The Influence of Food Abundance Patterns and Predation on Breeding Ducks with a Special Emphasis on the Interactions between Ducklings and Fish

Lisa Dessborn
Faculty of Forest Sciences
Department of Wildlife, Fish and Environmental Studies
Umeå

Doctoral Thesis
Swedish University of Agricultural Sciences
Umeå 2011

Acta Universitatis agriculturae Sueciae
2011:9

Cover: Mallard ducklings (photo: Lisa Dessborn)

ISSN 1652-6880
ISBN 978-91-576-7578-1

Print: SLU Service Alnarp 2011

The Influence of Food Abundance Patterns and Predation on Breeding Ducks with a Special Emphasis on the Interactions between Ducklings and Fish

Abstract

Ducks breeding in Fennoscandia represent a large part of the total population in Europe, and variations in reproductive success can affect continental population trajectories. It is therefore essential to understand processes affecting breeding success. In this thesis I have looked at temporal and spatial food abundance patterns and how these influence breeding ducks. Egg laying and hatching are often assumed to coincide with peaks in available food. No such peak in food abundance was evident in a boreal catchment based on six years of data. Even without clear food abundance peaks, changes in spring arrival can still lead to suboptimal breeding. I have investigated the importance of spring arrival and its effect on spring phenology and breeding success in two dabbling ducks (teal and mallard). Both species can change breeding time in response to variations in spring arrival; however, early springs have a negative effect on teal.

Total food abundance is also important, and fish are known to reduce invertebrates, thus potentially affecting survival of ducklings. In a descriptive study I was able to illustrate that fish reduce the availability of invertebrate prey. Fish also reduce the number of breeding ducks, which is probably a result of competition although pike predation on ducklings can also be of importance. To investigate the effects of pike predation, I introduced adult pike to two lakes that were previously fishless. The number of pairs that settled was not affected by pike, but the subsequent breeding success was reduced significantly. The negative impact of pike on breeding ducks is likely to favour adaptations of anti-predator behaviour.

In experimental trials, naïve ducklings recognised and responded to calls from predatory birds. They did not, however, avoid pike, although they displayed a very strong response to simulated pike attacks. They ran on the water, scattered and reassemble far from the initial attack. The lack of identification appears to be compensated by the ability to respond instantly to threat and thus reduce losses.

Keywords: dabbling ducks, diving ducks, diet, breeding success, mis-match, emergence peak, fish competition, pike predation, predator avoidance.

Author's address: Lisa Dessborn, 1)SLU, Department of Wildlife, Fish and Environmental studies, Swedish University of Agricultural Sciences, SE-901 83 UMEÅ, Sweden, 2) Kristianstad University, Aquatic Biology and Chemistry, SE-291 88 Kristianstad, Sweden. *E-mail:* lisa.dessborn@hkr.se

Dedication

To my parents,

For your love, support and encouragement which has given me the confidence to undertake and complete this thesis.

Contents

Appendix

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

Chapter 1: Diet of breeding ducks

I Dessborn L., Brochet A-L., Elmberg J., Legagneux P., Gauthier-Clerc M. and Guillemain M. 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 (submitted manuscript).

II Brochet A-L, Dessborn L., Elmberg J., Legagneux P., Gauthier-Clerc M., Fritz H. and Guillemain, M. Diet overlap in mallard, teal and pintail: seasonal patterns at the Western Palearctic flyway scale (manuscript).

Chapter 2: Breeding phenology

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

IV Arzel C., Dessborn L., Nummi P., Pöysä H., Elmberg J. and Sjöberg K. Early springs and breeding performance in two bird species with similar habitat requirement: Is adaptability to climate change related to migration distance? (manuscript)

Chapter 3: Interactions between fish and ducks

V Elmberg, J., Dessborn, L. and Englund, G. (2010). Presence of fish affects lake use and breeding success in ducks. *Hydrobiologia* 641, 215-223.

VI Dessborn, L., Elmberg, J. and Englund, G. Pike predation affects breeding success and habitat selection of ducks. *Freshwater Biology* (in press)

VII Dessborn, L., Englund, G. and Elmberg, J. Responses of mallard ducklings towards aerial, aquatic and terrestrial predators. (manuscript)

Papers III, V and VI are reproduced with the permission of the publishers.

Introduction

Ducks belong to the family *Anatidae*, which also includes geese and swans. The focal duck species in this thesis belong to two subfamilies; *Anatinae* (dabbling ducks) and *Aythyinae* (diving ducks). Both dabbling and diving ducks are widespread and common in the northern hemisphere, although only one species of diving ducks has been considered in this thesis (goldeneye, *Bucephala clangula*) Several taxa are also important quarry species, which is one of the reasons why they have received much attention in the scientific literature, particularly in North America and Europe (e.g. Batt *et al.*, 1992; Kear, 2005). Much of the European waterfowl research has been carried out in areas with large congregations of wintering ducks and with a long tradition of extensive duck hunting. However, to understand population fluctuations and to maintain a viable stock for hunters, it is crucial to understand the breeding ecology of ducks. The conditions in the breeding areas will influence annual recruitment, and many ducks migrate considerable distances to breed (Cramp and Simmons, 2004). The European boreal region has many breeding ducks, and factors influencing reproductive success need to be identified and understood in order to maintain viable populations on a continental scale. It is important to identify important life history events and assess how sensitive breeding ducks are to changes in food availability and predation pressure during different stages of the breeding cycle. Ducks are versatile organisms that are found over vast geographic areas. Their ability to utilise different habitats and to adapt to local environments makes them interesting subjects of investigation. As many duck species are spread over large geographical areas, they experience a wide variety of adaptive pressures. The behaviour and breeding patterns would therefore tell us about both past and present influences that have lead to adaptations in the breeding ecology of the species.

Breeding ecology

Although some individuals and populations are sedentary, most ducks are seasonal migrants (Cramp and Simmons, 2004). Breeding ducks are often found in high densities in biologically productive lakes in mid-latitudes (Cramp and Simmons, 2004), but breeding also takes place in many oligotrophic lakes at higher latitudes. Pairs are formed on the wintering sites, and the female is generally philopatric, in other words she has a strong tendency to return to her natal area to breed, whilst the accompanying male will follow the female (Anderson *et al.*, 1992). When the incubation starts, males often leave the rearing lake and congregate on larger lakes or in coastal areas (Cramp and Simmons, 2004) and new pair bonds are formed the following winter.

Ducks generally mature during their first year, though not all females reproduce during their first breeding season. Young females cannot rely on experience to find food and they may also have to compete with older ducks for the best feeding sites, not just in the breeding areas but also during wintering and staging when reserves are built up prior to breeding (Owen and Black, 1990). A weakened body condition can also be a result of disease to which the first year ducks have not previously been exposed and are therefore not immune (eg. Wallensten *et al.*, 2007). The energy costs of producing a clutch are quite high for waterfowl as they lay large eggs in relation to female body size (Alisauskas and Ankney, 1992). This reproductive strategy is likely to have evolved to increase the independence of ducklings. Unlike many other birds, ducklings are precocial, in other words they are semi-independent after hatching and they can swim and find food by themselves. Mallards (*Anas platyrhynchos*) produce 6 -12 eggs in a clutch, and clutch size often increases with female age (Owen and Black, 1990).

The high energy costs of egg-laying and risks of predation on brooding females have a large influence on the reproductive output of a breeding population. Nest predation is often high, particularly for ground nesting birds such as dabbling ducks. The destruction of nests by predators is often the most important cause of reproductive failure and exerts a great effect on population trends (Sargeant and Raveling, 1992 pp. 406-407), but predation rates remain high even after the eggs have hatched and the ducklings have left the nest.

Duckling mortality

Ducklings have low surival rates during the first two weeks after hatching. Energy requirements are high and food shortage often leads to starvation or increased chance to succumb to disease or cold weather. During this period the ducklings easily become prey to predators such as pike (*Esox lucius*), goshawk (*Accipiter gentilis*) mink (*Mustela* spp.), large gulls (*Laridae* sp.) and skuas (*Stercorarius* spp.) (Sargeant and Raveling, 1992). Solman (1945) discovered that pike ate almost 10% of the annual duckling production in the Saskatchewan River delta. Diving ducks were eaten more frequently than dabbling ducks, but the presence of large pike could impact the annual recruitment of both groups of species. American mink (*Vison neovison*) can also have a large impact on both nests and ducklings and can be the principal cause of duckling mortality in some areas (Talent *et al.*, 1983; Bartoszewicz and Zalewski, 2003). Even though gulls and corvids pose no direct threat to adult ducks, they can prey upon ducklings and eggs (Sargeant and Raveling, 1992) and thus impact reproductive success.

Nest destruction, starvation and predation-related mortality in ducklings have strong effects on the reproductive success of breeding ducks. Food availability and predation are the two most important influences on duckling survival, and their relative importance varies between landscapes and habitats. A female that can successfully identify areas of high food abundance and low predation risk is more likely to avoid brood losses. The female may communicate predation threats to her ducklings by using alarm calls, which often induces a freezing, scattering or aggregating reaction in the brood (Miller *et al.*, 1990; Afton and Paulus, 1992 pp. 88-89). There is naturally also a strong fitness advantage for individual ducklings that can acquire as much food as possible while avoiding predation. These behaviours are traded off against each other, as increased foraging often leads to reduced vigilance (Guillemain *et al.*, 2007). The ability to detect predation risk is particularly important when ducklings are not in the immediate vicinity of the female. This is especially the case for some diving duck species where ducklings are frequently feeding on their own, but also in dabbling ducks where the brood is often feeding some distance from the female.

