Introductory Research Essay

Ecological and genetic consequences of introductions of native species: the mallard as a model system

Pär Söderquist

2012
Introductory Research Essay **No. 15**
Department of Wildlife, Fish, and Environmental Studies
Swedish University of Agricultural Sciences
901 83 Umeå, Sweden

Contents

1. General about the Mallard

A species´ pattern of distribution and abundance can be caused both by natural forces and by humans or human activities. Dispersal caused by humans can in turn both be deliberate and involuntary. Most introduced non-native species, deliberately introduced or not, have negative effects on their new ecosystem in one way or another (Mack et al. 2000). Introducing new species but also relocating native species to a new area has been practiced ever since man learned how to cultivate crops and tame and domesticate animals. It is however during the last 500 years that most of all relocations and introductions have occurred (Mack et al. 2000).

There are many reasons to why man deliberately relocates animals. For purely aesthetical reasons some birds, for example Peafowl (*Pavo cristatus*) and some trees, for example Horse-chestnut (*Aesculus hippocastanum*) have been introduced in parks all over the world. In conservation biology it is also a common practice to relocate species to enhance non-viable or weak populations. This can be done by a so called genetic rescue, for example to outbreed a small inbred Swedish populations of adder, (*Vipera berus*) (Madsen et al. 1996) or simply by increasing the breeding population with the help of captive breeding and restocking the population to larger and viable size, sometimes to permit harvest (see examples in Frankham et al., 2010).

Even though there are examples of introductions of alien species that are considered successful with little or no negative impact on the indigenous flora and fauna, for example the fallow deer in central Europe (Myrberget 1990), introduction of alien species is considered as one of the major threats to biodiversity (Chapin et al. 2000). However, “the alien problem” does not have to concern a new or even invasive species, but may also consist of genetically different populations of native species, i.e. units below species level (Laikre et al. 2006). The risks that these genetically different populations can pose on the natural wild populations are for example increased competition, disease transmission, predation, habitat alteration and genetic change, which can lead to decreased genetic diversity, maladaptation and unwanted side effects (Laikre et al. 2006).

In Sweden, but also in the rest of Europe, many native species are farmed and released into the wild to increase natural populations and the possibility to exploit them. In Swedish forestry the indigenous species Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) are the main species cultivated, but non-local provenance have been used for well over 100 years (Almäng 1996). In fishery management in Sweden it is a common procedure that hydropower exploitation is allowed only if fish stocking is carried out to compensate for reduced return migration, reproduction or a decrease in fish population due to disturbance from hydro plants. Millions of fish, some with unknown origin, are released each year in Swedish waters. The most common species are brown trout (*Salmo trutta*), Arctic char (*Salvelinus alpinus*) and grayling (*Thymallus thymallus*) (Laikre et al. 2006). There are also massive releases of hand-reared game birds in Sweden. Gray partridges (*Perdix perdix*) and pheasant (*Phasianus colchicus*), often of unknown genetic origin, are hand-reared and released in summer in Sweden to boost the population for hunters during the hunting season. Fertilized eggs are also imported from other European countries to be reared and the hatchlings used for breeding purposes on farms or to be released (Laikre et al. 2006). The common denominator for all these examples is the lack of information about provenance and quantities of released individuals. Unfortunately the obligation to report and regulations in general about releases of alien populations is very poor in Sweden (Laikre et al. 2006).

So far, there is very little known about the effects of releases of alien populations in Sweden (Laikre et al. 2006). One species, which can be found all over Europe, including Sweden is the mallard (*Anas platyrhynchos*). This game bird is farmed and released for hunting purposes on a massive scale in Europe and Sweden, but there are few studies on how this affects the original population and ecosystem. In this introductory essay, the mallard will be used as a model species for studies on the effects of releases of native species with a potentially alien genetic structure.

1.1 The species

The mallard is one of about 40 *Anas* species (dabbling ducks) in the world and is besides wigeon (*A. penelope*), gadwall (*A. strepera*), teal (*A. crecca*), pintail (*A. acuta*), garganey (*A. querquedula*) and shoveler (*A .clypeata*) one of seven breeding dabbling ducks in Fennoscandia.

The mallard is the biggest of the seven breeding dabbling ducks in Fennoscandia with a length of 50-65 cm and a weight of about 850-1450 g for males and 750-1200 g for females. The mallard drake has an unmistakable plumage from fall through early summer with a greenish head and a white collar separating it from the reddish purple breast. It also has characteristic curled black tail feathers and a yellow bill. The female is mottled brown with a darker line through the eyes that separate brighter sides of the head. The female also has a more brownish bill with a black ridge, a fact that can be used to distinguish between the male and female also when the male is in his nondescript eclipse plumage, similar to that of females. During this period in the summer the birds are flightless for 3-4 weeks and have to rely on their camouflage. Both male and females have orange legs and a blue speculum bordered with white lines at front and rear. A juvenile mallard is very similar to an adult female (Cramp and Simmons 1977).

The adaptability of mallards to different habitats is extreme; they are found from the tundra to the sub-tropical areas in the northern hemisphere (Cramp and Simmons 1977). You can find them in fresh, brackish and salt waters, in lakes, rivers and by the coasts, even in cities and parks. However, they prefer shallow waters, where most feeding occurs. Young mallards mostly catch insects above the surface and on land, but with age they increase their feeding in water by dabbling in the water surface and later on completely up-ending in the water in their search for invertebrates and seeds (Pehrsson 1979). Dabbling ducks use lamellae in their bill to sieve out seeds and insects from the water. Nevertheless, mallards are highly omnivorous and opportunistic and their diet, which changes by season, age and availability, consists of molluscs crustaceans, annelids, amphibians, roots, tubers, leaves, seeds and buds (Cramp and Simmons 1977; Pehrsson 1979; Dessborn et al. 2011).

The mallard is the most common and numerous duck in Sweden, especially in the southern parts. Because the mallard is a migrating bird in most parts of Europe, the number of mallards in the country changes dramatically from season to season, but also over the years. The trends are that the number of mallards in January has increased in Sweden while the number in September has decreased during the last 40 years (Nilsson 2009). The overall size of the breeding population in Sweden is about 200 000 pairs (Ottosson et al. in press). For such a widely distributed and numerous species like the mallard, it is very difficult to estimate the total population in Europe. The Western Eurasian population is often divided into five subpopulations based on their main wintering areas; four out of five of these are mainly located in Europe. Midwinter counts across Europe indicate that the total European population is about 7 million mallards (Delany and Scott 2006). At any rate, the mallard is the world's most abundant dabbling duck with an estimated global population of 18 million (Delany and Scott 2006). It is a common quarry species over most of its range and intensively managed in parts of North America and Europe.

1.2 Vital rates

There are four basic natural parameters to take into consideration when working with population models: mortality, nativity, immigration and emigration. However, when dealing with mallards and other animals that are manipulated by humans there are two additional major factors that have to be considered, hunting mortality and released hand-reared animals.

Introductions of hand-reared mallards have during a long time been a way for hunters in both Sweden and elsewhere to increase their hunting bag. Because there are, as in most countries, no obligation for breeders to report how many mallards they release into the wild it is very hard to assess an accurate total number of released mallards in Sweden. However, after interviews with some of the biggest breeders in Sweden, it is most probable that more than 200.000 young mallards released each year in Sweden (Söderquist et al. unpublished), see more under *Management and Humans*.

The survival of mallards from year to year largely fluctuates and depends on which country and habitat the duck lives in but also on the age and sex of the duck (Blohm et al. 1987; Reynolds et al. 1995; Gunnarsson et al. 2008). Ring recovery data from Sweden shows that about 50% of wild mallards ringed in their first year of life survive to a second year. The yearly survival after the two first years is a bit higher, roughly 60% (Olsson 1960; Bentz 1985; Fransson and Pettersson 2001). When looking at crude calculations of ring recoveries from hand-reared mallards in Sweden, the percentage of surviving mallards is different, only 25% of ringed mallards survive their first year and about 40% of those a second (Fransson and Pettersson 2001). An early study (Brakhage 1953), in which wild mallards were compared to mallards that were hand-reared from wild collected eggs, showed a computed first year survival rate of 30% in wild and only 9% in hand-reared mallards. One explanation for the difference between wild and hand-reared mallards in Brakhage's study could be that the wild mallards were ringed later in the season than the hand-reared. Mortality is higher when the ducklings are younger and more exposed to cold, starvation and predators. This could also explain the differences between Brakhage's study and the Swedish studies. Gunnarsson et al. (2008) made capture-recapture analysis on Finnish mallard ringing data from 1973-2005. In this study they estimated that the annual survival rate of mallard pulli was 21-42%. The average mallard has a life expectancy of between one and two years (Fransson and Pettersson 2001; Gunnarsson et al. 2008). However there are ducks in Sweden that have reached an age of at least 25 years (Gunnarsson et al. 2008).

