Survival Patterns and Density-dependent Processes in Breeding Mallards *Anas platyrhynchos*

Gunnar Gunnarsson

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

Doctoral thesis
*Swedish University of Agricultural Sciences*
*Umeå 2007*
Abstract


Measuring and assessing vital rates such as births and deaths are prerequisites for understanding population dynamics. Vital rates may be affected by the density of individuals, even though the importance of density dependence on population dynamics has been debated for a long time. The mallard *Anas platyrhynchos* is one of the foremost game species in the Holarctic, with millions of birds in hunters’ bags annually. Still, basic knowledge about regulation of mallards’ vital rates is poor, and experimental studies on this topic are rare.

In this thesis I have studied survival patterns and density dependence in mallards breeding in Sweden and Finland. Long-term ringing data from both countries were analysed for mortality patterns and causation, as well as for e.g. survival rate estimation. Most of the studies were, though, experiments run over two years involving manipulations of the density of nests, broods and/or adults, in southern and northern Sweden, comprising different biotic regions. Common response variables were survival of nests, ducklings and hens, mainly analysed with program MARK.

About 90% of the recovered mallards in Finland and Sweden were hunting kills. However, survival rates were high, ranging from 0.66 to 0.81 for most groups (sex*age). The generality of density dependence was evident since such processes were detected in all studies. Consequently, depredation rate was higher in high nest density compared to low nest density. Survival of ducklings was density-dependent in both boreal and nemoral biotic regions, with food limitation being evident in the former region but not in the latter. In spite of their generality, density-dependent patterns varied within as well between years, and for nest predation rates also between landscape types.

The findings about density dependence in breeding mallards in this thesis are novel since they are based on experiments. They are potentially of general interest for management because they embrace a variety of lakes in two geographically distant areas, each being representative for large temperate areas in the northern hemisphere. Detection of density dependence at the local scale may be important at larger scales, too, following the principle of ‘ideal preemptive distribution’ in a source-sink dynamic system.

*Key words*: broods, dabbling ducks, density dependence, ducklings, experiments, models, mortality, nest predation, regulation, survival

*Author’s address*: Gunnar Gunnarsson, 1) Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 UMEÅ, Sweden, 2) Department of Mathematics and Science, Kristianstad University, SE-291 88 KRISTIANSTAD, Sweden
To Ebba
Contents

Introduction, 7
Density dependence, 7
Mallard ecology and density dependence, 10
Objectives, 13

Materials and methods, 14
Dabbling ducks, which are they?, 14
Study sites, 15
Experiments, 16
Analysing survival, 19
Invertebrate sampling, 21

Results and discussion, 21
Mallard mortality and population growth (Paper I), 21
Density dependence in nesting mallards (Papers III & IV), 23
Density dependence in brood rearing mallards (Papers V–VII), 24

Harvest and management implications, 26

Conclusions and future perspectives, 28

References, 30

Acknowledgements, 37
Tack, 38
Appendix

Papers I–VII

The present thesis is based on the following papers, which will be referred to by their Roman numerals:


III. Gunnarsson, G. & Elmberg, J. Density-dependent nest predation – an experiment with simulated mallard nests in contrasting landscapes. (Submitted manuscript).

IV. Elmberg, J. & Gunnarsson, G. Are mallards ducking for predators? Local pair density affects nest survival differently in different landscapes. (Submitted manuscript).


Papers II, V, VI, and VII are reproduced with kind permission of the journals concerned.
Introduction

All organisms die, some sooner and some later; that is an inevitable truth. However, a natural and immediate question arises: Why do some die young while others when old? Besides the fact that all organisms are genetically different (identical twins and clones excluded) and consequently have different prospects of getting old, the external environment plays a crucial role. As such, survival is affected by both non-biological (abiotic) factors, such as weather conditions, and biological (biotic) factors (e.g. Krebs, 1994; Newton, 1998). Competition for food and other resources, predation, and disease are examples of the latter. In this context two fundamental processes are often mentioned; ‘limitation’ and ‘regulation’. By definition, limiting factors are those that, in any way, suppress population growth. Both biotic and abiotic factors can act upon populations as limiting factors. Cold spells in late winter killing early arriving migrants, foxes acting as predators robbing birds’ nests, disease resulting in death or reduced future reproductive success, traffic taking the lives of animals on roads; all are examples of limiting factors. Regulation on the other hand, does not include abiotic factors, but only biotic, and is by definition the result of density-dependent intra- or interspecific factors (e.g. Royama, 1977; Turchin, 1995; Begon, Harper & Townsend, 1996).