Habitat selection - the choice of local breeding sites

In nutrient rich lakes with high production of seeds and invertebrates, the concentration of breeding ducks can be quite high. However, in the boreal regions of Fennoscandia densities of nesting ducks are generally low. The region contains many lakes, but many of these do not support any breeding ducks (Sjöberg *et al.*, 2000). In spring, females generally return to their natal area, where they choose a suitable breeding lake (Pöysä *et al.*, 1997). Food availability is of great importance as much of duckling mortality can be linked to food shortage (Gunnarsson *et al.*, 2004). It is also likely that low predator density and abundant vegetation cover are used as cues of good breeding habitat by females, as these reduce predation losses. Females generally prefer lakes with more invertebrates and more extensive vegetation cover (Nummi and Pöysä, 1993). Additionally, availability of nest sites such as tree cavities are particularly important to some diving ducks, and the number of breeding pairs in an area can be increased by adding nest boxes, although it does not necessarily increase the reproductive output (Pöysä and Pöysä, 2002).

Diet of ducks

As suggested by their name, dabbling ducks mainly feed by dabbling, often in shallow water. They can also dip their head under water or up-end their body to reach deeper, but unlike diving ducks, they rarely dive. They are omnivorous and will eat a variety of food items. The adult dabbling duck is primarily herbivorous and seeds make up a large part of the diet, but the female will increase consumption of invertebrates before and during egg- laying (Andersson *et al.*, 1975, Owen and Black, 1990). The ducklings feed primarily on newly hatched invertebrates, but their diet gradually includes more plant items as they approach fledging (Cramp and Simmons, 2004). During the first week after hatching, the dabbling ducks feed exclusively above the water surface. In this early stage they also catch food items from vegetation above the surface and on land (Pehrsson, 1984). After a few weeks they start feeding on more aquatic invertebrates, first by just putting their bills under the water, and later by up-ending (Chura, 1961). Particularly mallard ducklings also feed on terrestrial invertebrates either from the water or from land. When feeding on land, ducklings can jump up to three times their normal standing height (Chura, 1961).

Goldeneye ducks are also omnivorous but feed primarily on benthic and nectonic invertebrates, although macrophytes and seeds also make up a significant part of the diet (Cramp and Simmons, 2004). Diving duck ducklings start diving for food directly after they have hatched and are therefore not dependent on emerging insects to the same degree as the young of dabbling ducks.

The proportion of invertebrates in the adult diet increases during the spring, as egg production and duckling growth require protein rich foods (Thompson *et al.*, 1992; Baldassarre and Bolen, 2006; Pehrsson, 1991). Although preferences will influence the diet of breeding ducks, diet is naturally also dictated by availability. During spring, and early summer invertebrates are often abundant and/or conspicuous, whereas seed availability increases from late summer and onwards. One of the indications that ducklings are specifically choosing protein rich foods rather than just eating what is most available is that females eat comparatively more seeds and plant matter during the same period (Chura, 1961). Although these general trends can be observed, ducks are opportunistic and invertebrates can be found in great numbers in the diet during non-breeding season (Mazzucchi, 1971).

Importance of food availability for egg production and survival of ducklings.

Ducks are primarily migratory and are generally referred to as income breeders (eg. Bond *et al.*, 2007). In other words, unlike capital breeders such as geese, they do not store much energy reserves on their bodies from food ingested on the wintering and staging areas. They are therefore largely dependent on food available in the breeding areas for egg production and other energy expenditure related to breeding. Females need at least 18.6% protein in the diet to produce eggs that have a reasonable hatch rate according to Andersson *et al.* (1975), and protein content of female diet prior to egg-laying determining clutch and egg size (Pehrsson, 1991).

Protein rich food availability is also important to growth and survival of ducklings (Cox *et al.*, 1998; Gunnarsson *et al.*, 2004). Street (1977) found a mortality rate of 77% in lakes where predation was controlled, and concluded that the main mortality in ducklings is a result of food resource limitation and weather.

Some invertebrate taxa can be of special importance to ducklings due to their general availability. Chironomids belong to one such taxonomic group as they are abundant in many wetland systems as well as being rich in protein (Baldassarre and Bolen, 2006). The local availability of chironomids may therefore have strong impacts on breeding ducks. This has been illustrated for some boreal wetlands (Danell and Sjöberg, 1977)

Competition for food between duck species

Competition between individuals can be either a question of exploiting the same resources or actively excluding a competitor from a shared resource, for example through territoriality. The first type of interaction is called exploitation competition and the second interference competition (Begon *et al.*, 2006).

Diving ducks feed mainly in the benthos and can reach considerable depths, whereas dabbling ducks feed primarily in shallow areas. These groups thus have clearly separated niches due mostly to their foraging methods. In many oligotrophic lakes, goldeneye is often the only diving duck species and competition between other members of the diving duck guild is therefore limited.

Several dabbling duck species can be found in the same wetland and habitat and they feed largely on the same food items. However, there are some adaptations that could reduce niche overlap. Interspecific differences in bill lamellar density indicate an adaptation to different prey size; e.g. Nudds and Bowlby (1984) showed a negative correlation between lamellar density and prey size. Pöysä *et al.* (1994), on the other hand, found no support for the hypothesis that bill lamellar density affects species coexistence. The differences in neck and body length between dabbling duck species also means that they can forage at different depths when up-ending, which may facilitate resource partitioning (Pöysä, 1983). However, niche differentiation is not altogether straightforward among dabbling duck species (Gurd, 2008) and especially ducklings have very overlapping diets (Cramp and Simmons, 2004). It is possible that niche differentiation is not observed in dabbling ducks because they are generally not close to carrying capacity and food is thus not a limiting factor; hence no interspecific competition. There are many lakes in the boreal region, and many lakes lack breeding ducks altogether. Yet, others can have several broods of the same or closely related species with similar requirements (Elmberg *et al.*, 2005), indicating that competition avoidance is not the most important factor influencing habitat choice of ducks in the boreal region.

Aggressive territoriality in ducks may be a way to exclude competitors through interference. Savard and Smith (1987) showed that Barrow's goldeneye was more aggressive towards other diving ducks than to dabbling ducks. They suggested that the reason may be stronger competition among diving ducks. On the other hand, the presence of other duck species often seems to attract rather than deter individuals. Ducks prospecting for breeding wetlands are presumed to use the presence of closely related species as an indicator of habitat quality, which is sometimes referred to as heterospecific attraction (Sebastián-González *et al.*, 2010; Pöysä *et al.*, 1998).

Breeding time in relation to food availability

Determining the optimal breeding time is not necessarily straightforward. Theoretically, the best evolutionary strategy should be to time the hatching of ducklings to peaks in food supply, and some efforts have been made to investigate the presence of such patterns. However, it may not be the ducklings' food requirements that are the hardest to meet and which dictate the optimal breeding time. Females arriving on the breeding grounds have little extra reserves and need food to be accessible and plentiful for egg production. If the first arrivals turn up in early spring when wetlands and lakes are still covered with ice, it is suboptimal timing although early hatching may be advantageous for ducklings. The condition of the female prior to egg-laying could influence breeding time. Several studies have illustrated that earlier breeders have greater reproductive success, indicating that the average female breeds sub-optimally in many areas and that early breeding is a privilege of females in great condition (Elmberg *et al.*, 2005).

Additionally, the optimal time of breeding with respect to duckling survival may not be easy to predict for breeding birds. Conditions can change from year to year and there are studies showing reduced survival in early breeders due to increased weather related mortality (Street, 1977). There may therefore be a trade-off between optimising food abundance and avoiding brood losses induced by inclement weather. There is also a risk of ducklings hatching before the peak in food abundance in years with prolonged winter conditions, which would also reduce duckling survival rates (Street, 1977). Pehrsson (1984) placed broods of wild ducklings in lakes at different times and noticed that ducklings that were on the lake prior to the peak in insect emergence suffer high mortality rates, but ducklings placed on lakes after the main emergence peak actually had a better survival rate despite missing this potentially important time in terms of food supply.

Most emerging insect species have a very narrow window during which they emerge and swarm, however even closely related species do not necessarily swarm at the same time (Learner and Potter, 1974). Many studies have indicated that fish have a negative impact on abundance of invertebrate prey, but they may also change the observable pattern of emergence (Hornung and Foote, 2006). The fish can potentially reduce the abundance of dominant species and therefore remove the visible peak as each emerging insect species will have a different swarming period.