In contrast to released, shot mallards are reported and the total number of shot birds is estimated each year by the Swedish Association for Hunting and Wildlife Management. According to data from the Swedish Association for Hunting and Wildlife Management (2012), the estimated hunting bag of mallards decreased from close to 120.000 mallards in 1945 to 65.000 mallards in the end of the 1970s, since then the estimated hunting bag has increased to about 100 000 mallards shot each year for the last ten years. Hunting is the most common cause of death for recovered ringed Swedish mallards, 72% of all recovered Swedish mallards are reported as dead by hunting (Fransson and Pettersson 2001); of mallards ringed in Malmö between 1938-1982, 89.2% were reported as shot (Bentz 1985). These numbers suggest that hunting has important effects on the mallard population. But what role does it have on population size? It has been discussed for a long time whether hunting mortality is additive or compensatory, i.e. if hunting mortality adds on to the natural causes of deaths or if it is compensated, keeping the total mortality at the same level as it would have been without hunting (Anderson and Burnham 1976; Burnham and Anderson 1984; Pöysä et al. 2004), see more under *Management and humans*. In any case, both hunting and releases of hand-reared mallards are likely to have large effects on the population of mallards and need attention to fully understand the development of the mallard population.

What also affect the survival of mallards are of course their predators. Depending on where mallards live, there are many different predators that pose a threat to eggs, ducklings, and adults. Predation has the greatest impact during egg-laying and incubation and when the juveniles are flightless, which will be discussed later on in the section about breeding ecology and brood rearing. During a pilot study with radio transmitters on Öland, Sweden, autumn 2010, several mallards were taken by goshawk (*Accipiter gentilis*) and others were taken by mink (*Mustela vison*) (Söderquist et al. unpublished). Other common predators on adult European mallards are Red fox (*Vulpes vulpes*), and some birds of prey, such as White-tailed Eagle (*Haliaeetus albicilla*), Gyrfalcon (*Falco rusticolus*) and Peregrine Falcon (*Falco peregrinus*) (Errington 1961). Nevertheless, the animal that poses the biggest threat to adult mallards is the human.

1.3 Migration

Throughout the years, ring recoveries have given us the most information about the migration of mallards. In Sweden alone 57 533 mallards were ringed 1911-2008, of these were 5858 recovered, giving a recovery proportion of 10.2% (Swedish Bird Ringing Centre 2009).From these recoveries we can learn a lot about movements, winter quarters, time spent at different places and so on.

During autumn migration, recovered Swedish mallards have in average left the country by November. The general direction of these migrating birds are southwest and they move at a speed of about 40 km per day (Fransson and Pettersson 2001). Recoveries that are above 25 km from ringing sites are most often in the general migration direction, whereas shorter movements are more random (Olsson 1960).

The mallard on Greenland *A. platyrhynchos conboschas* is considered a subspecies of *A. platyrhynchos*. It is sedentary and does not migrate for the winter (Scott and Rose 1996). Parts of the Icelandic population are also sedentary and do not migrate; the ones that do migrate spend their winter in Great Britain and on Ireland (Scott and Rose 1996). Where the Swedish mallards migrate depend on where they breed, how cold the winter is and on the age of the mallard. Even though the differences are small, northern ducks seem to migrate farther than more southern, a higher proportion of the northern ducks end up in Great Britain than the southern ducks that end up in the northwest of France. Mallards ringed in Sweden in summer migrate farther south in a cold winter than they would do in a mild winter, Swedish first-year mallards seem to migrate farther south than older mallards (Fransson and Pettersson 2001). Other mallards from Fennoscandia, northwest Russia and the Baltic usually winter in Denmark and down to northern France (Scott and Rose 1996). However, some mallards in this area are sedentary, leaving only if the winter is really harsh. Estimates say that about 40-50% of the mallards in Sweden migrate during winter, this number is probably decreasing with milder winters and better conditions (Olsson 1960). Mallards further southwest in Europe are sedentary with only regional movements. In the more central parts of Europe, some mallards stay if the conditions are good enough during winter while other migrate to the northern shoreline of the Mediterranean Sea and other migrate southeast along the Danube river and may intermix in the Black Sea with mallards from further east (Scott and Rose 1996).

Spring migration is much faster than the autumn migration and the ducks can return from their winter quarter in just a couple of days (Olsson 1960; Fransson and Pettersson 2001). Ducks are mostly income breeders, i.e. they rely on the food on their breeding grounds. But there is a trade-off between leaving winter quarters early with low energy reserves to arrive early on breeding grounds or staying longer at wintering quarters to store energy and return later at breeding sites (Arzel et al. 2006). On average, mallards are back in Sweden in the second half of February (Fransson and Pettersson 2001).

1.4 Pair formation and breeding ecology

Pair-formation in mallards occurs in late fall on staging sites or in winter quarters where ducks from many different places aggregate (Olsson 1960; Cramp and Simmons 1977). There are many different attributes that are important for mate choice in mallards, however it is the female that chooses her partner (Holmberg et al. 1989). It is important that mallards get enough food at the wintering site to make the migration to the breeding grounds with as much energy left as possible. To be able to concentrate on feeding, early pair-formation among ducks is one way to do it. Paired mallards have a higher rank and therefore better access to food at the wintering grounds, the male also watches over and guards the female during winter and migration, leaving her with more time to feed (Guillemain et al. 2003). Later on, the male follows the female back to her breeding grounds, often far away from his area of origin; such dispersal from one breeding area to another is called abmigration (Olsson 1960). Because females are more philopatric than males, i.e. they return to their original breeding site, males are often found further away form their birthplace than females (Lincoln 1934a; Fransson and Pettersson 2001).

Advantages have been seen for ducks arriving early at breeding sites. For example, teals arriving early can choose the best nesting sites and therefore get higher reproductive success than later arriving teals (Elmberg et al. 2005). It has been claimed that ducks time their nesting to the phenology of emerging invertebrates (Danell and Sjöberg 1977; Pehrsson 1984). However, a recent study (Dessborn et al. 2009) could not find any such correlation. The more probable explanation is that ducks rely on cues related to photoperiod, deciding on when to nest. Still, the amount of chironomids does have a positive correlation with duck brood use on lakes (Dessborn et al. 2009). When deciding where to nest, some lakes are considered as bad brood habitats. These lakes do not have enough food to sustain ducklings and this will affect the distribution of nesting pairs per lake (Pöysä et al. 2001; Dessborn et al. 2009). For a lake to be chosen as a nesting site, it should also be free from fish. Fishless lakes increase the breeding success in ducks (Elmberg et al. 2010). Presence of fish may affect breeding success in several ways. (Pehrsson 1979) noticed a decrease in feeding efficiency in ducklings in the presence of perch (*Perca fluviatilis*) and rudd (*Scardinius erythrophthalmus*). He explained this decrease in feeding efficiency with competition of food between ducklings and fish. However, there is another, perhaps greater, impact on ducklings from fish, namely predation, the most common fish to predate on ducks is pike (*Esox lucius*).

Mallard nests are usually found in the vegetation on the ground but may also be placed a couple of meters up in a tree. Most often they are close to water but they can also be found a couple of kilometres inland. The size of the nest is about 30cm in diameters and about 7-8cm deep. It is often made from grass and twigs and covered with down (Cramp and Simmons 1977). A normal clutch size is between 8-12 eggs, however clutch size and egg size can be affected by food quality prior to egg production (Pehrsson 1991). The female lays one egg each day and during this period the male is guarding the female. When the incubation starts the male and female spend less time together and the male soon leaves her (Holmberg and Klint 1991b). After the drakes leave their females, they gather in larger flocks to moult all their flight feathers, resulting in 4 weeks of flightless state. Also the females moult all their feathers a couple of weeks after hatching and are flightless for about a month (Cramp and Simmons 1977). After about 27 days the eggs start to hatch, normally all eggs hatch within the same day, if the clutch is lost during incubation the female can re-lay later the same summer (Cramp and Simmons 1977; Holmberg and Klint 1991a). The ducklings leave the nest within a day and are self-feeding from day one (Pehrsson 1979). During the incubation and the rearing period of ducklings there are many threats for the young and the mother.

The sex ratio of adult mallards is somewhat skewed; although males are more likely to get shot than females (Eygenraam 1957; Bentz 1985) there are more adult males than females (55% versus 45%) for most parts of the year (Eygenraam 1957; Ohde et al. 1983). According to Eygenraam's observations (1957) the sex-ratio is not that skewed from the beginning, which agrees well with that females have lower annual survival than males despite that more males than female are shot during hunting (Bentz 1985; Gunnarsson et al. 2008). The lower survival rate for females can be explained by the cost for the female to take care of her offspring. During egg laying and brood rearing she is more exposed to predation and has higher energy demands than during the rest of the year (Johnson et al. 1992).

