuals tend to change in captive environments; recorded changes include reduction in brain size and traits related to diet, such as skull morphology, teeth, or digestive system (O'Regan & Kitchener, 2005).

For mallard, several changes of behavior have been recorded in captive breeding stock, including habituation to humans (Desforges & Wood-Gush, 1975), sexual behavior (Desforges & Wood-Gush, 1976), and mate preferences (Cheng *et al.*, 1979; Cheng *et al.*, 1978). Morphological changes, similar to those in other species in captivity have also been documented for captive mallards, e.g. a reduction in brain volume (Guay & Iwaniuk, 2008), larger body size (Pehrsson, 1982), and changes in their digestive systems (cf. Champagnon *et al.*, 2011).

1.4 General about the mallard

The mallard is one of about 50 dabbling ducks (genus *Anas*) around the world and one of seven breeding dabbling ducks in Europe. It is highly adaptable and its natural distribution range include fresh, brackish and salt waters, lakes, and rivers, from arctic tundra to the subtropical areas in the northern hemisphere (Cramp & Simmons, 1977).

Because of its adaptability, and some help from humans, the mallard is the most widespread and numerous duck in the world, with a total estimated population of more than 19 million individuals of which more than 7.5 million breed in Europe, and over nine million in North America (Wetlands International, 2015). Migration strategies differ within the range; northern breeders are long- to medium-distance migrants while birds breeding further south are more sedentary. Because of these differences local population size changes over the year, but also from year to year with severity of winter, and can therefore be hard to estimate.

To measure mallard vital rates, extensive ringing schemes and analyses of hunting bags have occurred in many places around Europe for a long time, but, ringing efforts have declined drastically since the 1970s (Guillemain *et al.*, 2011; Fransson & Pettersson, 2001). Still, for sustainable management of a harvested free-living population, high-quality data on vital rates are essential, and a more detailed understanding of the current status of mallards in Europe is needed (Elmberg *et al.*, 2006).

With the growing interest for releases of farmed mallards in Europe, and the lack of reliable data on vital rates, migration, and numbers of released farmed mallards it is hard to assess the effect these releases have on the population size of the mallard.

1.4.1 Migration and movements

Migratory behavior of the mallard can be studied by ring recoveries, isotopes, and telemetry. The recovery rate of ringed wild mallards is relatively high, but differs depending on e.g. where and at what age they are ringed, and may also change over years (Guillemain *et al.*, 2011). In Sweden, the recovery rate for wild mallards is about 10 % (Fransson & Pettersson, 2001). A similar rate has been found in France, while the recovery rate in UK and Ireland is about 12.5 % (Guillemain *et al.*, 2011). The general direction of migration for mallards breeding in northern Europe is southwest. Where they winter depends on where they bred, with more northern breeders migrating farther than more southern breeders (Fransson & Pettersson, 2001). It has also been shown that during very harsh winters the movements are longer than in milder winters (Sauter *et al.*, 2010). Even though mallards in northern Europe normally start their migration during autumn, there are sedentary populations on Greenland (which is considered a subspecies, *Anas platyrhynchos conboschas*) and Iceland (Scott & Rose, 1996), as well as in northern Norway (Nygård *et al.*, 1988).

The migration and movements of mallards are in constant change. With a changing climate leading to milder winters, the migration distance will probably decrease, a term called short-stopping (Sauter *et al.*, 2010; Olsson, 1960). Also the releases of farmed mallards may have an effect on the migration of mallard populations. Ever since restocking of mallard for hunting purposes started, the movement and migration of released mallards have been studied, in North America (Lee & Kruse, 1973; Brakhage, 1953; Lincoln, 1934), in Great Britain (Boyd & Harrison, 1962), in France (Champagnon *et al.*, 2011), in Denmark (Fog, 1964), and in Sweden (Fransson & Pettersson, 2001; Olsson, 1960). Most of these studies show that released mallards have a shorter migration than wild mallards and that they tend to stay close to the site where they were released. However, in the investigations by Brakhage (1953) and in Lee and Kruse (1973) the released mallards showed similar migration patterns as wild.

1.4.2 Feeding and diet

Mallards are omnivores and opportunistic in their feeding behavior, and shift their diet between seasons (Dessborn *et al.*, 2011), with age (Pehrsson, 1979), and sex (Nudds & Kaminski, 1984). In an adult mallard feeding most often takes place in shallow waters where they dabble for food which can consist of insect larvae, mollusks, crustaceans, annelids, amphibians, roots, tubers, leaves, seeds, and buds (Dessborn *et al.*, 2011; Pehrsson, 1979; Cramp & Simmons, 1977). Feeding comprises several complex mechanisms during which water is sucked in through the anterior opening of the bill and flows through the mandible and maxillae, after which food particles are sieved out by the maxillary lamellae as water and detritus are expelled (Kooloos *et al.*, 1989). It is hence the lamellar density that largely determines the size of food particles that are ingested (Nudds & Bowlby, 1984). However, if the lamellar spacing is too fine, the risk of clogging by detritus and mud increases (Tolkamp, 1993). Lamellar density is thus the result of a trade-off selection process. Differences in bill morphology can be seen among dabbling ducks and between sexes within species, and have most likely evolved to reduce competition and facilitate species coexistence through resource partitioning (Gurd, 2007; Guillemain *et al.*, 2002; Nudds *et al.*, 2000; Kehoe & Thomas, 1987; Pöysä, 1983).

When rearing mallards in captivity several natural conditions may be altered, among them the feeding process and diet. At farms mallards are often fed food items that are larger than their natural food, such as corn, wheat or food pellets (Champagnon *et al.*, 2010). This may lead to altered natural selection on the traits involved in feeding and may eventually lead to changed morphology in the feeding apparatus, such as the bill. Greenwood (1975) showed that the bill of farmed mallards was relatively shorter and wider compared to wild mallard bills. The same was observed by Pehrsson (1982) who claimed that farmed mallards had a "goose-like" bill that was more adapted for grazing, and grubbing for food on land, rather than dabbling for food in the water. Also, Champagnon *et al.* (2010) found a change in bill morphology in wild mallards in France when comparing two different time periods. The lamellar density was 10 % lower in wild mallards collected the winter of 2007-2008 compared to wild mallards collected before 1970, when no large-scale releases of farmed mallards occurred in the country. No changes could be seen in teals (*Anas crecca*) which were used as a control group. Champagnon *et al.* (2010) concluded that released farmed mallards had mixed with the wild mallard population which had caused a decrease in lamellar density due to a relaxed selection pressure for high lamellar density, as sieving small food items is not necessary in captivity.

1.4.3 Survival

The fact that survival is highly dependent on age, sex, and area, and also fluctuates largely within and between years makes it difficult to make general statements about mallard survival. Nevertheless, by analyzing ring recovery data from Sweden, about 50 % of wild mallards ringed during their first year survive to a second, and the annual survival after the second year is roughly 60 % (Fransson & Pettersson, 2001). Based on ring recoveries from Finland, the survival rate for juvenile males was 0.75 and for juvenile females 0.46 while the rates for adult males and females were 0.9 and 0.73 respectively, the life expectancy of a wild mallard is between one and two years (Gunnarsson *et al.*, 2008). Ring recoveries also show that about 90 % of all recovered mallards are shot (Gunnarsson *et al.*, 2008; Bentz, 1985).

What further could complicate estimates of survival is that released farmed mallards may have significantly different survival rates than wild. There are several studies from both North America and Europe that have compared survival rates between wild and farmed mallards, however, differences in releasing methods and analysis methodology make it hard to compare result from these studies. Already when releasing mallards was a relatively new practice in North America, Lincoln (1934) showed a lower survival in farmed mallards compared to wild, and Brakhage (1953) found that the survival rate of wild mallards in Canada was three times higher than in released mallards. Low survival rates in released mallards have thereafter been recorded in several studies in North America (e.g. Yerkes & Bluhm, 1998; Soutiere, 1989), in France (Champagnon *et al.*, 2011), and in Sweden (Fransson & Pettersson, 2001). The lower survival of released mallards can be explained by a "burden of captivity", due to maladapted genes acquired in breeding facilities, more dependence on anthropogenic food and a body condition (e.g. gizzard weight) different to wild mallards (Champagnon *et al.*, 2011).

To compare wild and released farmed mallards when analyzing ring recoveries, it is important to apply consistent filtering criteria to standardize age and time of ringing and also to obtain a clear wild sample without e.g. semi-domestic mallards ringed in city parks.