Spring phenology in breeding ducks

The northward migration and initiation of breeding in migrating species can be triggered by daylight hours or other cues related to spring. Some species have a spring migration that is generally at the same time every year and these are therefore very sensitive to seasonal changes due to natural fluctuations or human induced climate change (Coppack *et al.*, 2008). Other migratory species move north in steps and will halt the migration if winter conditions persist at stopover sites (Bauer *et al.*, 2008). The ability of a species to adjust its breeding to spring conditions at the breeding site is crucial in a changing world. Future changes in annual temperatures and timing of spring can lead to a trophic mismatch in species that are not able to change their migrating and breeding patterns in accordance to altered seasons. Mismatches between spring resources and timing of breeding have previously been identified in several bird species, and is most apparent in invertivorous, long distance migrants (Both *et al.*, 2010). The pre-emergent development of invertebrates such as chironomids is primarily dictated by water temperature (Danks and Oliver, 1972), and will therefore quickly respond to advancing springs due to global climate change. Many vertebrates on the other hand have longer generation times and will not be able to respond as quickly to changes in the environment. Migratory species also depend on the conditions at the wintering and staging areas (Arzel *et al.*, 2006) and these areas might not change to the same degree, as models of climate change predict greater changes at higher latitudes (Holland and Bitz, 2003, Sanderson *et al.*, 2011).

Ducks in the freshwater food web

Waterbirds are often studied as a separate entity from the rest of the limnological system. Ornithological research needs to be integrated with limnology to look at birds as integrated parts of the freshwater food web.

Waterbirds can influence the food web directly as predators of fish, invertebrates or macrophytes (eg. Hurlbert and Chang, 1983; Woollhead, 1994; Klaassen and Nolet, 2007). Ducks are omnivorous, and thus act on several trophic levels. They potentially compete with other groups of organisms that feed on seeds and invertebrates. Competition is more common between closely related species with highly overlapping niches, but also taxonomically distant species can influence each other through direct competition or alterations of the habitat. Fish communities have a strong impact on aquatic environments and can reduce invertebrate numbers both directly and indirectly and are therefore likely to affect breeding success of ducks (Phillips and Wright, 1993).

Waterbirds are unlikely to have a strong impact on invertebrate biomass in boreal lakes as the birds are found in very low densities and during a limited part of the year. Waterbirds can still have a strong influence on the freshwater habitat, however. Particularly piscivorous birds can reduce fish densities and thus indirectly influence the rest of the food web (Woollhead, 1994). Ducks and other waterbirds may also reduce macrophyte cover and increase turbidity in a wetland when they search for food in the sediments (Marklund *et al.*, 2002), which can indirectly affect invertebrate numbers and fish abundance.

In freshwater aquatic systems, a wetland is more or less isolated from other bodies of water. Inland wetlands are therefore essentially freshwater "islands". According to the island biogeography theory the numbers of species correlates positively with island size (MacArthur and Wilson, 1967). Immigration and extinction rates will also influence the number of species found on an island. Connecting streams or other factors increasing the transport of organisms between freshwater systems can therefore have strong influence on the diversity of a wetland. Organisms may also be able to colonise new wetlands by having a mobile, terrestrial phase, or by being transported by vectors or hosts. Darwin was one of the first to write about the potential effects of waterbirds as vectors of seeds (Darwin, 1859 pp 356-357). Ducks can also carry invertebrates in their guts or on their bodies and introduce them to new wetlands significant distances from the source (Brochet *et al.*, 2010). They can play an important role in increasing the number of species in wetlands, particularly in lakes that are isolated from other freshwater systems. By transporting seeds and invertebrates to new wetlands, waterbirds can also act as a vector for invasive species (Green and Figuerola, 2005; Wonham, 2006).

Waterfowl move freely in the landscape and can transport more than invertebrates and seeds. They can transport nutrients from other lakes or surrounding land areas. This is particularly true for birds such as geese and ducks that are opportunistic and tend to feed on agricultural land and then roost on lakes and ponds. Ducks have also been of public interest lately as a vector for disease. The ability of ducks to migrate long distances increases the threat of diseases spreading through these birds. Their roles as vectors for diseases that can affect humans and poultry and their importance as quarry species highlight the need to better understand their ecology and the interactions with other organisms in the wetlands.

Study area

The boreal zone as a duck breeding habitat

The boreal zone is one of the world's largest biomes, and it covers much of the northern temperate areas. The biome is dominated by conifers, but deciduous trees such as birch and alder are also common. The area is strongly influenced by seasonality, and the growing season is short. The Fennoscandian boreal forest grows on acid bedrock, and therefore the soil and wetlands generally have low pH. The last ice age has shaped the landscape and produced a network of lakes and wetlands. The abundance of lakes and the vastness of the biome make the contribution of annual duck recruits from this biome significant on a continental scale.

Evo area and research station, Finland.

Through collaboration with Finnish researchers, I have been able to use long term data from the Evo catchment (61°10' N, 25°05' E) north of Helsinki. For more than 20 years, 51 of the lakes in this area have been surveyed for waterbirds, vegetation, emerging and aquatic invertebrates (Nummi and Pöysä, 1993). The area is typical for the boreal region, and a dense patchwork of wetlands and lakes creates plenty of habitats for waterbirds. The density of breeding birds per lake is low in Evo, as in most of the boreal as the lakes have a relatively low production of invertebrates and seeds. The majority of research on ducks has been carried out in more productive systems, which makes the long term dataset all the more valueable as is it a good representation of a boreal system.

Evo Game and Fisheries Research Station belongs to the Finnish Game and Fisheries Research Institute and I was kindly offered to use some of the fish ponds and equipment for my experiments. These ponds have been constructed for fish and crayfish experiments, and the water level can be manipulated by altering inflow and outflow from a river running past. These ponds were used in experiments of predator avoidance behaviour in ducklings.

Fig. 1. Drained ponds at Evo research station.

Lake system, Västerbotten, Sweden.

Researchers at Umeå University have a well documented record of the fish communities in many lakes throughout Sweden. This data base is comprehensive and covers large areas, thus including all regional lake types including oligo- to mesotrophic lakes in the coastal areas of north-central Sweden, shallow coastal lakes and lakes above the historical coast line. The recorded fish status was the basis for a descriptive study of the influence of fish presence on breeding birds. Fishless lakes in this area are generally shallow lakes that do not have connecting streams and that frequently suffer from anoxic conditions during winter. Some of the fishless lakes were later used in a pike introduction experiment.

Materials and methods

Focal species

I have looked at both diving and dabbling ducks in some of my studies, however, the main focus is on dabbling ducks with particular emphasis on mallards as they are geographically widespread, locally common as well as a model species in animal ecology. Other dabbling ducks that are featured in this thesis are teal, wigeon and pintail. Goldeneye is the only diving duck species found breeding in significant numbers in the investigated oligotrophic lakes, and therefore the only diving duck represented in any of the studies. Mallard ducklings were chosen for the predator avoidance and feeding trials as they can be readily purchased from farms producing ducks for stocking by hunters. Teal, mallard and goldeneye are all common and important quarry species, and it is therefore important to find out more about their breeding ecology to manage them sustainably.

Trans-European collaboration and the French connection.

A French-Swedish information search on the diet of ducks on a European scale was the foundation for two diet review manuscripts. Through this collaboration we could do an efficient search of articles in peer-reviewed international journals, and more importantly, we were able to locate studies of a more regional nature and carry out searches in several languages. Through international contacts we were able to get a hold of unpublished data that further improved the basis for our conclusions.

20 year time series and the Finnish connection

There has been a well developed Swedish-Finish collaboration in duck research over the last 20 years resulting in 30 scientific articles to date. I was privileged to be able to work with this group of researchers, and through this cooperation that I had access to the long term data set from Evo. There has also been a weather station at Evo throughout this study period. Survey data can therefore be compared to local weather data to discern patterns in population fluctuation or changes in spring phenology. I was able to use part of this data to assess the timing of breeding in relation to peaks in invertebrate abundance. The data used for this analysis were only from 1989 to 1994, as these were the only years during which invertebrate surveys took place throughout most of the spring. The number of broods and the age of ducklings were used to estimate time of hatching of ducklings in relation to abundance of emerging insects, which had been collected in emergence traps. Emergence traps are made up of an upside down funnel which is covered by a net to catch emerging insects as they hatch and fly up the funnel.

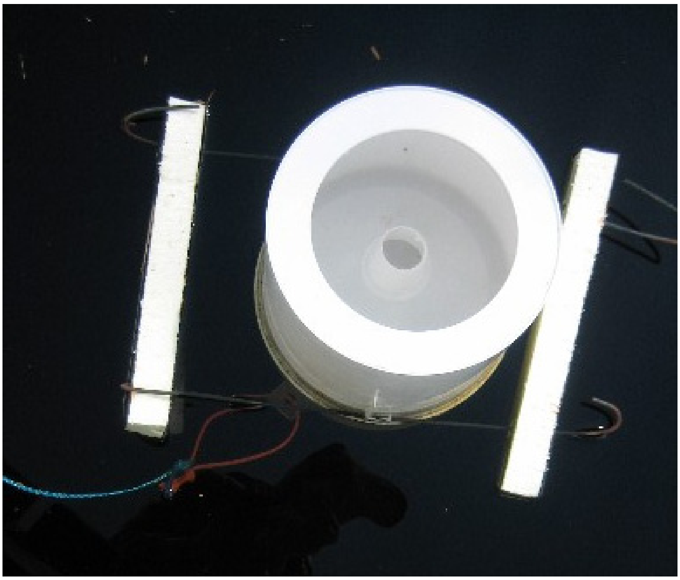

Fig. 2. An emergence trap floating on top of the water.