Density dependence

The outcome can be very similar for two populations subjected to either limitation or regulation, and it can hence be very hard to tell which process is taking place. In contrast to limitation, which may include both density-independent and density-dependent factors, regulation rests upon density dependence only (e.g. Royama, 1977; Turchin, 1995; Begon, Harper & Townsend, 1996).

A very simple population growth model is that of exponential (geometric) growth, i.e.

\[
\frac{dN}{dt} = rN
\]

(1)

In other words, the net rate of increase \((dN/dt)\) is equal to the intrinsic rate of natural increase \((r)\) multiplied by the population size \((N)\). However, hardly any species can grow unlimited; due to density dependence there is a balance between the ‘income factors’ (nativity and immigration) and ‘expense factors’ (mortality and emigration) limiting population growth (e.g. Cappuccino & Price, 1995; Begon, Harper & Townsend, 1996). A simple example is illustrated in Fig. 1 where density dependence leads to increased death rate when population size grows, in contrast to birth rate which decreases. In this context one should remember that, in reality, both birth and death rates may be density-dependent and/or density-independent, and the response does not have to be linear (Murray, 1994). Anyway, the consequence in Fig. 1 is an intersection point between the
Birth rate

Death rate

\[ \text{N} \]

\[ \text{N}^* \]

Fig. 1. Density dependence in an imagined population. In this example both birth and death rates are density-dependent; the population size (N) increases left of the dotted line and decreases right of it and hence goes to its equilibrium size (N*) as indicated by arrows.

lines which is often referred to as ‘equilibrium population size’ (N*) or ‘carrying capacity’. This leads us to the logistic equation (Verhulst, 1838),

\[
\frac{dN}{dt} = rN \left( \frac{N^* - N}{N^*} \right)
\]

(2)

which differs compared to eq. 1 in the expression (N*-N)/N* describing density dependence. When the actual population size gets closer to the equilibrium size, the expression approaches zero, and population growth thus slows down and is constrained not to exceed N* (Fig. 2A).

The above models are illustrative because of their simplicity, but true population dynamics are in most cases quite noisy and many factors must be included if one wants to describe it mathematically. Typical populations thus do not grow evenly and stabilise at a certain equilibrium size. The latter is decided by available resources (see below; e.g. Krebs, 1994), which in turn may also vary for other reasons than being regulated by its consumer. Moreover, density dependence is often not immediate but somewhat delayed. This may cause populations to overshoot N*, but regulation will make population growth decelerate and ultimately turn negative. The other side of regulation is the feed-back mechanisms once more making growth positive if N goes below N* (Fig. 2B). Through density dependence, regulatory mechanisms thus prevent both indefinite increase as well as extinction keeping the population within restricted limits (e.g. Newton, 1998).

What drives density dependence, i.e. what is forcing population growth not to go on unlimited? Several factors can be identified. Perhaps the most typical is the availability of resources (e.g. Krebs, 1978; Newton, 1998). All populations, no matter what species, depend on several resources, and the most fundamental one, called the “key resource” (White, 2001), is often food. In a population regulated by food availability a balance between individual numbers and resource
availability will ultimately be reached, assuming that external conditions remain fairly constant (Pulliam & Caraco, 1984). Food availability decides population equilibrium size such that the population increases when food is abundant due to low population size. Above $N^*$, population size is too big to be sustained by food resources, which will lead to negative population growth (cf. Fig. 1). Indeed, there is often a positive correlation between food abundance and population density (e.g. Newton, 1998). This can be studied for example in longitudinal studies of populations by comparing years with scarce and abundant food. However, the connection is not always that obvious because food quality rather than quantity is sometimes more important (Newton, 1998).