1.4.4 The phylogeography of the mallard

As explained above, the distribution of mallard in the world is Holarctic; it occurs widely in both the Palearctic and the Nearctic and within these two regions there are both migratory and more resident populations. From ringing, telemetry and isotope studies several different flyways have been recognized in North America (Flyways.us, 2015) and Eurasia (Scott & Rose, 1996), respectively. These flyways generally comprise a breeding area in the north and a nonbreeding area in the south. As female mallards are suggested to be the more strongly philopatric sex (Baldassarre & Bolen, 2006), i.e. she returns to her place of hatching, a potential genetic structure could be visualized by studying maternally inherited mitochondrial DNA (mtDNA). A first phylogeographic study of mallard mtDNA, including samples from Western Russia, North Asia, the Aleutian Islands, and mainland Alaska, was carried out by Kulikova (2005). The results showed one Asian clade and one North American clade with mixing within but not between continents. A more comprehensive study, additionally including samples from Europe, Greenland, and eastern North America, by Kraus *et al.* (2011b) confirmed the North American and Eurasian mitochondrial clades from Kulikova *et al.* (2005) in the global mallard population, and the low differentiation within each clade. The role of flyways for the phylogeography of the mallard is therefore of limited biological meaning as the flyway permeability, i.e. individuals are not obligated to one specific flyway (Guillemain *et al.*, 2005), seems to be high in Kraus *et al.* (2011b).

Single nucleotide polymorphisms (SNPs) are genetic markers where one nucleotide base change has occurred in a DNA sequence. SNPs are generally neutral markers that potentially can consist of any of the four nucleotides, however, in practice they are mostly biallelic (Vignal *et al.*, 2002). The simplicity and low cost of using SNPs has increased their popularity (Morin *et al.*, 2004; Vignal *et al.*, 2002) and Kraus *et al.* (2011a) discovered a large amount of SNPs distributed across the entire mallard genome that made it possible to study the genetic structure of the species with an appropriate nuclear marker. The SNPs from Kraus *et al.* (2011a) were used to study population structure in over 800 mallards from 45 locations worldwide (Kraus *et al.*, 2013). The results confirmed earlier studies that there is no or very little population structure on the continental levels, and analyses also suggested that there is a connectivity between the continents resulting in a nearly panmictic species, except for the Greenland population which seems to be clearly separated (Kraus *et al.*, 2013). To identify different mallard populations can be important in conservation management and for monitoring the spread of diseases such as the zoonotic avian influenza (Kraus, 2011; Olsen *et al.*, 2006).

The genetic variation among mallards can be further complicated by the release of farmed mallards with different genotypes. Individuals bred and reared in captivity always risk phenotypic and genotypic alteration, making them different from wild conspecifics. The effects of genetic drift, founder effects, inbreeding, and selection suggest that there indeed could be a genetic difference between wild and farmed released mallards. So far, only a handful studies on the genetic composition of farmed mallards have been conducted. A first study, concerning urban mallards which are a mix of wild and released farmed individuals, showed a significant genetic difference between wild and urban mallard populations in Italy when analyzing microsatellite DNA markers (Baratti *et al.*, 2009). In the Czech Republic, where the numbers of farmed released mallards by far exceeds the wild population, the two groups have been analyzed with both microsatellites and mtDNA. A clear genetic divergence was found between wild and farmed, as well as low genetic diversity within the farmed population (Čížková *et al.*, 2012). Hybrids between wild and farmed mallards were also found which confirms introgression of farmed genes into the wild population. Similar results were found in France where microsatellites showed a significant difference between farmed and wild mallards. Also here, hybrids between the two groups were found (Champagnon *et al.*, 2013a). However, when comparing mallards from before the era of large-scale releases in Europe with present-day mallards, the genetic differentiation was very low, suggesting low survival of the released farmed mallards (Champagnon *et al.*, 2013a). Baratti *et al.* (2014) investigated microsatellites markers in mallards from the wild, urban habitats, and breeding facilities. Large admixture between groups could be seen as well as a clear separation between urban samples and the other two groups. The patterns of wild and farmed mallards were more elusive; in one area, wild and farmed mallards were genetically similar whilst in another they were significantly differentiated (Baratti *et al.*, 2014). Most investigations suggest a clear genetic difference between wild and farmed mallards in different countries of continental Europe where releases of farmed mallards occur. In this thesis work, a more comprehensive study is presented, with samples from countries along the entire flyway, including countries in which releases occur as well as neighboring countries. The samples are analyzed with a common and powerful methodological framework to assess the genetic impact of releases on the wild mallard population in Europe.

2 Objectives

Despite the fact that the mallard is a common and well-studied species, an important game bird, and that releases of farmed mallards for hunting purposes has been practiced in Europe for many years (Boyd & Harrison, 1962; Fog, 1958), research on these farmed and released ducks and the potential effect on their wild conspecifics has for a long time been scarce in Europe. There is also a lack of knowledge about the number of released and shot farmed mallards in some countries.

The aim of this thesis is to study the effects of releases on the wild mallard population in Europe, with the Nordic countries in focus, and with a special emphasis on Sweden. The goal is also that acquired knowledge can be applied in other systems of restocking, e.g. fishery, and forestry management, or conservation of threatened species. As the introductions shows, there are several aspects in which releases of farmed mallards may have an effect on the wild population, therefore, this thesis encompasses both behavioral, morphological, and genetic effects of releases in an attempt to cover as many dimensions as possible.

In paper I, the status of the mallard in the Nordic countries was assessed by compiling national count data on breeding and wintering numbers, vital rates, and bag statistics. We also discuss knowledge gaps and the influence of releases of farmed individuals.

In paper II, recent and historical ringing data from Sweden and Finland were used to test: (1) if longevity is higher in wild than in farmed mallards, (2) if wild mallards migrate farther than farmed mallards, and (3) if migration distance in wild mallards has decreased the last 50 years. To determine the potential effect releases of farmed mallards will have on the wild population, it is important to study survival rates of farmed mallards and how they compare to their wild conspecifics. It is also important to study historical data sources to attain knowledge about which hypotheses that are important to address.

In paper III, bill morphology in historical wild, present-day wild, and farmed mallards was compared in a wide geographic area, i.e. not only restricted to release area (Sweden) but also neighboring countries (Norway and Finland). By using farmed and released mallards as a study system we can gain insight into how morphologically different captive-bred individuals may introgress the recipient population and alter their morphology. An earlier study on mallards showed a change in bill morphology over time, possibly due to introgression of farmed mallards, however this study was restricted to France (Champagnon *et al.*, 2010).

In paper IV, the aim was to determine genetic differences and potential gene flow between wild and farmed mallards in order to assess change in genetic structure in the wild population. During the last five years a handful studies on the genetics of farmed and wild mallard have been published (Baratti *et al.*, 2014; Champagnon *et al.*, 2013a; Čížková *et al.*, 2012; Baratti *et al.*, 2009). However, a more comprehensive study was needed, including samples from both release countries as well as neighboring countries, to assess the genetic impact of released mallards on the wild population in Europe.

By initiating a ringing program of farmed mallards in Sweden we want to study the number of mallards shot at release sites, their survival rates, and their dispersal. By also trapping and fitting wild and farmed mallards with GPS-loggers we can study movements and migration in more detail.

3 Material and methods

3.1 Model species

In this thesis the mallard is used as a model species to study ecologic and genetic impact of restocking management on wild populations. Provided knowledge can be applied on other species, both within restocking management such as fishery and forestry, or other game species, as well as in conservation management of threatened populations.

3.2 Study area

This thesis is focused on the European situation with a special emphasis on the Nordic countries and especially Sweden. However, because the mallard is such a numerous and widespread duck, the geographic area for which these results are relevant is most of the Holarctic region.

3.3 Data collection and analyses

3.3.1 Ringing program of farmed mallards

In 2011 a ringing program was initiated to gather data on survival and movement of released farmed mallards in Sweden. Mallard ducklings were ringed either on location just prior to release or at the location where they were reared. The ducklings were ringed and released unfledged at an age of 2-3 weeks. Between 2011 and 2014, 10034 farmed mallards were ringed and released in 14 different release areas. The different locations ranged from small-scale releases for leisure hunting to large-scale releases for commercial hunting (Table 1). Numbers and sex of shot farmed birds was reported by game managers at release sites. Collected data has so far only been compiled for basic interpretations and summaries.