The long term data series was also used to investigate fluctuations in spring arrival and the ability of breeding ducks to respond by changing their breeding initiation. Different quantitative measures were also used to assess the effects of early and late springs on breeding success in mallard and teal.

Something fishy going on in Västerbotten

Through the efforts of fish researchers in Västerbottten, the fish status of many lakes in the region is well documented. This enabled me to study relationships between breeding ducks and fish. Bird surveys were carried out once a week in spring and early summer so that nesting pairs as well as broods could be counted. Invertebrate data were collected using emergence and activity traps. All waterbirds were recorded and used as a "species richness" index. Three focal species (i.e. teal, mallard and goldeneye) were used for a more detailed analysis. The measure of lake use was "[Species name] days" which is the daily number of individuals of that species seen on a lake summed over all survey days. These numbers include adults, ducklings, and groups of adult birds. Thus, a hen with a brood of 6 ducklings produced "7 [species name] days" for a particular lake each day the hen and her brood were observed on it.

The data from the bird surveys of the descriptive study were later used as baseline information in a pike introduction study. Pike were added in natural densities to two of the previously fishless lakes, whereas the other nine remained as fishless controls. That way a before-after-control-impact study design could be used to investigate the impact of pike predation in a typical shallow boreal wetland.

Fig 3. Catching pike in Västerbotten prior to lake introductions.

The intriguing behaviour of ducklings

The impact of pike on breeding duck populations (Solman, 1945), and a documented lack of avoidance of such lakes by nesting pairs, is intriguing. It led to further questions about in situ responses of adults and ducklings. We wished to investigate whether ducklings avoid lakes with pike, either by recognizing their shape, or by using olfactory cues. To test this hypothesis I used a frozen pike in the water to assess the behaviour of ducklings. I also investigated their movements to see if they avoid the area of the pond where the frozen pike was placed. Additionally, I wanted to test the innate responses to other predators, such as birds and mammals. I used bird calls and a trapped mink to analyse predator response and avoidance behaviours. I also investigated the direct response to imminent threat from the air and from the water. A stuffed goshawk was strung to a wire and attack was simulated by sliding it in a downwards movement towards the ducklings in the pond. A simulated pike attack was also carried out with the frozen pike. The pike was either pushed using a pole or pulled with a fishing rod to break the surface near the ducklings.

Fig. 4. Placing the pike dummy in the ponds, and detailed recording of duckling behaviour.

Results and discussion

Diet of dabbling ducks (I-II).

The abundance of available studies on the diet of dabbling ducks in the Western Palaearctic provides insight into the amount of research that has been done on ducks in the last century or more. The amount of resources put into researching this group of species is strongly influenced by the interests of hunters and managers to maintain high stocks. Much of the research has also been concentrated to geographic areas that have a long tradition of hunting and with large quantities of wintering ducks. This is particularly the case in diet studies as many researchers have been able to collect data from shot birds by cooperating with local hunters.

The first scientific article published on the subject of dabbling duck diet is from the late 19th century (Hesselman, 1887). Since then there has been a major change in scientific writing and research focus. Many of the oldest articles have an anecdotal air about them, and resemble today's popular scientific writing and details are usually missing, particularly from the method and result sections. There is often a lack of replication in the samples, and some studies are even based on a single bird (Holmboe, 1900).

The papers from the latter part of the last century represent both a large quantity of studies and a large number of analysed birds. The popularity of these purely descriptive studies appear to have been somewhat reduced in the last few decades. It is possible that it has become harder to publish such studies because they are considered to add little new information to science. It could also be a result of a general trend in animal ecology to move from descriptive to more experimental studies.

Many researchers that have been analysing duck diet are primarily duck scientists, and the level of taxonomic resolution of taxa found in the diet therefore varies. Some studies have put a large effort into quantifying seeds, whereas many invertebrates are either ignored (Brouwer, 1980; Goyon Demonteil 2004) or given in very broad categories (Pirkola, 1966). Soft-bodied invertebrates are also hard to identify, particularly after they have passed the gizzard. Different studies have used different parts of the digestive system to analyse food content. The oesophagus and pro-ventriculus contain mostly intact and easily identified food items, whereas most soft tissue items will be destroyed and difficult to identify in the intestines. In the lower parts of the digestive system, it is potentially even hard to tell whether it is of animal or plant origin. For this reason, the oesophagus or pro-ventriculus would give the most accurate description of the diet content. However, if all other parts are ignored, we would get many "empty" birds as they do not always have any food in the upper parts of the digestive system. This is probably the reason why many studies have included the gizzard as well as the oesophagus and pro-ventriculus (eg. Campbell, 1946; Campredon, 1984)

The geographic distribution of duck diet studies accessible in the literature is skewed towards the south and west of Europe. This is where many ducks winter and also where many of them get shot. This means that we know very little about the diet of dabbling ducks in the central and eastern parts of Europe as well as in North Africa. Our knowledge about diet of dabbling ducks in the Western Palaearctic is therefore potentially biased as some geographic regions are overrepresented while other areas lack studies all together.

The compiled diet studies create the foundation for two review manuscripts. The first review summarizes knowledge about dabbling duck diet in the Western Palaearctic to date, and the second one compares the diets of different dabbling duck species in terms of food size distribution. The geographic distribution means that the knowledge of the diet of Palaearctic dabbling ducks is far from complete. It is also evident that there is a strong temporal bias towards autumn and winter. This is naturally determined by strict hunting regulations on breeding ducks; however it limits our knowledge about the diet of breeding birds. This period is potentially the most important in terms of the effects diet availability and composition could have on population trajectories. Ducks are known to eat a greater proportion of animal matter during breeding (Krapu and Reinecke, 1992), and this pattern can be seen in our review as well. Comparing studies from breeding and non-breeding seasons is difficult due to the differences in sampling methods, food quantification measurements and the taxonomic resolution of food items identified. Most studies use frequencies of sampled birds containing a certain food item. This value cannot be readily added or subtracted, and the proportion of animal *versus* plant matter cannot be estimated. However, where enough studies have used comparative measures, such as counts or dry weight, an analysis can be made. The increasing in invertebrate prey during breeding season concurs with previous studies from North America and Europe. It is uncertain how much of the change in diet is due to changes in the preference of the breeding birds, and how much is due to a shift in availability. It is only the breeding females and ducklings that have an increased protein demand during the early part of the breeding season and sex was not noted in any of the diet studies.

When comparing the diets of adults and ducklings during the breeding season, there is a difference in the type of invertebrates ingested. Adult ducks eat a larger proportion of benthic invertebrates, whereas ducklings eat relatively more emerging invertebrates.

There is a strong geographical influence on plant species found in the diet, likely due to availability patterns. Dabbling duck digestive tracts often contain cultivated crops such as barley (*Hordeum vulgare*) in the northern latitudes and rice (*Oryza sativa*) in the south. Species growing in or near water naturally make up a large part of the duck diet. In the southern areas, many plant species found in saline or brackish water are commonly ingested. Many of the plants in the northern areas are calcifuge, indicating that ducks mainly feed on acidic and oligotrophic lakes. However, it could also be a case of sampling bias, as the species found in the diet are dictated by where the birds were shot. *Carex* seeds were very important in the northern latitudes, whereas *Scirpus* species were more important in the south.

Despite the many articles on duck diet during the last century, our review yielded surprisingly little synthetic information. This is partly because of the discrepancies in sampling techniques, identification level of food items and method of quantification. It is also due to a lack of studies that actually compare diet to food availability (however; see Nummi, 1993). The duck feeding methods of filtering particles through their bill lamellae is not very discriminating in terms of the species of seeds and invertebrates they consume. Diet analysis based on contents of the digestive tract is therefore not only a measure of diet preference, but also availability and distribution of prey species.

In the second diet review we compare the average seed item sizes between mallard, teal and pintail. There was a clear division of seed size between the largest and smallest duck species (mallard and teal) based on all seed size measurements (weight, length and width). Mean seed length also differed between mallard and pintail, and mean width between pintail and teal.

Our results indicate that there is a certain amount of food size differentiation in the investigated dabbling duck species. If so, this may not be the only method of minimising niche overlap. Differences in feeding method and microhabitat could also lead to a division of resources (Nummi, 1993). Bill lamellar density, body length and feeding habits are all likely to be important for food partitioning in areas with high competition levels to facilitate the coexistence of species with overlapping diet requirements if resources are limiting.

The number of articles that have been published about the diet of ducks has reduced in the last few decades, and it is possible that it is hard to publish such articles due to the lack of apparent news value. To publish diet papers today, novel angles need to be addressed. Comparison of the available food and diet are likely to shed new light on diet preference. Non-intrusive method of analysing duck diet could improve available data, particularly from breeding areas and during the summer, when there is no access to shot birds. Faecal sampling is one such method; however, the level of identification would naturally be reduced as most soft tissue species would not be identified. A relatively new technique that could prove useful in determining dominating food sources and feeding habitats is isotope analysis (Collier and Lyon, 1991).

The effects of food availability and spring phenology on breeding dabbling ducks (III-IV)

In the temperate parts of the world, seasonal changes dictate productivity and activity patterns. At high latitudes the growing season is compressed to a few months as primary production is limited to periods of above-freezing temperatures. The lack of food resources concurs with high energy requirement in homoeothermic, or warm blooded, animals. Animals can develop different methods of surviving the winter, and many bird species avoid the coldest months by migrating to warmer regions where food is more readily available and where they have access to open water. When the growing season is short it is essential to optimise breeding time to enable birds to complete breeding and moult before the winter. Young birds also need to be fledged and in good condition before the winter migration.