1.5 Management and humans

There are many points of contact between mallards and man. In Europe alone there are about 9 000 000 hunters that potentially see the mallard as a game species (Elmberg 2009). There are also millions of interested birdwatchers in Europe who enjoy watching waterfowl and innumerable families and other people visit parks and feed ducks every year. As stated above, mallards are also carriers of pathogens which some may be transmitted to humans. All this makes the mallard an interesting species for humans. Accordingly, the mallard is one of the most well-studied animals in ecology (Elmberg 2009). But it is also important to be aware about that what we do also may affect mallards. For example, changes in agricultural practices may affect the population dynamics of mallards and other *anatidae* by altering their food supply, we also severely affect them, especially in migration times, by disturbing them by hunting and other human activities in nature (Arzel et al. 2006).

As stated earlier there has been a discussion whether mallard harvesting has an additive or a compensatory effect on mortality. An additive effect suggests that the total number of mallards that are shot and killed by hunters adds to the natural mortality and leads to higher total mortality than it would have been without hunting (Baldassarre and Bolen 2006). The opposite would be that hunting has compensatory effects such as compensatory natality and compensatory mortality. Compensatory natality occurs when a population increases its reproductive rate as a consequence of that hunting takes the population below its carrying capacity. Compensatory mortality means that when hunting lowers the population size below carrying capacity, the mortality is compensated by an increased survival of the individuals that escape hunting. This will keep the population almost at the same size as without hunting (Boyce et al. 1999; Williams et al. 2002; Pöysä et al. 2004). In North America the view was for a long time that hunting has an additive effect on mortality. However, after an extensive ringing study by Anderson and Burnham (1976) the opinion changed in favour to that hunting has a more compensatory effect, at least up to some point. Hunting mortality will of course be additive if it gets high enough; therefore it is important to adjust the hunting bag with respect to estimates of recruitment and previous bag statistics and to continuously evaluate the management strategy (Elmberg 2009).

It is important to know more about vital rates and density dependent processes to understand population changes, especially in hunted species. It is also important that estimates of population size are made before fall migration and harvesting starts. Exact information about bag statistics is also important for understanding changes in population size (Elmberg et al. 2006). However, due to releases of hand-reared mallards, the interpretation of bag statistics and the assessments of population sizes are much more complicated. The problem is rooted in that no distinction is made between hand-reared and wild mallards in censuses and bag statistics. At the present time, hardly any hand-reared mallards are ringed or marked in any way making it nearly impossible for hunters to know if the shot bird is a truly wild mallard or if it is a hand-reared released duck.

Using hand-reared mallards to increase the potential hunting bag seems like a working strategy, at least in the short term. However, that introduction of hand-reared mallards leads to a more permanent increase of the wild breeding population has little support in the published literature (Batt and Nelson 1990). According to Brakhage (1953) it is more justifiable with restoration or improvement of habitats than releasing hand-reared ducks if the objective is to increase the breeding population. Please read more about released hand-reared mallards in next section.

2. Restocking: a history

Even though some people see the pheasant and grey partridge as native Swedish species, both have been introduced by man. Although they may have occurred naturally and sparsely shortly after the glacial withdrawal, Grey partridges were probably introduced to Öland and Gotland already around 500 A.D. by Vikings, and pheasants were introduced in Sweden in the beginning of the 1700s (Myrberget 1990). Not only were they brought here by man, they have also been managed by us during hundreds of years for food and hunting purposes. In Great Britain, pheasants were kept in captivity already in the 11th century and mallards have been reared and released in Great Britain at least since 1651 (Myrberget 1990). Also in Sweden these birds were controlled early, during winter in Sweden, grey partridges were held indoor already in the 1760s (Myrberget 1990). As one can see, pheasant, grey partridge and mallard have been an interest for man for a long time. However, following sections are focusing on bag statistics, released numbers and trends for the mallard only.

2.1 Sweden

As stated before, bag statistics show that the hunting bag for mallards in Sweden was close to 120.000 birds per year right after the Second World War. During the following years the hunting bag decreased until 1980 when it was at its lowest with about 65.000 mallards shot per year, roughly the same as just before the Second World War. After 1980 the hunting bag has increased again, however the last 10 years it has fluctuated greatly. Today, more than 100.000 mallards are shot each year in Sweden (Dalby et al. in prep.). It was probably around the mid-20th century that releases of hand-reared mallards for hunting purposes became a bigger business in Sweden. IN order to keep and breed wild animals in Sweden you have to have permission from the Swedish Board of Agriculture. However, there is no need for permission to release hand-reared mallards in Sweden, nor any obligation to report how many are released. Accordingly, the extent or trends of releases are very hard to assess. In a study by Wiberg and Gunnarsson (2007) it is stated that at least 87.000 hand-reared mallards were released in Sweden 2005 based on questionnaires answered by breeders. However, after our own interviews with some breeders in southern part of Sweden, where releases are most common, it is most likely that more than 200.000 hand-reared mallards are released in the country each year (Söderquist et al. submitted).

Swedish hand-reared mallards can originate from either wild-caught birds or from imported eggs. Before September 2006 breeders could capture wild mallards and use as breeding birds. This was a good way to renew and increase the number of breeding birds on the farms and decrease the risk of inbreeding. However, in spring 2006 the first outbreak of high-pathogenic avian influenza occurred in Sweden (SVA 2010). After that, all mallard farms have to be completely closed for wild birds (Statens Jordbruksverk 2007). To renew breeding birds, breeders now have to trade with other farmers instead of capturing wild ones. As mentioned above, eggs are also imported from other countries, in 2010 and 2011 (until April) 39.000 and 30.000 eggs respectively, were registered as imported mallard eggs. All these eggs were imported from Denmark (Jönsson, pers. com). That these eggs were imported from Denmark does not mean that their true origin is Denmark, a country that in turn imports eggs from France. Hence, it is hard to know if the imported eggs originate from Denmark or France. Anyway, Sweden has imported mallard eggs directly from France before 2010 (Laikre et al. 2006).

Swedish hand-reared mallards are normally released in June—July when they are about 3 weeks old (Wiberg and Gunnarsson 2007). This is a couple of weeks earlier than for example in France. When to release the young mallards is a trade off; if they are released too early, the mortality is too high, and if they are kept to long on the farm they will be less wild and more used to humans. When they are released they have to have good access to food, usually corn or wheat is used in Sweden. The hunting season for mallards in the southern parts of Sweden is between 21st of August and 31st of December, in the northern parts the season ends the 30th of November (Sveriges Riksdag 1987)

2.2 Other Nordic countries

Among the Nordic countries Denmark is by far the one releasing the highest number of hand-reared mallards, and this have been a large business in Denmark at least since the 1950s (Søndergaard et al. 2006). It is estimated that Denmark released about 500 000 young mallards into the wild annually for hunting purposes at the end of 1990s (Vildtforvaltningsrådet 2006). However, in 2001 a regulation was introduced that only one duckling/50m^2 water surface can be released. This probably decreased the number to 400 000 mallards released per year, which is the present estimate. In 2007 the limit was adjusted to one duckling/150m^2 (Noer et al. 2008). The breeding population of wild mallards in Denmark is about 20 000 pairs and the winter population is about 135 000 individuals, and each year 600 000 mallards are shot in Denmark (Dalby et al. in prep.), which means that a large proportion of the shot birds are migrants. Until the beginning of 1970s the hunting bag for mallard in Denmark was about 350 000-400 000 individuals, ten years later the number increased to about 700 000 individuals each year, during the last ten years it has dropped again to about 600 000 (Noer et al. 2008; Dalby et al. in prep.).

Also in Finland, hunting mallards is a large business with 300 000 licensed hunters (Finnish Hunters' Association 2011). 250-300 000 mallards get shot each year in Finland and this number has been stable during at least the last 15 years (Dalby et al. in prep). Ring recovery data indicate that hand-reared mallards have been released in Finland at least between 1970-1990 (Söderquist et al. submitted). Currently, no or hardly any hand-reared mallards are released in Finland for hunting purposes. The breeding mallard population in Finland is about 160 000 pairs and the wintering population is only about 10 000 mallards, but it is slowly increasing (Dalby et al. in prep). Instead of releasing hand-reared mallards, Finland has chosen to use an alternative way to get a sustainable harvest. Each summer, breeding pairs and broods are estimated based on observations, from these estimations, hunting bag limits are recommended to the hunters for keeping the harvest at a sustainable level. This management is a type of adaptive harvest management (AHM) (Baldassarre and Bolen 2006). Read more about AHM under *North America*.