Table 1. *Numbers of ringed and released farmed mallards, 2011-2014, in 14 different release areas in Sweden. In one area, releases could occur on several different locations, e.g. five locations (7.1-7.5) in area 7. All mallards that were released at locations 1-10 were also ringed, at locations 11-14, additionally farmed mallards without rings were released. A total of 10034 farmed mallards were ringed and released. Three different types of hunts were held in the areas; educational hunts for teaching and training, small-scale leisure hunts at private estates, and large-scale commercials hunts on large estates that sell hunts.*

Location	Province	Ringed mallards				Hunting type
		2011	2012	2013	2014	
1.1	Scania	276	354	-	-	Educational hunts
1.2	Scania	75	150	-	-	Educational hunts
2	Uppland	60	-	-	-	Leisure hunts
3	Västmanland	400	-	400	-	Leisure hunts
4	Småland	200	200	200	150	Leisure hunts
5	Scania	101	123	-	-	Leisure hunts
6	Scania	315	-	-	-	Leisure hunts
7.1	Scania	-	251	150	201	Educational hunts
7.2	Scania	-	112	30	-	Educational hunts
7.3	Scania	-	394	558	500	Educational hunts
7.4	Scania	-	10	-	-	Leisure hunts
7.5	Scania	-	-	-	335	Leisure hunts
8.1	Småland	-	502	500	-	Educational hunts
8.2	Småland	-	511	500	-	Educational hunts
9.1	Scania	-	101	-	-	Leisure hunts
9.2	Scania	-	41	-	-	Leisure hunts
10	Scania	-	-	35	-	Leisure hunts
11	Scania	-	-	849	-	Commercial hunts
12	Blekinge	-	-	600	-	Commercial hunts
13	Scania	-	-	350	-	Commercial hunts
14	Scania	-	-	500	-	Commercial hunts
Total		1427	2749	4672	1186	
		10034				

3.3.2 Trapping of wild and farmed mallards

To get more detailed knowledge about movements and migration, bill morphology (paper III), and DNA samples (paper IV), a duck trap was built in 2011. The duck trap was set up in a small wetland, approximately 100x100 meters, in Osby, northern Scania, southern Sweden (WGS84, 56°26’24.2’’N, 13°59’32.5’’E). The surrounding area is composed of many small lakes surrounded by coniferous forests. The trap was 4x4x2 meters with three funnel entrances and was baited with barley and enclosed with electric wires (Figure 1). In the same area, two smaller traps, approximately one meter in diameter and one meter high, made by metal mesh net forming a circle with a funnel entrance, were also set up in 2013 (Figure 2). In the trapping area, ringed farmed mallards were released 2012-2014. If these ringed ducks were recaptured they could be distinguished from potentially wild ducks without rings.

Figure 1. A duck trap was built 2011 to capture wild and farmed ducks for ringing, bill measurements, DNA sampling, and fitting with GPS-loggers. The 4x4x2 meter trap with three funnel entrances is located in a small wetland in northern Scania, southern Sweden (WGS84, 56°26’24.2’’N, 13°59’32.5’’E). The trap was baited with barley and enclosed with electric wires. Photo: Pär Söderquist.

Figure 2. Two small duck traps, approximately one meter in diameter and one meter high, was set up in the same area as the larger trap, as a complement. The traps were made of a metal mesh net with a funnel entrance. The trap was baited with barley and checked every day when active. Photo: Pär Söderquist.

Both wild and farmed ducks caught in the traps 2012-2013 were measured, sampled for DNA, and fitted with a CatTrack GPS-logger (Catnip Technologies Ltd.) attached with a Teflon harness similar to the one used in Roshier and Asmus (2009). Loggers were embedded in a shrinking tube to be waterproof, the maximum size of the backpack was 95x30x15 mm and the weight with the harness included was 25 grams (Figure 3). Loggers were set to record one position every hour and had to be recovered to download stored data. In total 67 mallards (49 farmed and 18 wild) were fitted with loggers. Movement data from loggers have so far only been visualized in Google Earth (Google, Inc.).

Figure 3. Captured mallards were fitted with a CatTrack GPS-logger (Catnip Technologies Ltd.). The logger was put in a shrinking tube for waterproofing, with a maximum size of 95x30x15 millimeters and a weight of 25 grams, including the Teflon harness. An address was written on the shrinking tube and on paper inside the shrinking tube as information about where to send recovered loggers. Photo: Pär Söderquist.

3.3.3 Paper I

In paper I, we compiled available data on mallard from the Nordic countries from 1939-2010. Estimates of breeding and wintering numbers were based on annual surveys in all Nordic countries except for Iceland that lacks a national monitoring scheme for breeding dabbling ducks. Total hunting bag sizes have been estimated for all Nordic countries based on reports from hunters. Data from wing surveys was only available for Denmark and Iceland and data on brood productivity were only available for Finland.

The breeding indices for all countries, except Iceland, were calculated using a log-linear Poisson regression model in the software TRIM (Van Strien *et al.*, 2004). The same method was also used to calculate winter abundance indices for Norway and Finland. The winter abundance index for Denmark was calculated with a method from Underhill and Prys-Jones (1994) and for Sweden the chain method (Crawford, 1991) was used. All indices was set at 100 at the earliest common year between the countries.

3.3.4 Paper II

Paper II is based on nationwide, mallard ringing data in Sweden 1919-2004, and in Finland 1913-2006, provided by ringing centers in respective country. Several filtering steps were used, e.g., only using same age classes, same ringing and recovery months, and only using true wild mallards, excluding individuals ringed in city parks, to ensure that analyzed groups only differed in origin, i.e. wild or farmed.

After filtering the raw material, the longevity and migration distance of 588 individuals from Sweden and 378 individuals from Finland were analyzed. Longevity was defined as time from ringing until recovery, and migration distance as distance between ringing site and recovery site the first winter. In a first analysis, wild and farmed mallards within each country were compared for the two variables. In a second analysis, migration distance for wild Swedish mallards were compared between two time periods (1947-1972 and 1977-1993) to test changes over time. Independent *t* tests were run to analyze normally distributed data, for non-normally distributed data, Mann-Whitney *U* test was used instead. All analyses were run in SPSS 17.

3.3.5 Paper III

In paper III, bill morphology was analyzed in three different groups of mallards from Sweden, Finland, and Norway. A historical group contained 102 samples, from museums in Stockholm, Uppsala, Gothenburg, Jönköping, and Lund, originating from 1831-1946. Historical Finnish samples were from museums in Helsinki and Kuopio originating from 1848-1943, and samples from Tromsø, Norway, originated from 1880-1970. All historical samples in this paper and paper IV, were collected before large-scale releases of farmed mallards were initiated. The wild group in paper III consisted of 89 samples. Swedish wild samples came from Dalarna, collected at duck hunts in 2012, and from Scania trapped alive in the duck trap (Figure 1). The wild group also contained samples from a museum in Helsinki, Finland, collected 2004-2005, as well as samples from a museum in Tromsø, Norway, collected 2003-2010. To exclude a mixture of local birds, transient migrants, or winter visitors, only individuals from the breeding season were sampled. The farmed group consisted of 193 individuals originating from three different farms in Scania, Sweden, collected in 2011-2012 from duck hunts, the duck trap, and directly from a farm. Bill height, width, and length were measured for all birds when possible with a digital caliper (Figure 4A-B). A photograph of the underside of the bill was also taken to study the lamellar density in the first four centimeters (referred to as positions) of the bill (Figure 4C).

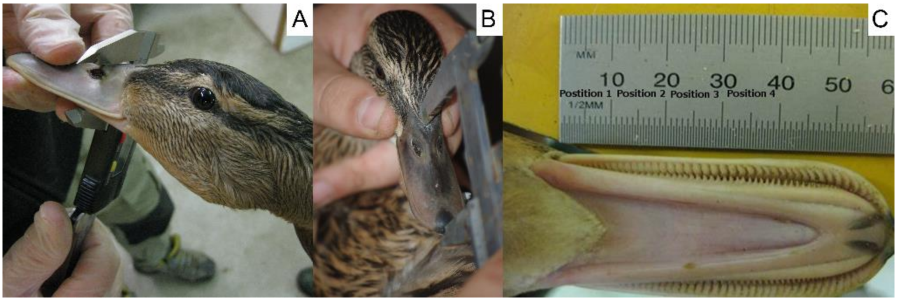

Figure 4. Bill height (A), bill length (B), and bill width were (to nearest 0.01 millimeter) measured along the dorsal side of the maxilla and over the center of the nostrils with a caliper. Figure (C) shows a scaled photography of the ventral view of the bill, used to count maxillar lamellae per centimeter. Positions 1-4 correspond to the first (i.e. proximate, here to the left) four centimeters of the bill. Photo: Pär Söderquist.

Due to desiccation, soft parts tend to shrink in museum specimens. Therefore, we corrected all bill measurements in museum samples by 1.6 %, based on the previously recorded shrinking rate in mallard (Champagnon *et al.*, 2010). After corrections, univariate general linear models (GLM) were used to test whether bill height, bill width, bill length, or lamellar density differed between sexes, and between groups (historical wild, present-day wild, or farmed mallards) within sexes for the 384 individuals measured. To separate between groups after significant model outcomes, pairwise Tukey's post-hoc tests were used.