The timing of reproduction is not just important for breeding birds, but also for many invertebrates. Spring time in the northern temperate regions is often characterised by large swarms of insects that hatch, emerge and deposit eggs within a short period of time. The swarming insects are often dominated by *Chironomidae* which are very numerous not only in the boreal, but in many parts of the world. I used 5 years of invertebrate and waterbird data collected in 12 lakes in Evo, southern Finland, to investigate these patterns. The combined data showed no peaks in emerging insects in relation to either date of ice break-up (a measure of spring arrival) or calendar date. In fact, chironomid emergence fluctuated from week to week and no detectable peak or predictable patterns were apparent. The development of chironomid larvae is affected by water temperatures and these vary between lakes depending on depth, size and shading. If the peak occurred at different times in different lakes it would dilute the effects of a peak in the pooled data. However, no peak was detectable at lake level either. Chironomids of the same species do swarm for only a short period in order to find a mate, but there are over 5000 known species of chironomids in the world (Cranston and Martin, 1989), with at least 500 species occurring in the boreal wetlands of Fennoscandia (Michailova, 1989). Each chironomid species will have a distinct swarming period, therefore clear peaks would only be detectable in wetlands or lakes with few dominating or several synchronous species. If the lake is species rich and no chironomid species is numerically dominant, then there will be no observable peak in emergence.

There are some major problems with measuring emergence as an assessment of food availability. For example, the traps used to catch invertebrates often catch insects when they emerge, which is not necessarily when they are available to ducklings. After the chironomids emerge they sometimes swarm near the water surface or around emergent vegetation. Insects tend to emerge in a patchy fashion, and the traps may therefore either represent a barren patch or a patch of unusually high abundance leading to great between-trap variation in insect catches.

We did not identify a narrow interval with abundant food supply for breeding ducks in the investigated habitats. However, timing of breeding might still be important for final breeding success. Early breeding females have a greater chance of renesting if her initial clutch or brood should fail. Predation pressure also generally increases as the season wears on (Elmberg *et al.*, 2009).

Peaks in total biomass of swarming chironomids has been illustrated in other types of wetlands (e.g. Danell and Sjöberg, 1977). Future studies should focus on identifying in what types of wetlands there might be a clear peak in invertebrate abundance and to what extent these habitats are used by breeding ducks. The uncertainty about the existence of a clear peak in available resources can influence future predictions about the sensitivity of ducks to phenological changes brought on by climate change.

When the environment changes rapidly, there is little time for organisms to evolve or alter their behaviour. This is particularly true for long lived organisms with long generation times. If timing of important life history events no longer fits with patterns of resource availability, it may influence survival or reproductive success in a species. As some organisms adapt faster to rapid changes, there can be a mismatch between trophic levels (Thackeray *et al.*, 2010). Onset of breeding can be dictated by date-fixed parameters (such as light) or by flexible parameters (such as ice break-up on the breeding grounds). If it is date-dependent, then breeding is more sensitive to changes in the climate and especially to arrival of spring. With present concerns of climate change and its effects on spring phenology, particularly at high latitudes, it is therefore important to know the general response in ducks. Our study shows that dabbling ducks (mallard and teal) breeding in the Evo area, onset of breeding changes in response to spring initiation measured as ice-out date of lakes. In other word they are not as sensitive to change as some other migrating birds (Both *et al.*, 2010). Although both mallard and teal are able to change their breeding to fluctuations in spring arrival, teal are negatively effected by early springs in terms of ducklings per brood. Arrival of spring is naturally fluctuating in the region of study (from 14th of April to 9th of May during our study period), which could explain the flexible nature of the onset of duck nesting. The reduced reproductive output in teal can however be a cause for concern for managers of this species.

Changes in the environment can alter the relative abundance of different species, and ultimately change species composition, through species-specific effects or by altered competition (Bowers and Harris, 1994). Competition between species can be asymmetric, where the negative effects of overlapping niches are mainly felt by one of the two species (Begon *et al.*, 2006). The effects of warmer and earlier springs on population trends in mallard and teal need to be followed up in the future to assure that earlier springs is not followed by a decline in the teal populations.

Ducks can successfully start breeding early in early springs, but we do not know to what extent this influences other life history events. Ducklings that hatch early are likely to become fully fledged before ducklings that hatch late. They would therefore be able to initiate moulting at an earlier stage as well. They might also be in better condition when they start the autumn migration. Such extended influence of early springs on different life history events and fitness aspects later on in the annual cycle are important and remain to be evaluated in future studies.

The effects of fish on boreal duck populations (V-VII)

Most boreal wetlands are oligotrophic, in other words relatively nutrient poor and with low productivity. Food availability may therefore be limiting for ducks breeding in these lakes (Gunnarsson *et al.* 2004). Fish can further reduce food availability and have a major influence on freshwater habitats. Invertivorous fish can reduce the total biomass of invertebrates (Giles *et al.*, 1995), as well as change the average size of the invertebrate community by selectively feeding on large individuals (Bertolo *et al.*, 2005; Rosenfeldt, 2000).

Fish can thus have a negative impact on breeding ducks through competition for invertebrate prey. To test the general effects of fish in typical boreal wetlands; a descriptive study was carried out with lakes of similar size and nutrient status. Some of these lakes were fishless, and others had a mixture of fish species including perch, roach and pike. There was a negative correlation between fish presence and the number of free-swimming and benthic invertebrates, which affected the abundance of breeding ducks as well as total species richness of waterfowl in the lakes with fish. Ironically, fish-eating species such as horned grebe were negatively affected by fish during the breeding season as their young are dependent on invertebrates. Lake utilization was greater in fishless lakes for both teal and goldeneye but there was no observed effect on breeding mallards. The difference in utilization in teal and goldeneye was observed both during the early parts of spring when ducks are in pairs and nesting, and later as the broods have hatched. The effects of fish were negative regardless of the combination of fish found in the lake.

The influence of invertivorous fish on aquatic habitats is likely to depend on fish species composition and density. Simple introduction or removal experiments of fish illustrate a clear negative effect on invertebrate abundance (Andersson, 1984). These experiments also unanimously show that fish have a strong negative effect on lake use and breeding success of ducks (e.g. Mallory *et al.*, 1994; Rask *et al.*, 2001). If a fish community is only limited by invertebrate food resources and is close to carrying capacity, it is likely to have a large impact on the invertebrate community. Piscivorous predators such as adult pike may keep the level of insectivorous fish lower than what would have been possible if food resource limitation was the only restriction on population size. A predator such as pike might therefore have indirect positive effects on ducklings as they reduce the number of competitors. In our study, fish had a negative impact on ducklings, even though pike were present. It is therefore unlikely that these aquatic systems are controlled by top predators.

Bottom-feeding and herbivorous fish can also increase turbidity and change lake characteristics by stirring up sediments and removing macrophytes. The latter can lead to a reduction in cover for broods and increase exposure to avian and terrestrial predators. Increased turbidity may also reduce the chances of catching aquatic prey.

Most studies have concluded that fish have a negative influence on breeding ducks and this is widely understood to be a result of competition between ducklings and fish for common invertebrate prey. Indeed, some studies have demonstrated a diet overlap (Winfield and Winfield, 1994) and a reduction in breeding ducks in waters with high fish densities (Haas *et al.*, 2007, Pehrsson, 1984). Fish removal experiments have resulted in an increased usage by broods and increased duckling survival (Giles, 1994). Other studies have shown that high densities of fish reduce suitability of a lake for ducks (Eriksson, 1983). However, fish density is not always a good predictor of a good breeding habitat. This is because a lake with naturally diverse and dense fish community has a resource base to support it (Paszkowski and Tonn, 2000). In other words, invertebrate levels are likely to be high and therefore it will still be a better breeding lake than a nutrient poor lake with fewer fish. However, the fish were removed, duck breeding success is likely to improve.

In our descriptive study, fish community consisted mainly of perch, roach and pike. Pike was present in all lakes with fish, which reflects the species' ability to colonise new habitats and tolerate a large environmental gradient. Many fishermen, hunters and ornithologists can give anecdotal accounts of pike attacks on broods. Pike are stalking predators that generally stay passive, and strike at moving prey size objects within a distance of less than 2.5m even if the object is a brightly painted lure (Solman, 1945). It is therefore fairly certain that pike would not avoid ducklings if they are moving nearby. Young diving ducks would be particularly vulnerable as they move through the water column. Paasivaara and Pöysä (2004) observed breeding goldeneyes and discovered that duckling survival was lower in lakes with high pike density. Very few studies have been carried out to try to quantify the effects of pike on breeding duck populations. However, Solman (1945), and Lagler (1956) used the gut contents of pike to estimate the annual number of ducklings lost due to piscivore predation. Solman estimated that as much as 9.7% of the waterfowl produced in the Saskatchewan River delta was taken by pike. The number of diving ducks consumed was three times higher than that of dabbling ducks. The study area had high abundance of both ducklings and pike and might therefore have had unusually high predation rates if pike specialize on ducklings in the spring.