Even if competition for resources is low, a population may still not start to grow to high numbers. This can be due to the impact of predators and parasites (e.g. Newton, 1998), and also of infectious disease. Mostly based on theoretical studies, it is suggested that the latter may be involved in the regulation of hosts although the knowledge is poor about how the dynamics of wild populations are affected (see review in Gulland, 1995). In contrast, there are many predator removal experiments showing that prey density is limited by predators; e.g. reducing the density of American mink *Mustela vison* resulted in increased number of waterfowl such as dabbling ducks *Anas spp.* (Nordström *et al.*, 2002). Such experiments indicate that density dependence is not just a theoretical concept but has biological significance. As such, density dependence, for example affecting survival, per capita growth rate or behaviour, has indeed been shown in numerous studies and for different taxa such as insects (e.g. Woiwod & Hanski, 1992), fish (e.g. Sibly *et al.*, 2005), birds (e.g. Krebs, 1970; Durell *et al.*, 2000) and mammals (e.g. Hansen, Stenseth & Henttonen, 1999; Kjellander *et al.*, 2004; Wauters *et al.*, 2004).

---

*Fig. 2. A) Logistic population growth; population size ($N$) cannot exceed its equilibrium size ($N^*$). B) Density dependence regulates population growth, i.e. population change will turn negative above the equilibrium size and positive below it.*
Mallard ecology and density dependence

Dabbling ducks are globally important game species and hunting mortality is a common cause of death. Based on data of recovered mallards *Anas platyrhynchos*, hunting mortality in Europe often stands for more than 90% of the deaths (Bentz, 1985; Wernham et al., 2002; see also Fransson & Pettersson, 2001; Bakken, Runde & Tjørve, 2003). The corresponding rate for North American mallards is also very high (85% in Hickey, 1952). These facts make hunting a process very likely to affect population dynamics (Anderson & Burnham, 1976). Of the natural mortality causes, predation is the major one being most prominent during incubation and early duckling life (Dzus & Clark, 1997a). Common predators on mallards’ nests and ducklings in Europe are raven *Corvus corax*, hooded crow *Corvus corone cornix*, American mink, red fox *Vulpes vulpes* and badger *Meles meles*. Adults may also fall victim to predators such as raptors and owls (Cramp et al., 1994).

One heavily debated question in waterfowl ecology is whether hunting mortality is additive to natural mortality or compensated for by lowered natural mortality (e.g. Anderson & Burnham, 1976; Rogers et al., 1979; Hill, 1983; Burnham & Anderson, 1984; Barker, Hines & Nichols, 1991; Smith & Reynolds, 1992; Trost, Dickson & Zavaleta, 1993; Boyce, Sinclair & White, 1999). Compensatory mortality requires, by definition, density dependence; if hunting mortality increases, density-dependent induced natural mortality decreases as a consequence (e.g. Anderson & Burnham, 1976; Williams, Nichols & Conroy, 2002). Most studies dealing with hunting effects on waterfowl confirm a compensation by lowered natural mortality, and indirectly so also for density dependence (e.g. Anderson & Burnham, 1976; Rogers et al., 1979). However, the degree of compensation through density dependence ought to be limited, and several authors claim that mortality through hunting will be additive above a certain level (Anderson & Burnham, 1976; Trost, Dickson & Zavaleta, 1993). It seems logical, and hence there are also many examples where populations have gone to extinction because of too high hunting pressure (see review in Caughley & Gunn, 1996). The concept can of course be applied on other limiting factors such as competition for resources, predation, and disease, too, and the conclusion is thus that understanding density dependence is important in management and conservation of all species, not only waterfowl.

As clarified in Nichols et al. (1984), the hypothesis of compensatory mortality does only deal with density-dependent mortality and should not be mixed with density-dependent reproduction. However, compensatory natality is indeed a relevant issue in this context since a temporal decrease in natural mortality due to hunting may be compensated for the following breeding season if reproductive output is density-dependent (Boyce, Sinclair & White, 1999; Williams, Nichols & Conroy, 2002).