3.3.6 Paper IV

The main data set in paper IV comprised 354 historical samples from 1831-1978 collected at museums in Sweden, France, Czech Republic, Norway, and Finland. From historical specimens, approximately 5 mm^2 skin from the toe pad was cut with a scalpel. The present-day wild group consisted of 440 samples from Sweden, France, Czech Republic, Norway, Finland, and the Netherlands collected 1995-2012. These samples consisted of tissue collected at duck hunts, blood extracted from live trapped birds, or egg membranes collected from shells in the wild. A farmed group comprised of 464 samples from Sweden, France, and Czech Republic collected 2009-2012, consisted of blood extracted at breeding facilities, tissue from shot birds, or egg membranes and feathers. Samples from France and Czech Republic had been collected for earlier studies and were kindly provided, both as tissue and DNA-aliquots, by the authors (Champagnon *et al.*, 2013a; Čížková *et al.*, 2012). An additional set of samples was also analyzed to provide a broader geographical coverage of the study, these samples had previously been analyzed in Kraus *et al.* (2013). In paper IV the breeding population was the intended focus of the study, and therefore only breeding birds were sampled in Sweden, Finland, and Norway.

However, this criteria could not be met in the samples provided from other countries.

After extracting DNA, using DNeasy Blood & Tissue kits (Qiagen, Hilden Germany) from all collected samples, 656 samples with sufficient DNA concentration and quality as well as a representative geographic distribution were selected for genotyping. Samples were genotyped using a previously published set of 384 SNPs (Kraus *et al.*, 2011a). After excluding individuals and SNPs with low output, 591 individuals and 360 SNPs remained for further analysis. Observed and expected heterozygosity together with inbreeding coefficient (as F_{IS} values) were calculated using *diveRsity* v1.9.5 (Keenan *et al.*, 2013) in R (R Development Core Team, 2009). To analyze the genetic population structure, Discriminant Analysis of Principle Components (DAPC) (Jombart *et al.*, 2010) from *adegenet* v1.4-1 (Jombart, 2008) in R, and STRUCTURE v2.3.4 (Pritchard *et al.*, 2000) was used. To find the most likely number of genetic clusters (*K*) in the data, the function *find.cluster* in DAPC, and the Evanno et al. method (2005) in STRUCTURE were used. The genetic structure of the additional set of 709 samples from Kraus *et al.* (2013) was also analyzed with STRUCTURE.

4 Results and discussion

4.1 Ringing program of released farmed mallards

The ringing program initiated in 2011, indicated that only one of five released mallards got shot on the location where they were released, even though the percentage differs a lot among sites and years. When sex was reported of the recovered mallards, the sex ratio was almost even (648 females *versus* 614 males. That only 20 % of all released mallards are shot on the location where they are released, suggests that a large proportion of the released mallards survives the hunting season and potentially reach the breeding season. However, Champagnon *et al.* (2011) show that survival of released farmed mallards, also at locations without hunting, is very low and only a fraction will survive until breeding season. By using the expected recovery rate for wild mallards of about 10 % (Fransson & Pettersson, 2001), 800 mallards should be recovered from the originally 10034 ringed birds (after subtracting the nearly 2000 mallards shot at the release sites). When compiling reports of recovered birds from outside the release sites, there are barely 75 recoveries (Figure 5). If 10 % is the recovery rate also for farmed mallards outside of their release site, these 75 recoveries correspond to 10 %, which would imply that only 750 of the 8000 farmed mallards that escaped hunting actually survived and dispersed, that corresponds to a survival rate of less than 10 %, which is similar to the survival rates found by e.g. Brakhage (1953) and Champagnon *et al.* (2011). It shall be noted that this is speculative and needs further analyzing with proper methods, e.g. capture-recapture (Seber, 1970). Nevertheless, when considering the massive number of released mallards, the actual number of mallards potentially surviving until the breeding season is still substantial, even if the survival rate is low. Despite the potential bias that all rings of shot mallards are not reported back by the hunters; this is a known problem and have to be considered when properly analyzing recovery data (Guillemain *et al.*, 2011; Guillemain, 2010).

4.2 Movements of wild and farmed mallards

Of the 67 mallards fitted with GPS-loggers (49 farmed and 18 wild), data were attained from 60. The daily movement pattern between roosting sites and foraging areas, with highest flight activity at dusk and dawn shown by e.g. Bengtsson *et al.* (2014) was also seen in our wild trapped mallards (Figure 6). This pattern could however not be seen in the released farmed mallards, that spent all their time in the same wetland they were released. However, ring recoveries from released mallards that later dispersed outside the release areas show that they can migrate in a similar manner as wild mallards (Figure 5). Detailed migration data were received from GPS-loggers for two wild mallards. One female fitted with a logger 5th of October 2012, was shot one month later, 75 kilometers south-southwest of the duck trap where it was initially caught. Another female, fitted with a logger 14th of October 2012 was shot 185 kilometer southwest in Denmark two months after capture (Figure 6).

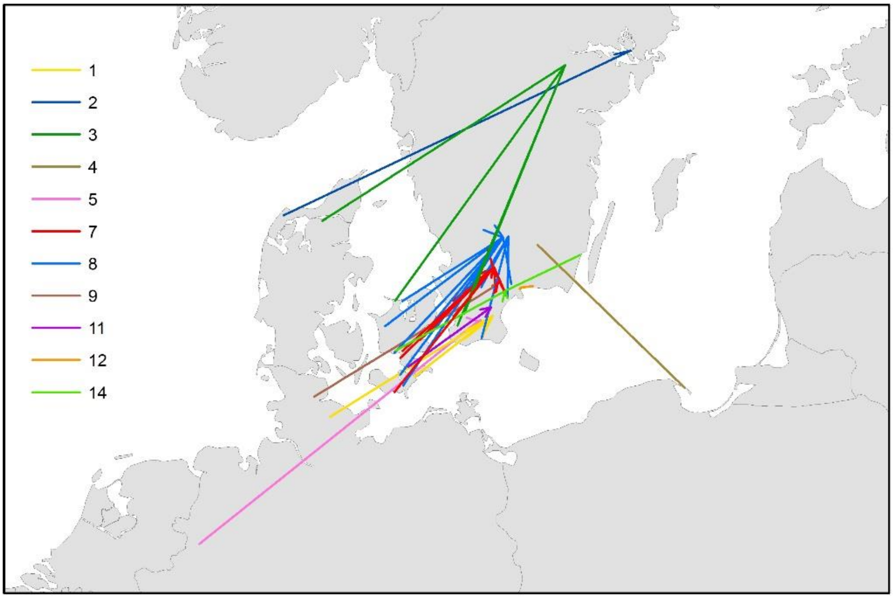

Figure 5. Recovery sites of 74 farmed mallards released in 14 different areas in Sweden. Recovery pattern show that farmed mallards can migrate in a similar manner as wild. Figure legend shows which colors represent the different release areas.

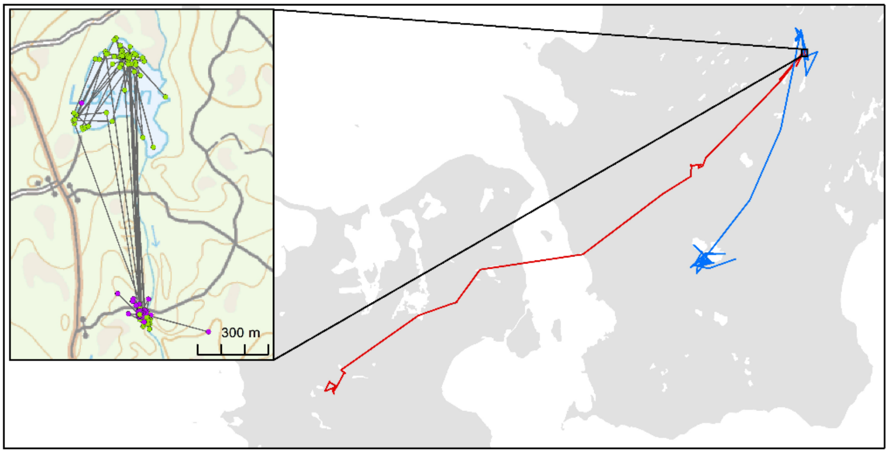

Figure 6. Detailed migration routes for two wild mallards (red and blue) fitted with GPS loggers in October 2012. Both mallards spent more than one week in the area where they later were shot, which suggests that they had completed their migration. Inset map show typical daily movement patterns of a wild mallard between the small wetland where the trap was located and a lake about 1 kilometer north of the trap. Green dots indicate the location during daytime and purple dots location during nighttime.