The pike introduction experiment was carried out to examine the effects of fish predation in isolation from competition effects. This is the first time a pike introduction has been used to study the impact on natural duck populations. We found that during the nesting phase, when male and female ducks are still in pairs, there was no change in lake use after pikes had been introduced. However, there was a clear decrease in the use of these lakes during the brood phase when the young had hatched. This trend was significant for teal and goldeneye, but not for mallard. The broods disappeared quickly in the pike lakes, and only one goldeneye brood of four ducklings remained throughout the study period. The results do not reveal if the pike are effectively consuming the ducklings or if females simply took their brood elsewhere as a response to pike presence and/or attacks. The effects of a female experiencing a pike attack might be overland movement with the brood to a safer rearing lake. This is an important aspect and similar studies in the future should make sure the female or ducklings can be traced through e.g. radio transmitters. That way it is possible to track the female to a nearby lake if she has moved her brood.

The term "ecological trap" was first coined by Dwernychuk and Boag in 1972 and is used to describe a situation where a species is attracted to a type of habitat despite its unsuitability. The species may be using cues indicating habitat quality that are no longer accurate due to changes in the environment. In a modern landscape where much of the natural habitats have been altered by human land use, the cues previously used to assess habitat quality may attract individuals to habitats that are in fact less suitable than other available areas. Choosing suboptimal breeding sites can influence the individual's breeding success and, if the habitat is consistently chosen, impact the population trajectory. Cues such as vegetation cover and food abundance are probably important when ducks choose rearing lakes. The presence of pike might keep the population of invertivorous fish low and thereby indirectly increase invertebrate abundance in the lake. Piscivorous fish would therefore increase the suitability based on food abundance cues and thus be favoured by breeding females, even though the total duckling mortality may be greater than on pike free lakes. It is also possible that the earliest arrivals, which are usually larger ducks such as mallards, do not suffer as much predation as smaller species and diving ducks. Many waterbirds are known to be attracted by con- and heterospecifics and use this as an indication of habitat quality (Sebastián-González *et al.*, 2010). The species that are more vulnerable to pike predation would therefore be attracted to a less suitable lake.

The lack of avoidance observed in nesting ducks is intriguing as pike appeared to have a great impact on breeding ducks. It is possible, however, that lakes with pike may not be avoided as there are too few alternatives (most lakes contain pike) and that pike avoidance can to some extent be achieved within a lake. Ducklings are potential prey of aquatic, terrestrial and aerial predators. They are likely to have a tailored response to each of the different types of predation, including responses to imminent threat such as predatory attack as well as a general avoidance of predators. As pike predation can have a significant impact on the recruitment of ducks, we would expect to see avoidance behaviour in the females or ducklings, however, no clear strategy for avoidance and response to fish predation has been described in ducks.

Breeding ducks do not avoid lakes with pike, but it is possible that they still identify pike large enough to pose a threat to ducklings. As pike is a stalking predator, avoiding predation by staying away from the area where it resides could be an efficient anti-predatory technique. Other prey species of pike have been shown to actively avoid pike by identifying olfactory cues in the water (Brown *et al.*, 1997). Paasivaara and Pöysä (2004) did not detect a general avoidance of lakes with high pike densities, but they noticed that goldeneye females appeared to be scouting for the ducklings by diving ahead of the brood. She could therefore reduce pike predation by avoiding areas where pike are present rather than trying to avoid entire lakes with pike. Beattie and Nudds (1989) also noticed a response of goldeneye ducklings to fish models in the water. The models were of large and small fish of both predatory and non-predatory species. The ducklings would respond by congregating and reducing their diving activity, but they were unable to distinguish between the predatory shapes and those of other fish dummies or objects. Many large fish live in freshwater ecosystems and, if mistakenly identified as a predatory threat, it would lead to many ”false positive” identification. If habitats were actively avoided, good habitat would subsequently be ignored and breeding possibilities missed.

The ability of ducklings to avoid areas smelling or tasting of pike was tested in the final manuscript of this thesis. We investigated duckling responses to a frozen pike dummy. The frozen pike was clearly visible from the shoreline and it could therefore easily have been identified and avoided either by visual or olfactory cues. The ducklings' innate reactions to avian and terrestrial predators were also tested. Ducklings exhibited neither apparent avoidance nor recognition of the pike or mink; however some broods displayed an innate reaction to predatory bird calls.

Immediate responses were also tested in relation to predation type. The pike dummy was moved towards the ducklings in an attempt to simulate a pike attack. As the pike broke the water, there was an instant reaction that was identical for all broods. They scattered by sprinting on the water to regroup far away from the initial attack, sometimes by the shore or even on land. This reaction is obviously an adaptation to aquatic predation as they reacted in a very different way when attacked by a predatory bird. During the avian attack they responded by diving and scattering under water. This reaction was not as strong as the pike reaction and several ducklings simply swam away from the approaching goshawk. The immediate response to a movement under the water might be well tailored response to aquatic predators. However, one could argue that this response might not be very effective as once an attack is initiated, the targeted duckling is unlikely to get away. It is still possible that if a pike attacks a brood, the rapid movement of feet might reduce the chances of catching or holding on to the targeted duckling. A single duckling on the other hand would be much more vulnerable, which may explain why diving ducks such as goldeneye have been known to be more frequently taken by pike (Solman, 1945) as these ducklings often feed independently.

It is possible that the reaction to predatory fish was not observed in our response study because it is the female that identifies aquatic predatory threat after experiencing attacks on her brood. In other words, it may be a conditioned response. However, the average age of recovered mallards ringed in Finland is around 1.2 years (Gunnarsson *et al.*, 2008), based on mark and recapture data. Thus, most females get one chance only to rear a brood, and innate predatory responses are likely to have a very strong selective value. The ability of naïve versus conditioned females to recognise different types of predatory threat has not been studied and is a great field of research for future studies.

There is a general consensus that ducks are negatively influenced by the presence of fish and that fish generally change a wetland or lake by reducing available invertebrate prey for other organisms. There have been many studies to date that could be used in a meta-analysis to examine the strength of different types of interactions. Dabbling and diving ducks are both influenced by fish, but it is possible that these groups are affected differently. The composition of the fish communities may also be important to the effects on breeding ducks. A complex food web with many different fish species may have a smaller or greater impact on breeding ducks than a lake with only one fish species.

Duckling survival therefore needs to be analysed in a more complex food web to determine the effects of pike on breeding ducks in a natural environment.

Summary

There are strong selection pressures on breeding ducks to increase brood survival by optimizing food intake and reducing predator related mortality. Food availability depends largely on the local habitat chosen by the breeding female and the time of breeding. As no clear peak in emerging invertebrates was identified, food availability in ducklings may not be the primary driving force behind breeding times in these habitat types. However, changing springs may still influence the breeding success of ducks. Teal reproductive output was reduced, whereas mallards did not seem to be affected. Should climate change advance the springs it is therefore likely to have a negative effect on teal which means that such changes and the subsequent response in teal have to be carefully monitored.

Selecting a good breeding habitat is likely to have an effect on reproductive output, which will lead to increased fitness of individuals that can correctly identify such habitat cues. Although the density of breeding ducks is low in most boreal regions, the lakes with ducks often contain several broods of different species. We were able to identify a separation of seed size in the diet of some common species, which might enable co-existence in areas with strong competition.

Ducks are not only competing with other species within the same guild, but also distantly related species, particularly fish. Breeding ducks were found to favour lakes without fish, as these contain more invertebrate prey. However, large piscivores such as pike can also prey on ducklings and this might be another reason for the observed pattern. Both the female and ducklings should benefit from the ability to avoid areas of high predation risk. We were not able to identify any avoidance of lakes with pike in

breeding females during pair formation and egg-laying, despite strong effects on broods and ducklings later in the season. Neither was there any apparent recognition of pike by young and inexperienced ducklings, even though they recognised and displayed clear responses to avian predators. The lack of recognition is intriguing as it is likely to increase duckling losses to pike predation. Either ducks have not developed an optimal predatory response to pike and subsequently suffer from reduced reproductive success, or there are other factors that are of overriding importance for breeding ducks. Further work is needed to analyse the impacts of pike on duck populations and of the anti-predator responses in both ducklings and females. The results in this thesis indicate that pike may have a large influence on breeding ducks and that ducks are unable to recognise or avoid this type of predator. In order to manage good breeding habitats for waterbirds, it could therefore be necessary to actively work to minimise or remove pike populations, at least pike large enough to take ducklings.

References

Afton, A.D. and Paulus, S.L. (1992). Incubation and brood care. In: B.D. Batt *et al.* (Ed.) *Ecology and management of breeding waterfowl*. Minneapolis: University of Minnesota Press.62-108.

Alisauskas, R.T. and Ankney, C.D. (1992). Philopatry, dispersal and the genetic structure of waterfowl populations. In: B.D. Batt *et al.* (Ed.) *Ecology and management of breeding waterfowl*. Minneapolis: University of Minnesota Press. pp. 30-61.

Anderson, M.G., Rhymer, J.M. and Rohwer, F.C. (1992). Philopatry, dispersal and the genetic structure of waterfowl populations. In: B.D. Batt *et al.* (Ed.) *Ecology and management of breeding waterfowl*. Minneapolis: University of Minnesota Press. pp. 365-395.