In neither Norway nor Iceland, hunting for mallard is extensive today. Barely 17 000 mallards are shot in Norway each year, which is a dramatic decrease since 1988 when about 80 000 were shot, on Iceland about 10 000 mallards are shot each year. There are no hand-reared mallards released in any of the two countries (Dalby et al. in prep).

2.3 Europe

There are about 9 000 000 hunters in Europe, which makes the mallard a targeted species. (Elmberg 2009) Therefore it is a common practice in some European countries to hand-rear mallards and to release them for hunting purposes. In France large scale introduction of mallards to increase the huntable population has been a continuously growing business for almost 40 years (Champagnon et al. 2009). In the mid 1980s about 800 000 mallards were released each year (Myrberget 1990), and now days about 1 400 000 mallards are released in France, which can be compared with the wintering population of about 270 000 (Champagnon et al. 2010). In Camargue in southern France, which is an important wintering site for mallards and other ducks, at least 30 000 hand-reared mallards are released every year (Champagnon et al. 2009). In France, farmed mallards are generally released at the age of 6-9 weeks (in comparison to 3 weeks in Sweden) about 2 months prior to the start of hunting. In France, as well as in Sweden, released mallards are fed on the release site to keep them there until the start of the hunting season (Champagnon et al. 2009).

In France, Belgium, Holland and Germany, close to 2.5 million mallards are shot each year. How many of them that are hand-reared is hard to estimate (Bertelsen and Simonsen 1989). In the United Kingdom, hand-reared mallards have been released for at least 100 years at a bigger scale (Boyd and Harrison 1962) and in the beginning of 1980s, probably around 500 000 mallards were released (Harradine 1985). At the same time 525 000 were shot each year (Harradine 1982); about 175 000 of these were wild and 350 000 were hand-reared (Hill 1984). During this time the total hunting bag for Europe was about 6 million mallards per year (Myrberget 1990). Now, that figure is about 4.5 million (Guillemain et al. 2010). Also Italy should be mentioned as a country where hand-rearing and releases of mallards are a common practice. In the mid 1980s it was estimated that Italy released about 250 000 mallards per year (Myrberget 1990). As stated above eggs from hand-reared mallards are not only used in the country that they were laid but can be exported to other countries. This is the case for some of the eggs from France that are sold to Denmark and also Sweden (Laikre et al. 2006).

2.4 North America

Duck hunting has a long history in North America, all the way back to Native Americans who hunted them for food. But what really made duck hunting an extensive activity was the development of the shotgun in the late 19th century (Baldassarre and Bolen 2006). Around the turn of the century there were few restrictions on duck hunting and enormous numbers were shot. In 1960 2 million mallards were shot in the USA, ten years later the number was close to 5.5 million, another ten years later it had dropped to 2 million again. In 2000 it peaked at 6.2 million mallards per year only to drop to today's number at about 4 million. Number of mallards in USA, 2011, is estimated to 9.2million individuals in the breeding population which in historical terms is a high number (U.S. Fish and Wildlife 2011). In 2006 there were 1.1million duck hunters in the USA (U.S. Fish and Wildlife 2006).

In the first half of the 20th century hand-reared mallards were released in USA to increase the breeding population. After studies by, for example, Brakhage (1953) that showed that the survival of hand-reared mallards was low, releases were considered non-practical and expensive. Instead, Adaptive Harvest Management (AHM) was to be used to optimize the harvests of ducks without over-exploitation of the population. AHM consists of several different models predicting the effects of different regulatory alternatives, for example bag size and length-, opening- and closing of hunting season. The models are based on estimates of the breeding populations and habitat- and environmental conditions. When the next year's estimations of the breeding population arrives each model are contrasted, so the best model can be applied the coming year (Baldassarre and Bolen 2006). However, releases of hand-reared mallards still occur in a few places in USA, for example, in Maryland, 140 000 mallards were released in the end of the 1980s (Smith and Rohwer 1997).

3. Effects

When hand-rearing mallards in captivity there is a risk that they will become genetically, morphologically or behaviourally different compared to wild mallards. Even though wild mallards are used as breeding stock, differences can be seen already after a couple of generations. These differences can be passed on and affect the natural population if the released mallards survive and succeed during the breeding season. Introduction of these hand-reared animals may for example influence the genetic composition, behaviour and reproductive success of the natural population (Myrberget 1990). Here, some possible effects from introductions of hand-reared mallards on the wild population are treated.

3.1 Genetic

Both harvest and introduction of hand-reared animals can alter the genetic variation in a population (Laikre et al. 2006; Allendorf et al. 2008). Genetic effects from harvesting a population include reduction or even extinction of local gene pools due to over-harvesting in a certain area, selective genetic change due to that harvesting is a non-random process, and a decrease in effective population size (N_e) with potential inbreeding and genetic drift related problems (Allendorf et al. 2008). Hand-reared, released animals may originate from non-local populations or may have been reared during artificial selection pressure and therefore risk having an alien genetic composition. There are several genetic risks of releasing these potentially 'alien' into the wild. For example, hybridization and introgression of non-native genes may break down locally adapted genes in the natural population. There is also a risk that the local population will decrease due to competition or disease transmission, leading to a further decrease in genetic variation. The local population can even get extinct and completely displaced by the released alien population (Laikre and Palmé 2005; Laikre et al. 2006).

When talking about large scale releases of hand-reared mallards in Europe, all these genetic risks are possible. However, the pair formation of mallards tells us that this may not be the case. As stated before mallard females are philopatric, i.e. they return to their natal ground, but males instead go with their female to hers. As a result the population is constantly mixing, which would make the European population fairly panmictic.

When looking at mitochondrial DNA in mallards, Kraus et al. (2011b) found a difference in genetic structure between the North American continent and the Eurasian (F_{st}=0.51). However, hardly any differences was found within the North American or the Asian continent, but the authors leave the door open for genetic structuring to exist among flyways in Europe (Kraus et al. 2011b). Partly based on the same mitochondrial DNA, Greenland mallards were clearly differentiated from mallards sampled in Canada, Great Britain and The Netherlands (F_{st}=0.44, 0.48 and 0.62 respectively) while the difference between Great Britain and The Netherlands was rather small (F_{st}=0.048) (Zeddeman et al. 2009). Obviously, much remains to be elucidated when it comes to natural patterns of genetic structuring in the mallard.

In addition, there are few studies on the genetic effects of releasing hand-reared mallards into the wild (Viltforvaltningsrådet 2006). However, some studies do exist. When Baratti et al. (2008) looked at microsatellites, searching for genetic differences between presumably wild mallards, farmed mallards and urban mallards in Italy, they found a distinct separation between the urban group and the other two groups. The explanation for these differences could be a geographic differentiation or genetic drift, the explanation for the lack of difference between the wild and the farmed mallards could be that farmed mallards fly to wild areas and mix or the use of wild mallards as breeders on the farms (Baratti et al. 2009).

Another study on microsatellites explored the genetic effects of released mallards and was carried out by Champagnon et al. (2011). Their results showed that wild mallards sampled 2009-2010 were not significantly different to wild mallards sampled 1883-1975, i.e. before massive releases of hand-reared mallards begun. Still, hand-reared mallards were significantly different to wild mallards. Their results suggest that even though hand-reared mallards show a genetic difference compared to wild conspecifics they have little impact on the wild population (Champagnon et al. 2011).

3.2 Morphological

When breeding animals in captivity there is a risk that the selection pressure is different compared to the natural selection pressure in the wild. If this is the case there is also a risk that the animals reared will show phenotypic differences to wild conspecifics. These phenotypic traits may be transferred to the wild population if the released mallards hybridize with the wild. Hybridization among ducks is very common and can be observed in most city parks all over the world where mallards with strange colorations and sizes can be seen. These hybridizations are most often between mallards and different breeds of domesticated ducks (*Anas platyrhynchos domestica*) such as the Peking duck (*Anas peking*). Already in the early 1930s hand-reared, released mallards were heavier with a stocky body (Lincoln 1934b).

The bill of a dabbling duck is a complex structure and an important tool for the duck to obtain food. On the upper and lower mandible there are lamellae along the edges that help filtering the water and sieve out food particles (Champagnon et al. 2010). The density of the lamellae and hence, the space between the lamellae, decide how large food particles that can be retained in the bill. The shorter distance between the lamellae the smaller food particles can be sieved out, but also, the shorter distance the easier the lamellae can get clogged by mud and other non-digestible matter (Champagnon et al. 2010). Bill morphology among dabbling ducks is often different between species and may help the different species to maintain different food preferences, which is often thought to reduce inter-specific competition, allowing more species to coexist (see Nudds et al. 2000 and references therein).