4.3 Status of the Nordic populations of mallards (paper I)

By compiling available data such as breeding numbers, wintering numbers, bag statistics, productivity, and survival rates, the status and knowledge gaps of the Nordic mallard could be identified. Breeding numbers show stable or increasing trends in all Nordic countries, from 0.82 % in Finland to 7.5 % in Norway, and a total breeding population of 400000-605000 pairs. The wintering population in the same area is 369000-409000 individuals, with large variations between countries and years.

Close to 900000 mallards are shot each year in the Nordic countries and the indices show a stable or slightly declining recent trend. The Swedish hunting bag has been monitored since 1939, and peaked 1945 after which it declined until 1978, and increased again to present levels of about 100000 shot mallards each year. Noer *et al.* (2008) estimated that 400000 farmed mallards were released each year in Denmark, and in Sweden more than 200000 released mallards may be released (the number for Sweden is now adjusted to more than 250000 (P. Söderquist unpublished data)). No large-scale releases have occurred in Finland, Norway, or Iceland. Releases of farmed mallards may have a significant influence on the size hunting bags.

The analysis of wing surveys in Denmark showed a stable trend from 1982-2010 while the wing surveys from Iceland fluctuated widely with no apparent trend. The brood counts in Finland showed an annual increase of 2.14 % during 1989-2010.

According to the compiled data in paper I, the status of the Nordic mallard population is good. Despite that a reduction in wintering numbers suggests a decline in the population in North-western Europe, breeding numbers and productivity in the Nordic countries are increasing. The significant increase in breeding numbers in Norway may be due to a monitoring bias, it also coincide with a decline in Norwegian hunting bags, suggesting that hunting may have an additive effect on mortality in the Norwegian population. During the last 20 years the wintering numbers in the Nordic countries show stable or increasing trends, even though the variations are large. Milder winters may lead to shorter migrations (Gunnarsson *et al.*, 2012) which could explain an increase in wintering numbers in Northern Europe, however, a detailed flyway analysis is required to determine if the effect is due to changes in the population size or due to climate change.

Since 1990, hunting bags in Denmark have declined. During the same time releases of farmed mallards have also declined from 500000 to 400000 which could be a part of the explanation. Still, more than half of all mallards shot in the Nordic countries are shot in Denmark and a majority of these mallards are probably released farmed mallards. Releases of farmed mallards surely have a great influence on several aspects studied in this paper. The effect on the hunting bag is obvious, but it could also bias the wing surveys, as released mallards often are shot during their first year, and because survival rates for released mallards a largely unknown it is hard to assess their influence on wintering and breeding numbers.

To successfully manage the North-west European population of mallards it is crucial that monitoring programs, including hunting bag sizes, are harmonized across the entire flyway. It is also important that the potential effects of released farmed mallards are thoroughly researched, which could be facilitated if released mallards were ringed, and if numbers of released mallards are reported at a national level.

4.4 Longevity and migration in wild and farmed mallards in Northern Europe (paper II)

Nation-wide ringing data on farmed and wild mallards from Sweden and Finland showed a great variation concerning longevity. Most of the ducks from both categories were recovered during the first fall and winter and only 2-9 % lived to be four years or older. Seventy-seven percent of Swedish and 90 % of Finnish farmed mallards were recovered dead within one year. The corresponding values for wild mallards were 45 % for Swedish and 66 % for Finnish mallards (Figure 7). Longevity was significantly shorter for farmed than for wild mallards in Sweden (farmed, mean=258 days; wild, mean=575 days), and the same was true for Finland (farmed, mean=129 days; wild, mean=388 days).

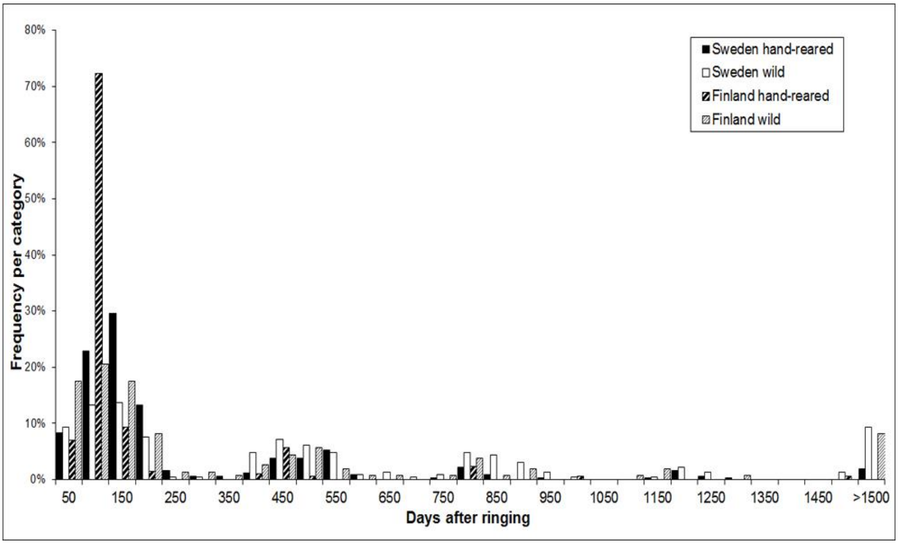

Figure 7. Frequency of longevity, expressed as the number of days from ringing until recovery, per category of mallards (Swedish farmed, Swedish wild, Finnish farmed, and Finnish wild).

Also the migration distance varied substantially within countries and groups, however, wild mallards were recovered significantly farther from the ringing site than farmed mallards in both countries (Sweden wild, mean=676 km; farmed, mean=523 km; Finland wild, mean=1213 km; farmed, mean=157 km). Also migration distance per day differed between wild and farmed mallards in both countries, (Sweden wild, mean=4.8 km day^{-1}; farmed, mean=3.5 km day^{-1}; Finland wild, mean=8.5 km day^{-1}; farmed, mean=0.8 km day^{-1}). Mean distance between ringing and recovery site was 787 km for wild Swedish mallards ringed 1947-1972 whereas it was 591 km for wild mallards ringed 1977-1993 (Figure 8), however, this difference was not statistically significant (p=0.114).

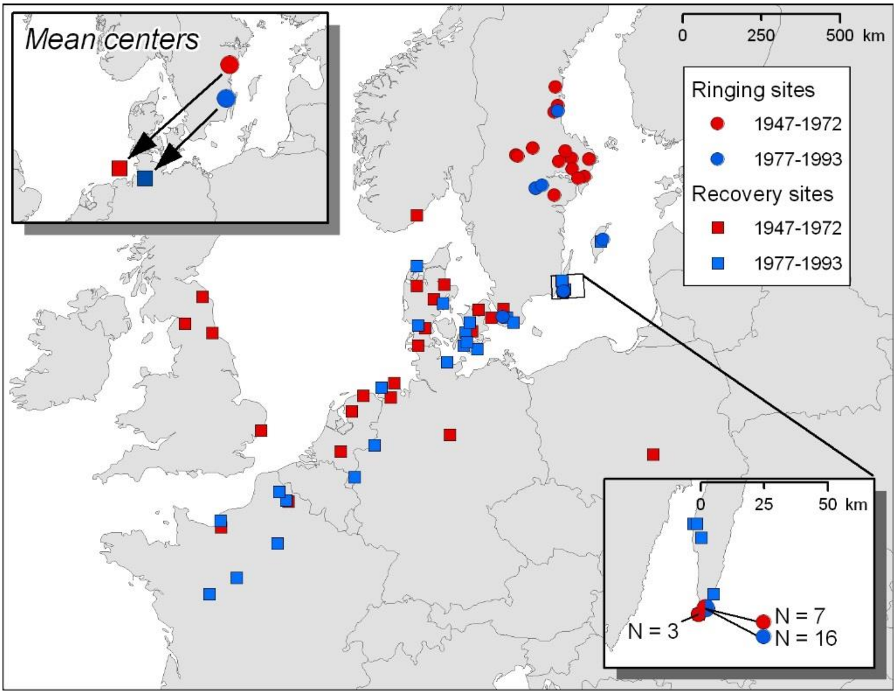

Figure 8. Ringing (*circles*) and recovery (*squares*) site for wild mallards ringed in the time periods 1947-1972 (*n*=25, *red*) and 1977-1993 (*n*=25, *blue*). Inset map shows mean positions for ringing and recovery site for the two periods.

The shorter longevity in farmed mallards compared to wild mallards found in paper II, corroborates earlier patterns that wild mallards live longer than farmed (Dunn *et al.*, 1995; Soutiere, 1989; Fog, 1964; Brakhage, 1953). However, we advise caution when comparing the longevity in this paper with survival estimates in other, as the longevity does not show true survival, and differences in release methods varies greatly between studies. The explanation for differences in longevity between wild and farmed mallards could be that farmed released mallards carry a "burden of captivity", a potential genetic maladaptation, resulting in bills less efficient for sieving, smaller gizzards, and a higher dependency on anthropogenic food, i.e. a reduced physiological fitness (Champagnon *et al.*, 2011). Similar patterns of shorter longevity has also been documented for other released game birds compared to their wild conspecifics, e.g. gray partridge, *Perdix perdix*, (Buner & Schaub, 2008) and ring-necked pheasant, *Phasianus colchicus*, (Brittas *et al.*, 1992; Hill & Robertson, 1986).