Density-dependent effects on breeding success have been debated since the study by Nicholson (1933), and even if the process is generally accepted, it is still central and controversial (e.g. Woiwod & Hanski, 1992; Newton, 1998; Shenk,
White & Burnham, 1998; Berryman & Turchin, 2001; White, 2001). Theoretically, density dependence could act during any stage of the breeding period, *i.e.* pair formation, nesting habitat selection, nest building, egg-laying, incubation, and chick-rearing (*cf.* Åström, Lundberg & Lundberg, 1996). Adults as well as ducklings may be affected, even though the inexperienced ducklings are most likely to be influenced. The effect of density dependence is certainly not only ‘life or death’: it may be less straightforward and operate through lowered body weight, reduced immunological defence (*i.e.* sub-lethal effects) *etc.*, which in turn may lead to lowered future fitness, or more dramatically increase mortality rate (Newton, 1998; *cf.* also Gulland, 1995; Wobeser, 1997).

For mallard survival and reproduction there is still no general consensus about the role of density-independent factors such as temperature and rainfall versus density-dependent factors (Anderson & Burnham, 1976; Burnham & Anderson, 1984; Kaminski & Gluesing, 1987; Bethke, 1993; Trost, Dickson & Zavaleta, 1993; Krapu *et al.*, 1997; Newton, 1998; Sheaffer, 1998; Miller, 2000). Indeed, there is evidence for weather impact on mallard duckling survival (*e.g.* Sheaffer, 1998; Miller, 2000; but see Pöysä *et al.*, 1993). Most studies on density dependence in mallard are based on long time-series from North America (*e.g.* Anderson & Burnham, 1976; Burnham & Anderson, 1984; Kaminski & Gluesing, 1987; Sheaffer, 1998), and also for the few European studies the results are somewhat contradictory. Hill (1983) argued that density dependence is most prominent on wintering sites, even though duckling mortality also tended to be density-dependent. Long-term observational data in Hill (1984) indicate density-dependent breeding success, as was also shown in a long-term study in Sweden (Elmberg, 2003). The latter study reports a density-dependent effect on per capita brood as well as per capita fledgling production (though the latter was not independent of the former). Studies on Finnish mallards with long-term data (Pöysä, 2001; Elmberg *et al.*, 2003) did not find any density dependence on breeding success, and also other studies on dabbling ducks in Europe give an inconsistent picture (Elmberg *et al.*, 2003; Pöysä & Pesonen, 2003). A summary of studies on density dependence in dabbling ducks are presented in Table 1 (papers in this thesis are not included).
Table 1. Studies on density dependence in breeding dabbling ducks. Density dependence was either detected (Yes), not detected (No), or not addressed at all (empty line). Except for the four last studies and Andrén (1991) specifically studying nest predation, all others are based on time series data; the number of years is given in parentheses in the ‘Area’ column. A modelling approach was used in Anderson & Burnham (1976), Burnham & Anderson (1984), Barker, Hines & Nichols (1991), Smith & Reynolds (1992), and Sheaffer (1998). Other studies have used traditional statistical testing to analyse data.