If hand-reared mallards are fed with different-sized food in captivity than in the wild, the selection pressure for lamellar density changes and a change in lamellar density will occur. Breeders in Sweden and other countries in Europe usually feed captive mallards large food items like food pellets, corn or wheat. This will relax the selection pressure for high lamellar density in the bill and may over time lead to fewer lamellae in the bill of hand-reared mallards. This may already have happened in France. Champagnon et al. (2010) compared bill morphology in three different groups of mallards. Museum specimens shot before 1970 when the releases of hand-reared mallards were few, wild-caught or shot mallards during winter of 2007-2008 whose origin could be either wild or hand-reared and hand-reared mallards studied during winter of 2007-2008. Their study showed that lamellar density was significantly lower in the wild population now than it was in the historical group of mallards, even though the difference was small in absolute numbers. To rule out other explanations than farming effects they used a control group consisting of teals. Teals have never been hand-reared in the same way and extent as mallards in Europe and no significant difference between historical and modern teals could be seen (Champagnon et al. 2010).

The body mass of migrating mallards fluctuates over the year because of behavioural adaptations to be able to cope with weather and demands related to migration. In mid-winter, the mallard is heavy, but as spring migration approaches it gets lighter (Guillemain et al. 2010). Even though there are very few studies available on hand-reared mallards, it has been presumed that they are bigger than true wild mallards (Pehrsson 1982). Guillemain et al. (2010) conducted a study where they compared the body mass of modern mallards and teals with historical mallards and teals. The results showed that both mallards and teals are heavier but not bigger now than before. The authors speculated that this is rather due to changes in climate and local habitat improvements than an effect of releases of hand-reared ducks (Guillemain et al. 2010). Nevertheless, morphometric changes in mallards because of released hand-reared birds are still possible and needs more attention(Gunnarsson et al. 2011). Byers and Cary (1991) found that North American wild mallards had narrower bills and shorter, narrower tarsi than game-farmed and urban mallards did. In Europe a similar study showed that hand-reared mallards had a shorter and higher bill than wild mallards, and the former were also bigger in general but with shorter wings making it harder for the duck to take off (Pehrsson 1982).

3.3 Migration

The migratory habits of mallards differ a lot between regions and climes. In northern Europe, large parts of the population migrate southwest during autumn (Scott and Rose 1996; Fransson and Pettersson 2001). However, as long as the mallards have open water and access to food some of them will stay over winter. With a changing climate leading to milder winters, the migration distance will probably decrease (called short-stopping) and the sedentary populations of mallards will increase in northern Europe (Olsson 1960; Sauter et al. 2010).

Another factor that could affect the migration of mallards is releases of hand-reared mallards. Both migration distance and homing effects have been studied and analyzed in released mallards in for example North America (Lincoln 1934b; Brakhage 1953; Lee and Kruse 1973), Sweden (Olsson 1960; Fransson and Pettersson 2001; Söderquist et al. submitted) and Britain (Boyd and Harrison 1962). Most of these studies show that hand-reared mallards migrate shorter distances than wild ones. However, the results from both Brakhage (1953) and Lee and Kruse (1973) showed similar migration behaviour for hand-reared and wild mallards. Hand-reared mallards may during generations on farms lose their innate natural migration behaviour leading to shorter migration distances. Another explanation for shorter migration distances in hand-reared mallards could be that eggs from non-migratory populations in central and southern Europe are exported to and used in countries where the population is naturally migratory, e.g. in Sweden. If hand-reared mallards with non-natural migration behaviour intermix with wild mallards there is a risk that the migrating populations become more sedentary. Depending on how climate will change, this may or may not lead to maladaptation, but definitely to some loss of present regional adaptations, if any.

3.4 Survival

There are only a few modern studies on survival in hand-reared mallards. However in a Danish report it is stated that about 90% of the released ducklings are still alive when the hunting begins the 1st of September. This high number can be explained by that they are fed and protected from predation (Vildtforvaltningsrådet 2006). When longevity was compared between wild and hand-reared mallards in Sweden and Finland, the latter lived much shorter than wild in both countries with a mean survival of 258 days for hand-reared Swedish mallards and 575 days for wild, in Finland the mean survival for hand-reared mallards was 129 days and 388 days for wild (Söderquist et al. submitted). That hand-reared mallards have a higher mortality rate than wild ones has also been confirmed by Brakhage (1953). The most common cause of death for both wild and hand-reared ringed mallards is hunting (Fransson and Pettersson 2001). Hand-reared mallards are more vulnerable to hunting than wild (Brakhage 1953) and may also have a higher vulnerability to predation because of inferior anti-predator behaviour than true wild birds (Schladweiler and Tester 1972; Parish and Sotherton 2007). Using hand-reared mallards to boost the huntable population that season is a working strategy, but releasing hand-reared mallards to increase the breeding population next year has little support in the published literature because of low survival (Batt and Nelson 1990). By releasing hand-reared mallards on hunting grounds it is possible that a greater part of the wild mallards avoid the gun and thereby the survival of wild mallards will increase to the cost of lower survival for the hand-reared.

3.5 Population ecology

How the releases of hand-reared mallards affect population ecology and population dynamics in mallards is not well studied. To achieve this, one has to know the current status of the population. Are the released hand-reared mallards an addition below or above carrying capacity? If the population has not reached its carrying capacity the releases are less likely to have negative effects. But if the releases are an addition above carrying capacity it is likely that some density dependent factors like availability of food, predation, hunting mortality and disease transmission will affect the population in a negative way from the mallard point of view. Another important question is then; which ones will suffer, hand-reared or wild mallards? When talking about hunting mortality, it is probably more hand-reared mallards that will be affected because they are released in areas where hunting occurs. However, the other factors are more elusive and need more scientific attention. A common example when talking about density dependence is how food abundance can affect the population size. When the population gets too big, the amount of food will not be enough to support the whole population. The result will then be a decrease in birth rate or an increase in mortality rate, or both. Studies of mallards indicate that this is the case, at least during the breeding period (Gunnarsson et al. 2004). In that case, the released mallards have to live long enough and increase the breeding population to contribute to this problem. However, with an increasing winter population due to milder winters and a potentially sedentary released hand-reared population there is a risk of food shortage also during winters leading to a reduced population (cf. Hill 1984). Other density dependent factors that can take effect due to releases are for example nest site limitations (Pöysä and Pöysä 2002) and nest predation (Hill 1984; Gunnarsson and Elmberg 2008). Both require that the hand-reared mallards survive long enough to become a part of the breeding population.

To do accurate estimations on sustainable harvests and achieve a working Adaptive Harvest Management, it is crucial to know how the density dependent factors are working and to have good understanding about population structures (Hill 1984; Pöysä et al. 2004). For more about Adaptive Harvest Management, see section 2.4 *North America.*

3.6 Effects on other species and the environment

Releases of hand-reared mallards may have effects on the water quality where they are released because their excrements contain nutrients, which may lead to eutrophication (Søndergaard et al. 2006). The ducks could also have an effect on flora and fauna by for example feeding on water plants and predation of tadpoles and newts (Søndergaard et al. 2006). Also the enormous loads of grain that are used to feed the ducks may lead to eutrophication if not eaten (Søndergaard et al. 2006). The increased nutrient level in the water will lead to an augmentation of plankton. More plankton will in turn lead to lower visibility and plants on the bottom will die if not getting enough sunlight. These plants are also important for other life such as fish, newts and tadpoles. Most often it is phosphorus that is the limiting nutrient in lakes (Søndergaard et al. 2006).

Anther possible problem is that rat poison sometimes is used at the feeding place. This might be a problem for some birds of prey that mainly live on rodents, like Eurasian Kestrel (*Falco tinnunculus*) and Common Buzzard (*Buteo buteo*) (Vildtforvaltningsrådet 2006). However, there are also possible positive side effects from mallard releases: more wildlife reserves are created, which can help protecting other animals. Also, more wetlands and ponds are constructed, which will help increasing the biological diversity locally (amphibians, other waterbirds). By focussing the hunting on species that are hand-reared and released, hunting pressure on other wild species may be relieved (Vildtforvaltningsrådet 2006). However, the contrary has also been suggested; shooting intensity in an area increases when more hand-reared ducks are released leading to more wild ducks shot as well (Hill and Robertson 1987). It is also known that introduced mallards may attract wild conspecifics and increase the biological diversity at the release site (Pöysä et al. 2001).