As was predicted, migration distance between ringing and recovery sites was significantly shorter for farmed than wild mallards in both countries. A shorter time between ringing and recovery may of course explain the shorter distance covered. However, also the migration speed was lower for farmed mallards, suggesting that migration distance is a result of both shorter life and slower migration. The last prediction that migration distance of wild mallards have changed over time could not be supported by our data. The low sample size could be a contributing factor for this. Also the fact that mean ringing site for the two time periods differed significantly, complicates the interpretation of data. Even if migration distance in wild mallards has changed since releases of farmed mallards begun, it can be difficult to separate introgression of non-migratory farmed mallards from the response to climate change and milder winters (cf. Gunnarsson *et al.*, 2012; Lehikoinen & Jaatinen, 2012; Sauter *et al.*, 2010).

4.5 Bill morphology in wild and farmed mallards (paper III)

There were significant differences in lamellar density between sexes for each position of the bill, with females always having denser lamellae than males. In the second centimeter (position 2), historical wild males had higher lamellar density than farmed males, and they also tended to have a higher density than present-day wild males (p=0.051). No other significant differences for lamellar density were found in any other position in either sex.

Male mallards consistently had higher, wider, and longer bills than female mallards (Figure 9A-C). Historical males had flatter bills than both present-day wild and farmed mallards, also female historical wild mallard bills were flatter than farmed bills. However, there was only a tendency (p=0.068) for historical wild bills to be flatter than present-day wild bills in females (Figure 9A). Bill width was consistently widest for farmed mallards and narrowest for historical wild mallards in both sexes (Figure 9B). For both sexes, historical wild mallards had the longest bills and farmed mallards the shortest, while present-day wild mallards could not be separated from any of the two groups (Figure 9C).

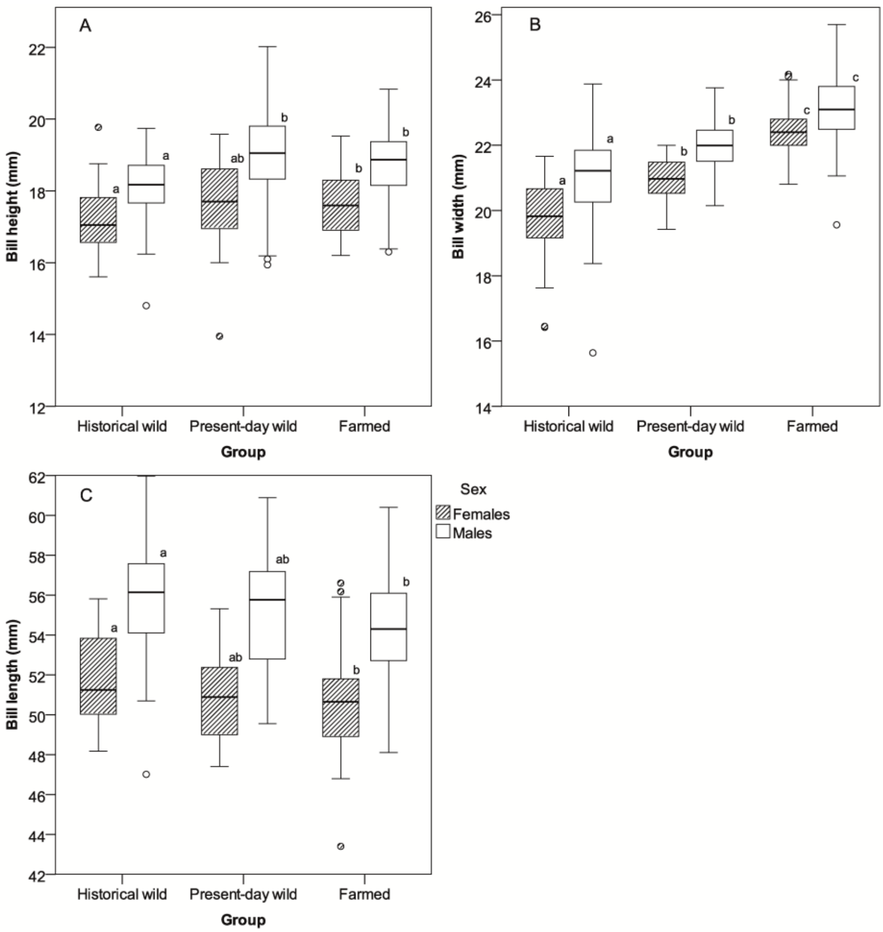

Figure 9. Box plots showing median and quartiles of mallard bill measurements by group and sex; A) height, B) width and C) length, in millimeter. Different letters indicate significant difference of means within each group and sex.

The overall higher lamellar density for females can be a cause or an effect of feeding niche divergence and may reduce inter-sexual competition (Nudds & Kaminski, 1984). We found a lower lamellar density for male farmed mallards in position 2, and similar results were found by Champagnon *et al.* (2010) in France, who discussed the possible explanation that farmed mallards are fed large food-pellets which may relax the selection for denser lamellae. This would also apply in Sweden where feeding with pellets is also practiced at breeding facilities.

The consistently bigger bill (wider, higher, and longer) found in males could be explained by simple allometry as males are generally larger than females. Shorter bills found in farmed mallards were also found by Pehrsson

(1982) but the consequences for such a change is not clear, however, it could have importance for which food items the ducks collect (e.g. Gurd, 2007; Guillemain *et al.*, 2002; Pöysä, 1983). Historical wild mallards generally had flatter bills than present-day mallards, and historically wild mallards also had the narrowest bills, while farmed mallards had the widest. This is consistent with results by Pehrsson (1982) and Greenwood (1975) and it has been proposed that these "goose-like" bills in farmed mallards are more adapted to feeding on larger food particles on land, such as agricultural crops or food pellets, rather than filtering for food in water (Champagnon *et al.*, 2010; Pehrsson, 1982).

The paper shows that farmed mallards have "goose-like" bill proportions and that present-day wild mallards are changing in the direction of farmed mallards. This change is not limited to where the releases occur but also includes release-free zones. Such cryptic introgression of farmed mallard traits may lead to a maladapted and genetically compromised wild mallard population.

4.6 The genetic landscape of wild and farmed mallards (Paper IV)

Observed and expected heterozygosity were similar between all groups of mallard. However, F_{IS} values (inbreeding coefficient) for historical wild, Swedish wild, French wild, Czech wild, Swedish farmed, and Czech farmed showed signs of heterozygote deficits while the French farmed, the combined Norwegian and Finnish wild, and the Dutch wild did not.

The most likely number of clusters for STRUCTURE was K=2, while for DAPC K=3 was the most probable number of K. The inferences of K=2 to K=4 from both assignment methods were similar with the exception that DAPC was more decisive and showed fewer admixed individuals (Figure 10 and 11). For K=2, one cluster consisted of historically and wild samples while the other consisted of farmed samples. For K=3, the Czech farmed samples formed a separated cluster, and for K=4, all three farmed groups from Sweden, France, and Czech Republic formed separate clusters beside the historical and wild cluster. For higher K, patterns were less clear. When STRUCTURE assigned an individual to one cluster with an assignment probability (q) higher than 0.7, we arbitrarily considered that individual as belonging to that certain cluster, and an individual with a $q \leq 0.7$ was hence considered admixed. Based on the assignments of K=4 in STRUCTURE, historical wild samples almost exclusively belonged to the historical and wild cluster, with only one admixed individual, compared to the wild samples, i.e. the proportion of admixed individuals in the wild population has increased since the releases of farmed mallards started (Figure 12). Within the wild populations of Sweden, France, and Czech Republic, individuals assigned to respective country's farmed cluster could be found (Figure 12).