Andersson, G. (1984). The role of fish in lake ecosystems – and in limnology. In Fagerfjell (Ed.) *Interaksjoner mellom trofiske nivåer i ferskvann*. Oslo: Norsk Limnologforening. pp. 189-197.

Andersson Å., Danell, K., Pehrsson, O. and Sjöberg, K. (1975). Gräsandens häckningsekologi. *Statens Naturvårdsverk*. SNV PM 611, 50.

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

Baldassarre, G.A. and Bolen, G.A. (2006). *Waterfowl ecology and management*. 2nd edition. Florida: Krieger Publishing company.

Bartoszewicz, M. and Zalewski, A. (2003). American mink, Mustela vison diet and predation on waterfowl in the Słońsk Reserve, western Poland. *Folia Zool.* 52(3), 225-238.

Batt, B.D., Afton, A.D., Andersson, M.G. Ankney, C.D., Johnson, D.H., Kadlec, J.A. and Krapu, G.L. (1992). *Ecology and management of breeding waterfowl*. Minneapolis: University of Minnesota Press.

Bauer, S., Gienapp, P. and Madsen, J. (2008). The relevance of environmental conditions for departure decision changes en route in migrating geese. *Ecology* 89(7), 1953-1960.
Beattie, L.A. and Nudds, T.D. (1989). Differential habitat occupancy by goldeneye ducklings (*Bucephala clangula*) and fish: Predator avoidance or competition? *Can. J. Zool.* 67(2), 475-482.
Begon, M., Townsend, C.R. and Harper, J.L. (2006). *Ecology: From individuals to ecosystems*. 4th edition. Malden, USA: Blackwell Publishing.
Bertolo, A. Carignan, R. Pinel-Alloul, B. Planas, D. and Garcia, E. (2005). Decoupling of pelargic and littoral food webs in oligotrophic Canadian Shield lakes. *Oikos*. 111, 534-546.
Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Siepel, H., Van Strien, A.J. and Foppen, R.P.B. (2010). Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proc. R. Soc. B* 277, 1259-1266.
Bond, J.C., Esler, D. and Hobson, K.A., (2007). Isotopic evidence for sources of nutrients allocated to clutch formation by harlequin ducks. *Condor* 109(3), 698-704.
Bowers, M.A. and Harris, L.C. (1994). A large-scale metapopulation model of interspecific competition and environmental change. *Ecological Modelling* 72, 251-273.
Brochet, A.L., Gauthier-Clerc, M., Guillemain, M., Fritz, H., Waterkeyn, A., Baltanás, Á. and Green, A.J. (2010). Field evidence of dispersal of brachiopods, ostrachods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). *Hydrobiologia* 637, 255-261.
Brouwer, C. (1980) Contribution à l'étude du régime alimentaire des sarcelles d'hiver (Anas crecca) en Bretagne Méridionale. *Anatides de Bretagne Meridionale*, rapport d'activité 1979/1980, St Biol Paimpont: 10.
Brown, G.E., Chivers, D.P. and Smith, R.J.F (1997). Differential learning rates of chemical versus visual cues of northern pike by fathead minnows in a natural habitat. *Environmental Biology of Fishes*. 49, 89-96.
Campbell, J.W. (1946) The food of the Wigeon and Brent goose. *British Birds* 39, 194-200.
Campredon, P. (1984) Régime alimentaire du canard siffleur pendant son hivernage en Camargue. *L'Oiseau et la Revue Française d'Ornithologie* 54,189-200.
Chura, N.J. (1961). Food availability and preference of juvenile mallards. *Trans.N.Am. Wildl. Conf.* 26,121-134.
Collier, K.J. and Lyon, G.L. (1991). Trophic pathways and diet of the blue duck (Hymenolaimus malacorhynchos) on Manganuiateao river – a stable

isotope study. *New Zealand Journal of Marine and Freshwater Research*. 25(2), 181-186.

Coppack, T., Tindemans, I., Czisch, M., van der Linden, A., Berthold, P. and Pulido, F. (2008). Can long-distance migratory birds adjust to the advancement of spring by shortening migration distance? The response of the pied flycatcher to latitudinal photoperiodic variation. *Global Change Biology* 14, 2516-2522.

Cox, R.R. Jr., Hanson, M.A., Roy, C.C., Euliss, N.H. Jr., Johnson, D.H. and Butler, M.G. (1998). Mallard duckling growth and survival in relation to aquatic invertebrates. *J. Wildl. Man.* 62(1), 124-133.

Cramp, S. and Simmons, K.E.L (2004). *The Birds of the Western Palearctic on interactive DVD-ROM.* Oxford: BirdGuides Ltd and Oxford University Press.

Cranston, P.S. and Martin, J. (1989). Family *Chironomidae*. In N.L. Evenhuis (Ed.) *Catalog of the Diptera of the Australasian and Oceanian regions*. (Ed. N.L. Evenhuis) Honolulu: Bishop Museum Press, Leiden: E.J.Brill, Leiden pp. 252-274.

Danell, K. and Sjöberg, K. (1977). Seasonal emergence of chironomids in relation to egg-laying and hatching of ducks in a restored lake (northern Sweden). *Wildfowl* 28, 129–135.

Danks, H.V. and Oliver, D.R. (1972). Seasonal emergence of some high arctic *Chironomidae* (Diptera). *The Canadian Entomologist* 104, 661-686.

Darwin, C. (1859). *The origin of species by means of natural selection or the preservation of favoured races in the struggle for life.* Ed. J.W. Burrow 1968. London: Penguin books.

Dwernychuk, L.W. and Boag, D.A. (1972). Ducks nesting in association with gulls – an ecological trap? *Can. J. Zool.* 50, 559-563.

Elmberg, J., Folkesson, K., Guillemain, M. and Gunnarsson, G. (2009). Putting density dependence in perspective: nest density, nesting phenology, and biome all matter to survival of simulated mallard Anas platyrhynchos nests. *J. Avian. Biol.* 40, 317-326.

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

Eriksson, M.O.G. (1983). The role of fish in the selection of lakes by nonpiscivorous ducks. *Wildfowl* 34, 27-32.

Giles, N. (1994). Tufted duck (*Aythya fuligula*) habitat use and brood survival increases after fish removal from gravel pit lakes. Aquatic birds in the trophic web of lakes. *Hydrobiologia* 279/280, 387-392.

Giles, N., Wright, R.M. and Shoesmith, E.A. (1995). The effects of perch, *Perca fluviatilis* L., and bronze beam, *Abramis brama* (L.), on insect emergence and benthic invertebrate abundance in experimental ponds. *Fisheries Management and Ecology* 2, 17-25.

Goyon Demonteil M.C. (2004). *Examen du contenu stomacal des canards sauvages de la Dombes: conséquences pour la gestion floristique des étangs*. Ecole Nationale Vétérinaire. Lyon: Université Claude Bernard.

Green, A. and Figuerola, J. (2005). Recent advances in the study of long-distance dispersal of aquatic invertebrates via birds. *Diversity and Distributions* 11, 149-156.

Guillemain, M., Arzel, C., Legagneux, P., Elmberg, J., Fritz, H., Lepley, M., Pin, C., Arnaud, A. and Massez, G. (2007). Predation risk constrains the plasticity of foraging behaviour in teals, *Anas crecca*: a flyway-level circumannual approach. *Animal Behaviour* 73, 845-854.

Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. and Nummi, P. (2004). Why are there so many empty lakes? Food limits of mallard ducklings. *Can. J. Zool.* 82, 1698-1703.

Gunnarsson, G., Elmberg, J., Dessborn, L., Jonzén, N., Pöysä, H. and Valkama, J. (2008). Survival estimates, mortlity patterns, and population growth of Fennoscandian mallards *Anas platyrhynchos*. *Ann. Zool. Fenneci* 45, 483-495.

Gurd, D.B. (2008). Mechanistic analysis of interspecific competition using foraging trade-offs: Implications for duck assemblages. *Ecology* 89(2), 495-505.

Haas, K., Köhler, U., Diehl, S., Köhler, P., Dietrich, S., Holler, S., Jaensch, A., Niedermaier, M. and Vilsmeier, J. (2007). Influence of fish on habitat choice of water birds: A whole system experiment. *Ecology* 88(11), 2915-2925.

Hesselman, H.L. (1897). Några iakttagelser öfver växternas spridning. *Bot.notiser* 97, 97-112.

Holland M.M., Bitz C.M. (2003) Polar amplification of climate change in coupled models. *Climate Dynamics* 21, 221-232.

Holmboe, J. (1900). Notizen über die endozoische Samenverbreitung der Vögel. *Nyt Magazin f. Naturvidensk* 38, 303-320.

Hornung, J.P. and Foote, A.L. (2006). Aquatic invertebrate response to fish presence and vegetation complexity in western boreal wetlands, with implications for waterbird productivity. *Wetlands*. 26(1), 1-12.

Hurlbert, S.H. and Chang, C.C.Y. (1983). Ornitholimnology: Effects of grazing by the Andean flamingo (*Phoenicoparrus andinus*). *Proc. Natl. Acad. Sci. USA* 80, 4766-4769.

Kear, J. (2005). *Ducks, geese and swans*. Volume 2. Oxford: Oxford University Press.