3.7 Disease transmission

There are generally four reasons why waterfowl are prone to pick up and pass on diseases. First, most are gregarious during some part of the year when they gather in big flocks. In these flocks it is easy to get infected and spread diseases. Second, due to environmental changes many crucial habitats for these birds are getting fewer, increasing crowding and infection spread. Third, waterfowl are migrating birds moving great distances and may therefore also spread diseases over large areas. They also stop at many different places and risk to pick up pathogens on the way. Fourth, some waterfowl species seem to be inherently more susceptible to pathogens than others and many diseases within these species can spread fast (Baldassarre and Bolen 2006). The transmission occurs when birds come in contact with discharges of infected birds, for example faeces, and can spread through a population very fast, especially in a high density population such as on a farm.

When hand-reared mallards are released into the wild there will be a higher concentration of individuals than usual in a confined area, this will increase the risk of outbreaks of diseases and parasites among the mallards (Baldassarre and Bolen 2006; Vildtforvaltningsrådet 2006). Furthermore, if releases of hand-reared mallards leads to shorter migrations and more sedentary populations, this can lead to a higher risk of outbreaks of zoonotic pathogens in humans (Altizer et al. 2011). Influenza A virus can cause diseases in birds as well as mammals and the influenza that is adapted to birds is often referred to as avian influenza virus (AIV). In ducks, the AIV spreads easily between wildfowl by the fecal-oral transmission way, i.e. when they ingest faeces. Low pathogenic avian influenza virus (LPAIV) does not affect ducks very much; infected ducks have a lower body mass and get a small fever (Latorre-Margalef et al. 2009; Jourdain et al. 2010). Some LPAIV can infect poultry and among them mutate into high pathogenic avian influenza virus (HPAIV), which may rarely be transmitted to humans with a deadly outcome. Duck plague is also one of the diseases that can occur within captive waterfowl, no hand-reared mallards should therefore be released if there has been a history of disease within that population (Baldassarre and Bolen 2006). However, in Sweden there has never really been a problem with diseases on mallard farms and no vaccinations occur on released hand-reared Swedish mallards (Wiberg and Gunnarsson 2007). Always when releasing hand reared mallards into the wild, supplemental food such as food pellets, corn or wheat is also placed at the release site to enhance the chance of survival for the ducks. Large piles of food lies near the water during several weeks, this food risk attacks by fungi such as *Aspergillus* and increase the risk of outbreaks of aspergillosis.

3.8 Economical

With 9 million potential duck hunters in Europe, there is no question that duck hunting in general and hunting of mallards in particular is a big business. Accordingly, the possibility to increase the turnover increases significantly with releases of hand-reared mallards. Releases of hand-reared mallards make it possible to invite more hunters to bigger hunting sessions more often. In Sweden the hunting on released mallards alone generates close to 10 million euros per year (Laikre et al. 2007). In Denmark, 160 000 hunters are registered and hunting in Denmark yields 250 million euros per year (Vildtforvaltningsrådet 2006). If releases of hand-reared mallards in Denmark will come to a stop, this figure will dramatically decrease. The same is probably true for all countries releasing hand-reared mallards for hunting purposes. This kind of hunting is a major source of income for many landowners around Europe. Rearing mallards on farms and also feeding them and taking care of them after the release, with for example predation protection, is a costly business which generates work and money in other sectors as well. Not to be forgotten is the recreational effect this business encourages as well, with much outdoor and physical activity for hunters as well as dog owners and landowners.

4. Discussion

4.1 Summary

The accumulated knowledge about the mallard is substantial. It is the world's most widespread duck and a model species in many biological research areas. It is also an economical important game species with a yearly hunting bag of 4.5million ducks in Europe alone.

Because the mallard is heavily hunted in many European countries it has also been subject to extensive management and conservation programs such as wetland restoration, but also large-scale introductions of hand-reared mallards into the wild. Even though the latter has been practiced more or less for more than half a century, surprisingly little is known about the extent of releases in Europe. Estimations of released mallards per year in some European countries are; Sweden 200 000, Denmark 400 000 and France 1 400 000.

The effects of these large-scale introductions of hand-reared mallards into the wild to augment the potential hunting bag are even less examined. Some studies show that there is a potential genetic effect on the wild mallard population due to hand-reared mallards possibly having a different genetic composition compared to wild conspecifics. Other studies show that there may also be morphological differences between wild and hand-reared mallards, possibly leading to maladaptation spreading into the wild population. Many more potential effects of releasing hand-reared mallards into the wild need to be studied; is the survival of hand-reared mallards significantly lower than that of wild mallards? Is migration of hand-reared shorter than in wild? A few studies also look at how the releases can affect other species and the environment where they are released and also the potential disease transmission between mallards and other species. Because of the large number of released and consequentially shot hand-reared mallards, this practice yields a lot of money, however, it is hard to assess the actual economical costs and benefits of rearing and releasing mallards.

4.2 Research needs and future studies

In comparison to the gross number of scientific mallard studies there are rather few about the effects of released hand-reared birds, leaving a gap in knowledge in this area (Søndergaard et al. 2006). It is essential and fundamental to know the extent of the practice of releasing hand-reared mallards into the wild. At present, there are no restrictions in Sweden on how many mallards that can be released at one time or in one place. There are also no obligations to report how many ducklings that are released during one season. This would be an easy thing to do and would be of great use for researchers working with for example population ecology or population trends to be able to understand the fluctuations in population sizes.

To get basic information on how hand-reared mallards manage in the wild, large scale ringing was conducted for many years in Sweden (Fransson and Pettersson 2001). Unfortunately, this has stopped. Nowadays only ringing of wild mallards occurs. However, to understand how hand-reared mallards cope in the wild today compared to wild ones, it is essential to continue large-scale ringing. We plan to ring all hand-reared mallards released in certain areas to be able to estimate survival, dispersal and proportion shot. To get even more data and also more knowledge about migration, habitat use and time budgets, we will use GPS-loggers fitted to both wild and hand-reared mallards. By using ringing data together with our GPS-loggers we will increase sample size and get more accurate and valid results (Lindberg and Walker 2007).

There are probably some genetic effects of releasing hand-reared mallards into the wild, but the extent of this is not well studied and needs more attention (Vildtforvaltningsrådet 2006). With relatively new techniques we will study the possible introgression from hand-reared mallards to the wild population. With a set of Single Nucleotide Polymorphisms (SNPs) produced for mallards by Kraus et al. (2011a) it is now possible to study mallard population genetic in a cost and time efficient way (Vignal et al. 2002; Morin et al. 2004; DeYoung and Honeycutt 2005; Wink 2006; Kraus et al. 2011a). With the help of this SNP-set our aim is to create a genetic map of wild and hand-reared mallards in Europe, including samples from Sweden, Denmark, France and Czech Republic.

To complement studies from France demonstrating a morphological change in wild mallards during the last 30 years, morphological studies will also be carried out here in Sweden. It has for a long time been suspected that hand-reared mallards are morphologically different compared to their wild conspecifics (Lincoln 1934b; Pehrsson 1982) but more studies are needed to answer this question. Another very important question needs to be addressed, namely if wild and hand-reared mallards readily mate. This is a fundamental question to answer, if no mating occurs between the two, no introgression will occur. So far, there are only few studies of mate choice between hand-reared and wild mallards and this needs further attention (Cheng et al. 1979) .

5. Acknowledgements

I would like to thank Johan Elmberg and Gunnar Gunnarsson for all the comments on the manuscript improving it greatly. I am also grateful for all the encouragement from my supervisors; Carl-Gustaf Thulin, Johan Elmberg and Gunnar Gunnarsson, who have supported me and answered all my questions during the introduction of my PhD.

6. References

Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N (2008) Genetic effects of harvest on wild animal populations. Trends Ecol Evol 23 (6):327-337.

Almäng A (1996) Utländska gran- och tallprovenienser i svenskt skogsbruk. Sveriges Lantbruksuniversitet,

Altizer S, Bartel R, Barbara AH (2011) Animal migration and infections disease risk. Science 331:296-302.

Anderson DR, Burnham KP (1976) Population ecology of the mallard. VI. The effect of exploitation on survival. US Fish and Wildlife Service Resource Publication 128.

Arzel C, Elmberg J, Guillemain M (2006) Ecology of spring-migrating Anatidae: a review. Journal of Ornithology 147:167-184.

Baldassarre GA, Bolen EG (2006) Waterfowl ecology and management. Second edn. Krieger Publishing Company, Malabar, Florida

Baratti M, Cordaro M, Dessi-Fulgheri F, Vannini M, Fratini S (2009) Molecular and ecological characterization of urban populations of the mallard (Anas platyrhynchos L.) in Italy. Italian Journal of Zoology 76 (3):330-339.

Batt BDJ, Nelson JW (1990) The role of hand-reared mallards in breeding waterfowl conservation. Transactions of the North American Wildlife and Natural resources Conference 55:558-568.