<table>
<thead>
<tr>
<th>Species</th>
<th>Area (years)</th>
<th>Breeding pairs</th>
<th>Nest failure</th>
<th>Brood survival</th>
<th>Duckling survival</th>
<th>Recruitment to population</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mallard Anas platyrhynchos</td>
<td>England (16)</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Hill, 1984</td>
</tr>
<tr>
<td></td>
<td>Sweden (13)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Elmberg, 2003</td>
</tr>
<tr>
<td></td>
<td>Sweden (1)</td>
<td>No</td>
<td></td>
<td>No</td>
<td></td>
<td></td>
<td>Andrén, 1991</td>
</tr>
<tr>
<td></td>
<td>Finland (16)</td>
<td>No</td>
<td></td>
<td>No</td>
<td></td>
<td></td>
<td>Poysä, 2001</td>
</tr>
<tr>
<td></td>
<td>Finland (12)</td>
<td>No</td>
<td></td>
<td>No</td>
<td></td>
<td></td>
<td>Elmberg et al., 2003</td>
</tr>
<tr>
<td></td>
<td>N.Amer. (26)</td>
<td></td>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>Kaminski &amp; Gluesing, 1987</td>
</tr>
<tr>
<td></td>
<td>N.Amer. (30)</td>
<td></td>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>Burnham &amp; Anderson, 1984</td>
</tr>
<tr>
<td></td>
<td>N. Amer (15)</td>
<td></td>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>Sheaffer, 1998</td>
</tr>
<tr>
<td></td>
<td>N.Amer. (12)</td>
<td></td>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>Anderson &amp; Burnham, 1976</td>
</tr>
<tr>
<td></td>
<td>N.Amer. (11)</td>
<td></td>
<td></td>
<td>Yes</td>
<td></td>
<td></td>
<td>Smith &amp; Reynolds, 1992</td>
</tr>
<tr>
<td>Wigeon A. Penelope</td>
<td>Finland (12)</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td></td>
<td></td>
<td>Elmberg et al., 2003</td>
</tr>
<tr>
<td></td>
<td>Finland (17)</td>
<td>No</td>
<td></td>
<td>No</td>
<td></td>
<td></td>
<td>Poysä &amp; Pesonen, 2003</td>
</tr>
<tr>
<td></td>
<td>Iceland (21)</td>
<td>Yes</td>
<td></td>
<td>No</td>
<td></td>
<td></td>
<td>Poysä &amp; Pesonen, 2003</td>
</tr>
<tr>
<td>Teal A. crecca</td>
<td>Finland (12)</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Elmberg et al., 2003</td>
</tr>
<tr>
<td>Blue-winged teal A. discors</td>
<td>N.Amer (13)</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Weller, 1979</td>
</tr>
<tr>
<td>Anatinae spp.</td>
<td>N.Amer (2)</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sugden &amp; Beyersbergen, 1986</td>
</tr>
<tr>
<td></td>
<td>N.Amer (1)</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Esler &amp; Grand, 1993</td>
</tr>
<tr>
<td></td>
<td>N.Amer (1)</td>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Larivière &amp; Messier, 1998</td>
</tr>
<tr>
<td></td>
<td>N.Amer (5)</td>
<td>No</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Ackerman, Blackmer &amp; Eadie, 2004</td>
</tr>
</tbody>
</table>

1 Results are not statistically independent of each other; 2Studies using artificial duck nests, usually resembling those of mallard.
Objectives

Knowledge about the frequency and impact of density dependence is basic to understanding the ecology of any species and a prerequisite for successful management and conservation (Caughley & Sinclair, 1994; Kokko et al., 1998; Boyce, Sinclair & White, 1999). Jonzén & Lundberg (1999) emphasise, however, that in order to be able to understand the influence of density dependence on population fluctuations, it is important to collect data on per capita birth and death rates as related to population density. Hence, I have focused my studies on density dependence to the breeding season and as study species I have chosen mallard.

Ducks are important study objects since they are numerous and can be used as indicator species of wetlands, many of which have high species diversity and hence have high biological values. Duck research has a long and productive history for conservation, for general ecological understanding, and also for management. A considerable proportion of many duck populations are harvested each year. Moreover, ducks are the natural vectors of some diseases such as avian influenza that may potentially be hazardous to man (Olsen et al., 2006).

Mallard is the most common duck worldwide, and as such also in many aspects thoroughly studied. Previous research has addressed many questions that still need investigation, for example the impact of density dependence. In particular, experimental studies are rare, but nevertheless important and necessary to test and to establish such patterns. Many species cannot be used for experiments, e.g. due to practical problems such as difficulties in collecting specimens in low populations sizes. Mallard is a perfect species in this sense since it is numerous and also because it is a commonly bred species in captivity. The studies in this thesis are thus mainly experimental and my contribution to waterfowl ecology is a natural continuation of preceding waterfowl research, but along partly new paths.

The reason why there is no general conclusion concerning density dependence may be that such processes may differ because of differences in temporal and/or spatial structure of populations (e.g. Turchin, 1990; Hanski & Woiwod, 1991; Ray & Hastings, 1996; Berryman & Turchin, 1997; Rodenhouse, Sherry & Holmes, 1997; Paradis et al., 2002; Pöysä & Pesonen, 2003). In addition, because Europe have different breeding conditions for mallards compared to North America in terms of permanency of wetlands, predation pressure etc., we need to gain a separate understanding of population limitation and regulation in European populations of dabbling ducks.