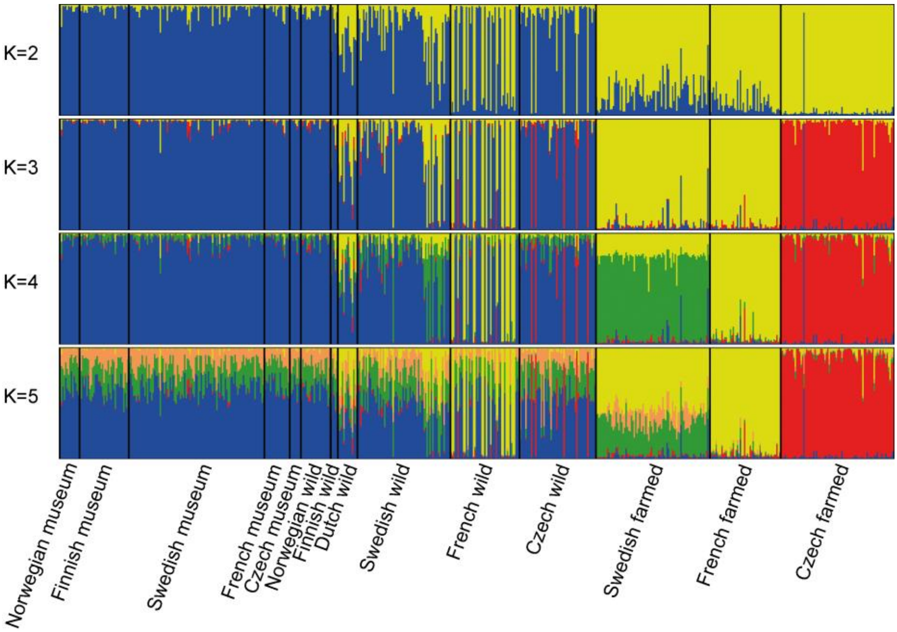

Figure 10. STRUCTURE assignments of 591 individual genotypes for *K*=2 to *K*=5. Each individual genotype is represented by one vertical bar. Black bars separate the 14 different groups of mallards included in the study. The most likely number of clusters is *K*=2, where predominantly blue bars represent historical and wild mallards and yellow bars farmed mallards. In addition, *K*=3 show that Czech farmed mallards (red) split from other farmed (yellow), and for *K*=4, all farmed mallards (Swedish; green, French; yellow, and Czech; red) are separated. Throughout higher levels of *K* the assignment of mallards from farms to the farm clusters remains stable while the resolution of wild mallard clusters is obscured.

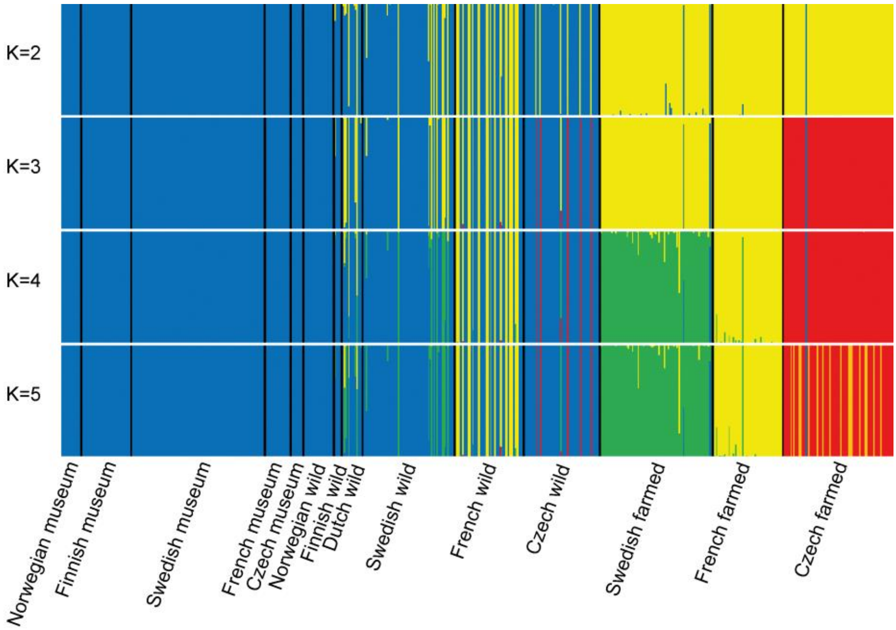

Figure 11. Discriminant Analysis of Principal Components (DAPC) assignment for *K*=2 to *K*=5 for 591 individual genotypes, each represented by one vertical bar. Black bars separate the 14 different groups of mallards included in the study. The most likely number of clusters is *K*=3, where historical and wild mallards form a blue cluster, farmed mallards from Sweden and France a yellow-, and the Czech farmed mallards a red cluster. At *K*=4, Swedish farmed mallards (green) split from the farmed yellow cluster in *K*=3 separating all farmed groups. As for the STRUCTURE results (Figure 10), mallards from the wild cannot be assigned to clusters in a meaningful way for higher estimates of *K*.

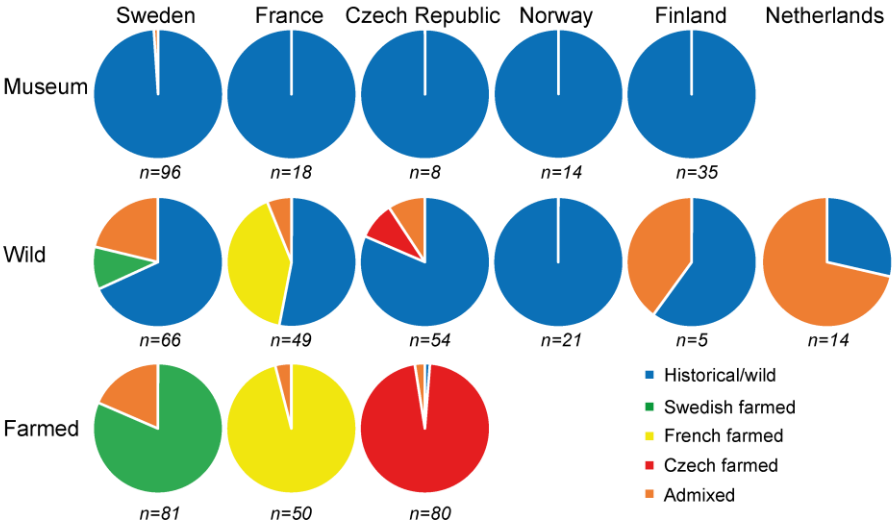

Figure 12. Proportion of mallards with an arbitrary assignment probability of q>0.7 from historical, wild, or farmed mallards from six countries, belonging to either of K=4 genetic clusters from STRUCTURE; historical/wild (blue), Czech farmed (red), French farmed (yellow) or Swedish farmed (green), or admixed specimens (orange), i.e. when q≤0.7. Sample sizes for each group are found under respective pie chart, N.B. low sample size for *Finnish wild* and *Dutch wild* may lead to non-representative results.

When including previously analyzed global samples, the continent-wide lack of geographical structure, except for the mallard population of Greenland, reported by Kraus *et al.* (2013) was confirmed. However, signs of assignment to the farmed cluster was observed in wild samples of some countries (Figure 13).

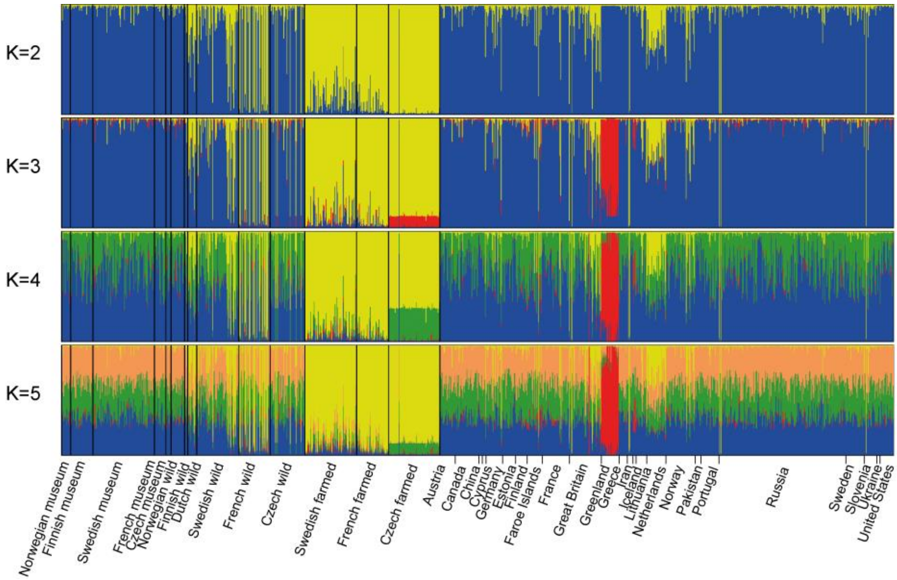

Figure 13. STRUCTURE assignment for *K*=2 to *K*=5 for the 591 individuals from this study combined with the 709 individuals from Kraus et al. (2013), resulting in a total of 1300 individuals. Each individual genotype is represented by one vertical bar. Black bars separate the 15 different groups of mallards. For *K*=3 the blue cluster shows historical/wild mallards, the yellow cluster shows the three farmed groups (Swedish, French, and Czech) and the red cluster shows wild mallards from Greenland. As for Figure 10 and 11, in estimates of higher *K*, individuals cannot be assigned in a meaningful way.