Bentz P-G (1985) Studies on some urban Mallard *Anas platyrhynchos* populations in Scandinavia. Part I: Causes of death, mortality and longevity among Malmö Mallards as shown by ringing recoveries. Fauna Norvegica, Series C 8:44-56.

Bertelsen J, Simonsen NH (1989) Documentation on Bird Hunting and the conservation status of the species involved; situation in 1986 (Revised Edition). Copenhagen : Ministry of the Environment (Denmark), Game and Wildlife Administration.

Blohm RJ, Reynolds RE, Bladen JP, Nichols JD, Hines JE, Pollock KH, Eberhardt RT (1987) Mallard mortality rates on key breeding and wintering areas. Transactions of the North American Wildlife and Natural Resources Conference 52 (246-257).

Boyce MS, Sinclaire ARE, White GC (1999) Seasonal compensation of predation and harvesting. Oikos 8 (3):419-426.

Boyd H, Harrison J (1962) First-autumn dispersal of hand-reared Mallard. The Wildfowl Trust 12:70-73.

Brakhage GK (1953) Migration and mortality of ducks hand-reared and wild-trapped at Delta, Manitoba. J Wildl Manage 17 (4):465-477.

Burnham KP, Anderson DR (1984) Tests of compensatory vs. additive hypothesis of mortality in mallards. Ecology 65 (1):105-112.

Byers SM, Cary JR (1991) Discrimination of mallard strains on the basis of morphology. Journal of Wildlife Management 55 (4):580-586.

Champagnon J, Guillemain M, Gauthier-Clerc M, Lebreton J-D, Elmberg J (2009) Consequences of massive bird releases for hunting purposes: Mallard *Anas platyrhynchos* in the Camargue, southern France. Wildfowl 2:184-191.

Champagnon J, Guillemain M, Elmberg J, Folkesson K, Gauthier-Clerc M (2010) Changes in Mallard *Anas platyrhynchos* bill morphology after 30 years of supplemental stocking. Bird Study 57 (3):1-8.

Champagnon J, Crochet P-A, Kreisinger J, Cízková D, Gauthier-Clerc M, Massez G, Söderquist P, Albrecht T, Guillemain M (2011) Restricted genetic impact of massive restocking on wild mallard. Animal Conservation.

Chapin FS, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Diaz S (2000) Consequences of changing biodiversity. Nature 405:234-242.

Cheng KM, Shoffner RN, Phillips RE, Lee FB (1979) Mate preference in wild and domesticated (game-farm) mallards: II. Pairing success. Animal Behaviour 27, Part 2:417-425.

Cramp S, Simmons KEL (1977) The birds of the western Palearctic, vol 1. Clarendon Press, Oxford

Danell K, Sjöberg K (1977) Seasonal emergence of chironomids in relation to egglaying and hatching in a restored lake (northern Sweden). Wildfowl 28:129-135.

Delany S, Scott DA (2006) Waterbird population estimates, 4th edn. Wetlands International, Wageningen

Dessborn L, Elmberg J, Nummi P, Pöysä H, Sjöberg K (2009) Hatching in dabbling ducks and emergence in chironomids: a case of predator-prey synchrony? Hydrobiologia 636 (1):319-329.

Dessborn L, Brochet AL, Elmberg J, Legagneux P, Gauthier-Clerc M, Guillemain M (2011) Geographical and temporal patterns in the diet of pintail *Anas acuta*, wigeon *Anas penelope*, mallard *Anas platyrhynchos* and teal *Anas crecca* in the Western Palearctic. European Journal of Wildlife Research 57:1119-1129.

DeYoung RW, Honeycutt RL (2005) The molecular toolbox: Genetic techniques in wildlife ecology and management. J Wildl Manage 69 (4):1362-1384.

Elmberg J, Nummi P, Pöysä H, Gunnarsson G, Sjöberg K (2005) Early breeding Teal *Anas crecca* use the best lakes and have the highest reproductive success. Annales Zoologici Fennici 42:37-43.

Elmberg J, Nummi P, Pöysä H, Sjöberg K, Gunnarsson G, Clausen P, Guillemain M, Rodrigues D, Väänänen V-M (2006) The scientific basis for a new and sustainable management of migratory European ducks. Wildlife Biology 12:121-127.

Elmberg J (2009) Are dabbling ducks major players or merely noise in freshwater ecosystems? A European perspective, with references to population limitation and density dependence. Wildfowl (2):9-23.

Elmberg J, Dessborn L, Englund G (2010) Presence of fish affects lake use and breeding success in ducks. Hydrobiologia 641 (1):215-223.
Errington PL (1961) An American Visitor's Impressions of Scandinavian Waterfowl Problems. The Journal of Wildlife Management 25 (2):109-130.
Eygenraam JA (1957) The sex-ratio and the production of the mallard, Anas platyrhynchos L.:117-143.
Finnish Hunters' Association (2011) Finnish Hunting. http://www.metsastajaliitto.fi/?q=en/node/531. Accessed 2011-09-20
Fransson T, Pettersson J (2001) Svensk ringmärkningsatlas [Swedish Bird Ringing Atlas], vol 1. Ljungföretagen Tryckeri AB. (In Swedish, English summary). Örebro
Guillemain M, Caldow RWG, Hodder KH, Goss-Custard JD (2003) Increased vigilance of paired males in sexually dimorphic species: distinguishing between alternative explanations in wintering Eurasian wigeon. Behavioral Ecology 14 (5):724-729.
Guillemain M, Elmberg J, Gauthier-Clerc M, Massez G, Hearn R, Champagnon J, Simon G (2010) Wintering French Mallard and Teal Are Heavier and in Better Body Condition than 30 Years Ago: Effects of a Changing Environment? Ambio 39 (2):170-180.
Gunnarsson G, Elmberg J, Sjöberg K, Pöysä H, Nummi P (2004) Why are there so many empty lakes? Food limits survival of mallard ducklings. Canadian Journal of Zoology-Revue Canadienne De Zoologie 82:1698-1703.
Gunnarsson G, Elmberg J (2008) Density-dependent nest predation - an experiment with simulated Mallard nests in contrasting landscapes. Ibis 150 (2):259-269.
Gunnarsson G, Elmberg J, Dessborn L, Jonzen N, Pöysä H, Valkama J (2008) Survival estimates, mortality patterns, and population growth of Fennoscandian mallards *Anas platyrhynchos*. Ann Zool Fenn 45 (6):483-495.
Gunnarsson G, Elmberg J, Waldenström J (2011) Trends in body mass of ducks over time: The hypotheses in Guillemain et. Revisited. Ambio 40:338-340.
Harradine J (1982) Sporting shooting in the United Kingdom - some facts and figures. In: Proceedings of the second meeting of International Union of Game Biologists - Working group on Game Statistics, Netherlands, 1982. pp 63-83
Harradine J (1985) Duck shooting in the United Kingdom. Wildfowl 36:81-94.
Hill DA (1984) Population regulation in the mallard (Anas platyrhynchos). Journal of Animal Ecology 53:191-202.
Hill DA, Robertson P (1987) Hand reared pheasants: how they affect productivity. Game Conser Ann Rep 18:65-69.
Holmberg K, Edsman L, Klint T (1989) Female mate preferences and male attributes in mallard ducks (Anas platyrhynchos). Animal Behaviour 38 (1):1-7.
Holmberg K, Klint T (1991a) Female mallards maximize their breeding success by laying extra eggs. Mallard ducks - Mate choice and breeding success. Stockholm University
Holmberg K, Klint T (1991b) Mate guarding and female feeding efficiency among mallard pairs (Anas platyrhynchos). Mallard ducks - Mate choice and breeding success. Stockholm University
Johnson DH, Nichols JD, Schwartz MD (1992) Population dynamic of breeding waterfowl. In: Ecology and management of breeding waterfowl. University of Minnesota Press, pp 446-485
Jourdain E, Gunnarsson G, Wahlgren J, Latorre-Margalef N, Bröjer C, Sahlin S, Svensson L, Waldenström J, Lundkvist Å, Olsén B (2010) Influenza virus in a natural host, the mallard: Experimental infection data. Plos ONE 5 (1):e8950.
Kraus RHS, Kerstens HHD, Van Hooft P, Crooijmans RPMA, Van der Poel JJ, Elmberg J, Vignal A, Huang Y, Li N, Prins HHT, Groenen MAM (2011a) Genome wide SNP discovery, analysis and evaluation in mallard (Anas platyrhynchos). BMC Genomics 12:11.
Kraus RHS, Zeddeman A, van Hooft P, Sartakov D, Soloview SA, Ydenberg RC, Prins HHT (2011b) Evolution and connectivity in the world-wide migration system of the mallard: Interferences from mitochondrial DNA. BMC Genetics 12 (99).