Klaassen, M. and Nolet, B.A. (2007). The role of herbivorous water birds in aquatic systems through interactions with aquatic macrophytes, with special reference to the Bewick's Swan – Fennel Pondweed system. *Hydrobiologia* 584, 205-213.

Krapu G.L. and Reinecke, K.J. (1992). Foraging ecology and nutrietion. In: B.D. Batt et al. (Ed.) *Ecology and management of breeding waterfowl*. Minneapolis: University of Minnesota Press.

Lagler, K.F. (1956). The pike, *Esox lucius* Linnaeus, in relation to waterfowl on the Seney national wildlife refuge, Michigan. *Journal of Wildlife Management* 20(2), 114-124.

Learner, M.A. and Potter, D.W.B. (1974). The seasonal periodicity of emergence of insects from two ponds in Hertfordshire, England, with special reference to the *Chironomidae* (*Diptera: Nematocera*). *Hydrobiologia* 44(4), 495-510.

MacArthur, R.H. and Wilson, E.O. (1967). *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Mallory, M.L., Blancher, P.J., Weatherhead, P.J. and McNicol, D.K., (1994). Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia* 279/280, 345-351.

Marklund, O., Sandsten, H., Hansson, L., Blindow, I. and Marklund., O. (2002). Effects of waterfowl and fish on submerged vegetation and macroinvertebrates. *Freshwater Biol.* 47(11), 2049-2059.

Mazzucchi, L. (1971). Beitrag zur Nahrungsökologie in der Umgebung von Bern überwinternder Krinckenten *Anas crecca* L. *Der Ornithologische Beobachter* 68, 161-178.

Michailova P. (1989). The polytene chromosomes and their significance to the systematics of the family *Chironomidae*, *Diptera*. *Acta Zoologica Fennica* 186, 1-107.

Miller, D.B., Hicinbothom, G. and Blaich, C.F. (1990). Alarm call responsivity of mallard ducklings: multiple pathways in behavioural development. *Animal Behaviour* 39, 1207-1212.

Nudds, T.D. and Bowlby, J.N. (1984). Predator-prey relationship in North American dabbling ducks. *Can. J. Zool* 62(10), 2002-2008.

Nummi, P. (1993). Food-niche relationships of sympatric mallards and green-winged teals. *Can. J. Zool.* 71(1), 49-55

Nummi, P. and Pöysä, H. (1993). Habitat associations of ducks during different phases of the breeding season. *Ecography* 16(4), 319-328.

Owen, M. and Black, J.M. (1990). *Waterfowl ecology*. New York: Blackie.

Paasivaara, A. and Pöysä, H. (2004). Mortality of common goldeneye (*Bucephala clangula*) broods in relation to predation risk by northern pike (*Esox lucius*). *Ann. Zool. Fennici* 41, 513-523.

Paszkowski, C. A., Tonn, W.M. (2000). Community concordance between the fish and aquatic birds of lakes in northern Alberta, Canada: the relative importance of environmental and biotic factors. *Freshwater Biolog*y 43, 421–437.

Pehrsson O. (1984). Relationships of food to spatial and temporal breeding strategies of Mallards in Sweden. *J. Wildl. Manag.* 48, 322-339.

Pehrsson, O. (1991). Egg and clutch size in the mallard as related to food quality. *Can. J. Zool. review*. 69(1), 156-162.

Phillips, V.E., Wright, R.M. (1993). The differences in behaviour and feeding success of tame Mallard ducklings Anas platyrhynchos in presence of high and low fish populations at a gravel pit site, with reference to wild brood distribution. *Wildfowl* 44, 69-74.

Pirkola M.K. (1966) On the feeding habits of the mallard (Anas platyrhynchos) as revealed by crop and gizzard samples. *Suomen Riista* 18, 67-81.

Pöysä, H. (1983). Morphology-mediated niche organization in a guild of dabbling ducks. *Ornis Scandinavica* 14, 317-326.

Pöysä, H., Elmberg, J., Nummi, P., Sjöberg, K. (1994). Species composition of dabbling duck assemblages: ecomorphological patterns compared with null models. *Oecologia* 98, 193-200.

Pöysä, H., Elmberg, J., Sjöberg, K., Nummi, P. (1998). Habitat selection rules in breeding mallards (Anas platyrhynchos): a test of two competing hypothesis. *Oecologia* 114, 283-287.

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, 502-511.

Pöysä, H., Runko, P., Ruusila, V. (1997). Natal philopatry and the local resource competition hypothesis: data from the Common Goldeneye. *J. Avian. Biol.* 28, 63-67.

Rask, M., Pöysä, H., Nummi, P., Karppinen, C. (2001). Recovery of the perch (Perca fluviatilis) in an acidified lake and subsequent responses in macroinvertebrates and the goldeneye (Bucephala clangula). *Water, Air and Soil Pollution* 130, 1367-1372.

Rosenfeldt, J.S. (2000). Contrasting effects of fish predation in a fishless and fish-bearing stream. *Arch. Hydrobiol.*. 147(2), 129-142.

Sanderson, M.G., Hemming, D.L., Betts, R.A. (2011). Regional temperature and precipitation changes under high-end (≥4°C) global warming. *Phil. Trans. R. Soc. A*. 369, 85-98.

Sargeant, A.B. and Raveling, D.G. (1992). Mortality during the breeding season. In: B.D. Batt et al. (ed.) *Ecology and management of breeding waterfowl. Minneapolis*. University of Minnesota Press. pp 396-422.

Savard, J-P.L., Smith, J.N.M. (1987). Interspecific aggression by Barrow's Goldeneye: A descriptive and functional analysis. *Behaviour* 102, 168-184.

Sebastián-González, E., Sánchez-Zapata, J.A., Botella, F., Ovaskainen, O. (2010). Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. *Proc. R. Soc. B* 277, 2983-2990.

Sjöberg, K., Pöysä, H., Elmberg, J., Nummi, P. (2000). Response of mallard ducklings to variation in habitat quality: An experiment of food limitation. *Ecology* 81(2), 329-335.

Solman, V.E.F. (1945). Ecological relations of pike and waterfowl. Ecology. 26(2), 157-170.

Street, M. (1977). The food of mallard ducklings in a wet ravel quarry, and its relationship to duckling survival. *Wildfowl* 28, 113-125.

Talent, L.G., Jarvis, R.L., Krapu, G.L. (1983). Survival of mallard broods in south-central North Dakota. *Condor* 85, 74-78.

Thackeray, S.J., Sparks, T.H., Fredriksen, M., Burthe, S., Bacon, P.J., Bell, J.R., Botham, M.S., Brereton, T.M., Bright, P.W., Carvalhos, L., Clutton-Brock, T., Dawson, A., Edwards, M., Elliot, J.M., Harrington, R., Johns, D., Jones, I.D., Jones, J.T., Leech, D.I., Roy, D.B., Scott, W.A., Smith, M., Smithers, R.J., Winfield, I.J., Wanless, S. (2010). Trophic level asynchrony in rates of phonological change for marine, freshwater and terrestrial environments. *Global Change Biology*. 16, 3304-3313.

Thompson, J.D., Sheffer, B.J., Baldassarre G.A. (1992). Food habits of selected dabbling ducks wintering in Yucatan, Mexico. *J. Wildl. Manag.* 56, 740-744.

Wallensten, A., Munser, V.J., Latorre-Margalef, N., Brytting, M., Elmberg, J., Fouchier, R.A.M., Fransson, T., Haemig, P.D., Karlsson, M., Lundkvist, Å. Osterhaus, A.D.M.E., Stervander, M., Waldenström, J., Olsen, B. (2007). Surveillance of influenza A virus in migratory waterfowl in Northern Europe. *Emerging Infectious Diseases* 13(3), 404-411.

Winfield, D.K. and Winfield, I.J. (1994). Possible competitive interactions between overwintering tufted duck (*Aythya fuligula* (L)) and fish populations in Lough Neagh, Northern Ireland: evidence from diet studies. *Hydrobiologia* 279/280, 377-386.

Wonham, M. (2006). Species invasions. In: M.J. Groom et al. (Ed.) *Principles of conservation biology*. 3rd ed. Massachusetts U.S.A.: Sinauer Associates, Inc.

Woollhead, J. (1994). Birds in the trophic web of Lake Esrom, Denmark. *Hydrobiologia* 279/280, 29-38.

Acknowledgements

When I started as a PhD student, I was told that the work was very independent and even lonely at times. I was very fortunate to be incorporated into a group of researchers that meet up regularly to share ideas, work together and socialise. I have met researchers from around the world, which has been a great inspiration. Much of this has been made possible by the active role of my main supervisor, Johan Elmberg, who has not only guided me through the daunting task of writing scientific articles, but also made it possible for me to attend international meetings and conferences. Johan has been a great mentor, colleague and friend. If I manage to make myself a career in academia, I will have him to thank for it.

I therefore thank Johan for taking me on as a PhD student, for all his support and for including me in the Nordic duck research team.

I also wish to thank my other supervisors; Göran Englund for your knowledge of fish, your attention to detail and for letting me stay with your family. I would like to thank Hannu Pöysa and Kjell Sjöberg for inspirational discussions during our many meetings. I would also like to thank Carin Magnhagen for making sure I got through the maze of administration in order to graduate.

Above all I would like to thank those closest to me, my parents and my brother. Thank you for always being there for me.