The estimates of expected and observed heterozygosity do not indicate serious inbreeding in any of the groups, however, positive F_{IS} values show signs of heterozygote deficits in some of them. The surprising indication of decreasing heterozygosity in the historical wild mallards could be explained by global sampling of different subpopulations leading to a Wahlund effect (Wahlund, 1928). The same effect could also explain the positive F_{IS} in the Swedish, French, and Czech wild groups, where wild and released farmed mallards may have been collected simultaneously. More expected were the signs of decreasing heterozygosity in the Swedish and Czech farmed samples; the risk of inbreeding is higher at breeding facilities due to the limited number of breeding stock. Exchanges of breeding birds between breeding facilities reduce the risk of inbreeding, this is practiced at French farms and may explain their lack of heterozygote deficits. No large-scale releases have ever occurred in Norway and Finland which could help keeping their populations in natural states. The vast numbers of migratory birds that congregate in the Netherlands may help keeping the rate of heterozygosity at a high level in the Dutch wild population, despite the influence of French farmed mallards seen in Figure 12.

There were clear signs that farmed individuals released from breeding facilities are genetically different from both historical and present-day wild mallards. When breeding animals in captivity there is always a risk that founder effects, inbreeding, and genetic drift will influence the genetic structure of the animals (Price, 1999). Natural selection is also relaxed at breeding facilities leading to an altered selection that may affect the genetic structure of farmed mallards (Lynch & O'Hely, 2001). These genetic differences may have been translated to some of the morphological and behavioral changes documented for farmed mallards, concerning e.g. brain volume (Guay & Iwaniuk, 2008), digestive organs (Champagnon *et al.*, 2011; Moore & Battley, 2006), feeding apparatus (Champagnon *et al.*, 2010), sexual behavior (Desforges & Wood-Gush, 1976), mate preferences (Cheng *et al.*, 1979; Cheng *et al.*, 1978), and habituation to humans (Desforges & Wood-Gush, 1975).

Farmed individuals found in wild populations show that farmed mallards survive the hunting and intermix with wild mallards, and the significant part of admixed individuals also indicate hybridization between farmed and wild individuals. This is not restricted to the country of release *per se* but can also be seen in other close countries such as Finland and the Netherlands. By including data from Kraus *et al.* (2013) other regions potentially affected by introgression of farmed mallards could be identified. Signs of admixed or farmed individuals could be seen among wild samples from Great Britain, Iran and the Netherlands (Figure 13), however, to be ascertained more farmed references are needed.

The cryptic introgression of farmed mallard genes into the wild population shown in the current study may have negative effects on the fitness of the wild mallard population. Because of the economic values generated from releases of farmed mallards, this business will likely continue, and unless released mallards are sterilized, the hybridization will continue as well. However, the introgression is probably kept at a low rate due to the low survival of released mallards. Therefore, efforts to increase survival of released mallards should not be encouraged. Nevertheless, genetic monitoring, ringing, and documentation of numbers and provenances of released individuals will facilitate research and monitoring of released farmed mallards.

5 Conclusions and implications

The general status of the mallard in the Nordic countries is good. Breeding numbers are going up, and productivity measures and wintering numbers indicate stable or increasing trends during the last two decades. However, major knowledge gaps were identified that needs further attention, e.g., size of hunting bags, the role of short-stopping in explaining the changing patterns of wintering numbers in Europe, and the role of releases of farmed mallards.

Mallards bred in captivity and released for hunting purposes are different to their wild conspecifics, and this thesis highlights some of these differences; longevity and migration are significantly shorter for farmed mallards than wild, farmed mallards also have a bill morphology that separates them from their wild counterpart, and farmed mallards has different genotypes compared to wild mallards. These differences are however subtle, and it is still nearly impossible to discriminate between farmed and wild mallards just by observing phenotypes.

Traits of farmed mallards, concerning bill morphology, can be found in wild populations. Thus indicating a cryptic introgression of farmed mallard genes, which may alter the genetic structure of the wild mallard population. The genetic analyses also support a hybridization between the genetically diverged farmed and wild mallards. The effect on the wild population has been limited, probably due to low survival in farmed mallards. However, a continued pressure on the wild population from released farmed mallards may have future consequences.

When aiding threatened populations for conservational purposes by restocking, it is important that released stocks are as wild-like as possible with a high chance of survival. This can be facilitated with natural and wild-like conditions at breeding programs. Duck hunters and mallard breeders are also striving for as wild-like mallards as possible. However, bill morphology of farmed mallards indicates that conditions at breeding facilities, concerning feeding, are not natural and the recommendations in paper III could help improve this situation. However, with the wild mallard population in mind, and with the genetic and morphological results at hand, showing significant differences between wild and farmed mallards, no released mallards reaching the breeding season would be ideal. Therefore, no efforts to increase survival rates of farmed mallards should be encouraged, unless a practical solution to sterilize farmed mallards can be found.

To facilitate continued research on farmed mallards and their effects on wild populations, as well as assess their contribution to e.g. hunting bags, a national ringing scheme of farmed mallards should be considered, together with continuous genetic monitoring of both wild and farmed populations. A legislative change regarding registration of numbers of released farmed mallards, their provenance, and release sites should also be considered to be able to track outbreaks of avian influenza and to monitor trends and development of releases.

Because of the large numbers of released farmed mallards and the relative ease of gathering data on the effects of releases, the farmed mallard can be a useful model system to study different angles of restocking and its effects on wild populations, whether the purposes are for conservation or restocking game species.

6 Sammanfattning på svenska

6.1 Storskaliga utsättningar av inhemska arter: gräsanden som ett förutseende modellsystem

Människan har i alla tider påverkat sin omgivning. Konsekvenserna av den mänskliga påverkan ses idag som ett stort hot mot den biologiska mångfalden. Spridning av främmande arter har länge setts som ett av de största hoten mot biologisk mångfald men fokus har nu även riktats mot spridning av främmande populationer.

Gräsanden är den mest talrika och spridda anden i världen. Den har också en nära relation till människan, den är vanlig i parker och där en populär fågel att mata. Det förekommer också avel på tamänder och flera olika raser har avlats fram som i grunden är gräsänder, även den vita pekinganken som kan beställas på restaurang är en variant av gräsand. Gräsanden är även ett populärt jaktvillebråd. För att öka den jaktbara populationen föds den upp i fångenskap och sätts ut i våtmarker under sommaren. I Europa sätts det varje år ut över tre miljoner farmade gräsänder i jaktsyften, varav över 250000 i Sverige. Djur som avlas i fångenskap föds upp under omständigheter som skiljer sig från naturliga förhållanden. Därför finns det en risk att farmade änder efter bara ett par generationer kan skilja sig gentemot den vilda populationen. Eftersom det varje år skjuts så många vilda och farmade änder, finns det en stor tillgång till data som gör det möjligt att studera hur utsättningar av farmade gräsänder kan påverka den vilda populationen. Det gör gräsanden till ett lämpligt modellsystem för att studera hur utsättningar av djur uppföda i fångenskap kan påverka sina vilda artfränder.

Denna avhandling visar att statusen för gräsanden i de Nordiska länderna är generellt god men att ett gränsöverskridande samarbete behövs för att på ett bra sätt kunna övervaka hela den Europeiska gräsandspopulationen. Vilda och farmade änder skiljer sig signifikant vad gäller flyttlängd och livslängd. En farmad gräsand flyttar generellt kortare och har ett kortare liv än en vild gräsand. Näbben på en farmad and är också generellt bredare, högre och kortare än hos en vild gräsand. Det finns även genetiska skillnader mellan farmade och vilda gräsänder. Gener specifika för farmade gräsänder förekommer nu även i den vilda populationen, vilket kan leda till en sämre fitness. Denna effekt är troligtvis begränsad av att endast en bråkdel av de farmade änderna överlever till häcksäsongen och därmed har en möjlighet att korsa sig med den vilda populationen.

Naturliga förhållanden vid uppfödning i fångenskap är viktiga för att få vildlika individer med hög överlevnad efter utsättning. Om utsatta individer däremot riskerar att försämra den vilda populationen, genom spridning av sämre anpassade gener, är en låg överlevnad av de utsatta individerna mer gynnsamt för den vilda populationen.

För att bättre förstå effekter av utsättningar av farmade gräsänder är det önskvärt att obligatorisk rapportering av antal utsatta, ursprung samt utsättningslokal för farmade gräsänder införs. Praktiska lösningar för märkning och genetisk övervakning av utsatta änder bör också övervägas.

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