Laikre L, Palmé A (2005) Spridning av främmande populationer i Sverige. Rapport 5475. Naturvårdsverket, Stockholm

Laikre L, Palmé A, Josefsson M, Utter F, Ryman N (2006) Release of alien populations in Sweden. Ambio 35 (5):255-261.

Laikre L, Palme A, Larsson LC, Lindberg E (2007) Spridning av genetiskt främmande populationer i Sverige. Rapport 5683-2. Naturvårdsverket, Stockholm

Latorre-Margalef N, Gunnarsson G, Munster Vincent J, Fouchier Ron AM, Osterhaus Albert DME, Elmberg J, Olsen B, Wallensten A, Fransson T, Brudin L, Waldenstrom J (2009) Does influenza A affect body condition of wild mallard ducks, or vice versa? A reply to Flint and Franson. Proceedings - of the Royal Society Biological sciences 276 (1666):2347-2349.

Lee FB, Kruse AD (1973) High survival and homing rate of hand-reared Wild-strain mallards. J Wildl Manage 37 (2):154-159.

Lincoln FC (1934a) The operation of homing instinct. A Journal of Ornithological Investigation 5 (4):149-155.

Lincoln FC (1934b) Restocking of marshes with hand-reared mallards not proved practicable. Yearbook of Agriculture:310-313.

Lindberg MS, Walker J (2007) Satellite telemetry in avian research and management: sample size considerations. Journal of Wildlife Management 71 (3):1002-1009.

Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10 (3):689-710.

Madsen T, Stille B, Shine R (1996) Inbreeding depression in an isolated population of adders Vipera berus. Biological Conservation 75 (2):113-118.

Morin PA, Luikart G, Wayne RK, Group SNPW (2004) SNPs in ecology, evolution and conservation. Trends Ecol Evol 19 (4):208-216.

Myrberget S (1990) Wildlife management in Europe outside the Soviet Union. Norsk Institutt For Naturforskning, Trondheim

Nilsson L (2009) Internationella sjöfågel- och gåsinventeringarna i Sverige. Årsrapport för 2008/2009. Ekologiska Institutionen, Lunds Universitet, Lund

Noer H, Søndergaard M, Jørgensen TB (2008) Udsætning af gråænder i Danmark og påvirkning af søers fosforindhold. Danmarks Miljøundersøgelser, Aarhus Universitet - Faglig rapport fra DMU nr. 687, 44pp (in Danish),

Nudds TD, Elmberg J, Sjoberg K, Poysa H, Nummi P (2000) Ecomorphology in breeding Holarctic dabbling ducks: the importance of lamellar density and body length varies with habitat type. Oikos 91 (3):583-588.

Ohde BR, Bishop RA, Dinsmore JJ (1983) Mallard reproduction in relation to sex ratios. J Wildl Manage 47 (1):118-126.

Olsson V (1960) Märkningar och återfynd av Svenska gräsänder, *Anas platyrhynchos* L. Swedish Wildlife 2:87-152.

Ottosson U, Ottvall R, Elmberg J, Green M, Gustafsson R, Haas F, Holmqvist N, Lindström Å, Nilsson L, Svensson M, Svensson S, Tjernberg M (in press) Fåglarnas antal i Sverige - i ditt län och landskap.

Parish DMB, Sotherton NW (2007) The fate of released captive-reared grey partridges Perdix perdix: implications for reintroduction programmes. Wildlife Biology 13 (2):140-149.

Pehrsson O (1979) Feeding behaviour, feeding habitat utilization, and feeding efficiency of mallard ducklings (*Anas platyrhynchos* L.) as guided by a domestic duck. Swedish Wildlife 10:194-217.

Pehrsson O (1982) Vilka gräsänder skall vi ha i våra sjöar? Viltnytt 16:23-27.

Pehrsson O (1984) Relationships of food to spatial and temporal breeding strategies of mallards in Sweden. Journal of Wildlife Management 48:322-339.

Pehrsson O (1991) Egg and clutch size in the mallard as related to food quality. Canadian Journal of Zoology-Revue Canadienne De Zoologie 69 (1):156-162.

Pöysä H, Sjöberg K, Elmberg J, Nummi P (2001) Pair formation among experimentally introduced mallards Anas platyrhynchos reflects habitat quality. Ann Zool Fenn 38 (2):179-184.
Pöysä H, Pöysä S (2002) Nest-site limitation and density dependence of reproductive output in the common goldeneye Bucephala clangula: implications for the management of cavity-nesting birds. Journal of Applied Ecology 39 (3):502-510.
Pöysä H, Elmberg J, Gunnarsson G, Nummi P, Sjöberg K (2004) Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? Oikos 104 (3):612-615.
Reynolds RE, Blohm RJ, Nichols JD, Hines JE (1995) Spring-summer survival rates of yearling versus adult Mallard females. Journal of Wildlife Management 59 (4):691-696.
Sauter A, Korner-Nievergelt F, Jenni L (2010) Evidence of climate change effects on within-winter movements of European Mallards *Anas platyrhynchos*. Ibis 152 (3):600-609.
Schladweiler JL, Tester JR (1972) Behavior of hand-reared mallards released in the wild. J Wildl Manage 36 (4):1118-1127.
Scott DA, Rose P (1996) Atlas of anatidae populations in Africa and western Eurasia. Wetland International Publication No.41, Wageningen, The Netherlands
Smith DB, Rohwer FC (1997) Perceptions of releases of cative-reared mallards, with emphasis on an intensive program in Maryland. In: Transactions of the 62nd North American Wildlife and Natural Resources Conference, 1997. pp 403-411
Statens Jordbruksverk (2007) Statens jordbruksverks föreskrifter och allmänna råd om förebyggande åtgärder mot överföring av högpatogen aviär influensa från vilda fåglar till fjäderfä eller andra fåglar som hålls i fångenskap. SJVFS 2007:17
SVA (The National Veterinary Institute) (2010) Surveillance of zoonotic and other animal disease agents in Sweden 2010. SVA:s rapportserie 22.
Swedish Bird Ringing Centre (2009) Antal ringmärkta och återfunna fåglar år 1911-2008. http://www.nrm.se/sv/meny/forskningochsamlingar/enheter/vertebratzoologi/ringmarkningscentralen/antalringmarkta/totaltfran1911.435.html. Accessed 2011-09-20
Svenska Jägareförbundet (Swedish Association for Hunting and Wildlife Management) (2012) Avskjutningsstatistik. http://www.jagareforbundet.se/Viltet/Viltovervakningen/Avskjutningsstatistik/. Accessed 2012-01-04
Sveriges Riksdag (1987) Svensk författningssamling. Jaktförordning 1987:905
Söderquist P, Elmberg J, Gunnarsson G (submitted) Longevity and migration distance differ between wild and hand-reared Mallards Anas platyrhynchos in Northern Europe. European Journal of Wildlife Research.
Søndergaard M, Wiberg-Larsen P, Noer H (2006) Miljøpåvirkninger af søer som følge af udsætning af gråand. Danmarks Miljøundersøgelser,
U.S. Fish and Wildlife Service (2006) National Survey of Fishing, Hunting, and Wildlife-Associated Recreation.
U.S. Fish and Wildlife Service (2011) Waterfowl population status, 2011. U.S. Department of the Interior, Washington, D.C. USA.
Wiberg S, Gunnarsson S (2007) Inventering av hållning och uppfödning av viltfågel i Sverige [A survey of game bird rearing in Sweden]. Sveriges Lantbruksuniversitet. Institutionen för husdjurens miljö och hälsa. Avdelningen för husdjurshygien. Rapport 17. [Swedish University of Agricultural Sciences. Department of Animal Environment and Health. Section of Animal Hygiene. Report 17], 66pp (in Swedish, English summary), Skara
Vignal A, Milan D, SanCristobal M, Eggen A (2002) A review on SNP and other types of molecular markers and their use in animal genetics. Genetics Selection Evolution 34 (3):275-305.
Vildtforvaltningsrådet (2006) Indfangning, udsætning og jagt på fasan, agerhøne og gråand i Danmark. Rapport fra arbejdsgruppe nedsat af Vildtforvaltningsrådet:84 pp.
Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, San Diego

Wink M (2006) Use of DNA markers to study bird migration. Journal of Ornithology 147 (2):234-244.

Zeddeman A, Van Hooft P, Prins HHT, Kraus RHS (2009) Mallard (*Anas platyrhynchos*) gene pool connectivity between Greenland, eastern Canada, Great Britain and the Netherlands. In: L. M. Jensen and M. Rasch, eds. Nuuk Ecological Research Operations, 2nd Annual Report, 2008., National Environmental Research Institute, Aarhus University - Denmark, 2009.