In Paper I, mortality patterns for Fennoscandian mallards are presented using approximately 90 years of banding data from Sweden and Finland. I thereby report mortality causes, distribution of recovered birds by sex and age, and I also give estimates for e.g. survival rates. The latter is combined with pair and reproduction data from Finland, to model population growth.

Paper II reviews previous work dealing with hunting mortality and the long lasting question how it influences natural mortality. In this paper it is also
discussed whether there has been a trend in favour of either of the two hypotheses of compensatory and additive mortality.

The remaining papers (III–VII) are all based on experiments addressing density dependence in breeding success of mallards. Vital rates during the breeding season are perhaps the most important ones determining population growth and this is why I mainly focus on this period. For several reasons, I do not give threshold values for when density dependence starts to give negative feedback on population growth. First, such limits include a lot of noise due to spatial and temporal variability. Also, my experiments on density dependence are restricted to a quite small geographical scale and a confined set of habitat types.

## Materials and methods

### Dabbling ducks, which are they?

Although the number differs among taxonomies, Batt et al. (1992) recognise 36 dabbling duck species. Most of them share the characteristics of slender body size, sexual dimorphism (male often with bright colours whereas female is dull coloured), long and pointed wings, and quite long flattened bill with distinct lamellae for straining food in water (Cramp et al., 1994). Seven species breed in Fennoscandia: mallard, gadwall A. strepera, pintail A. acuta, northern shoveler A. clypeata, Eurasian wigeon A. penelope, Eurasian teal A. crecca, and garganey A. querquedula. Mallard, teal and wigeon are the most numerous species in Fennoscandia; the first two breed more or less in the entire area whereas wigeon mainly is restricted to the boreal region. The other four species have wide ranges too, but breed sparser and have much lower population sizes (Hagemeijer & Blair, 1997).

Dabbling ducks depend on wetlands as most foraging takes place there, although foraging on land also occurs (Cramp et al., 1994). They usually forage from the water surface or just below it by up-ending. Most of the European dabblers are omnivorous, having a diet largely reflected by its abundance. However, wigeon and gadwall are exceptions in being mainly vegetarians. Water-living animal prey comprises insects, molluscs, crustaceans, annelids, amphibians, and vegetarian food mainly roots, leaves, tubers, buds and seeds (Cramp et al., 1994).

Monogamous pair formation, with seasonal duration, takes place during the autumn and winter, or more seldom during early spring before migration (Cramp et al., 1994). For the mallard, a substantial part of the European population breeds in the northern countries of Fennoscandia and settles in wetlands areas in a wide range of habitats in nemoral as well as in boreal zones. The breeding season in Fennoscandia lasts from April to July and the number of eggs laid varies between species, but it is usually 8–10. The nest is most often on the ground close to water and consists of a cup of grass or other plant material collected near the nest site. After the incubation period (3.5–4 weeks), which the female alone takes care of,
the precocial ducklings hatch and almost immediately leave the nest. The female tends the brood alone, and ducklings fledge after 6–8 weeks (teal and garganey fledge after 3.5–4 weeks). Adults moult completely after breeding and this leads for a few weeks to incapability of flying, and males also develop female-like eclipse plumage during this period. The moult period is quite prolonged and the breeding plumage for the next season appears from mid autumn and is completed in early winter. Yearlings do not moult completely in their first calendar year, but as many breed as one year olds, breeding plumage is acquired during the winter (Cramp et al., 1994). The dabbling ducks breeding in Fennoscandia fly more or less far southwest for wintering, and in between they stop along the migration routes. Except for in some mallard populations, breeding, staging and wintering thus occur in separate areas (Fransson & Pettersson, 2001).

Study sites

Papers I & II are based on data that were not directly gathered by the people involved in the studies of my thesis; previous nationwide ringing data from Sweden and Finland, provided by the national ringing centres in these countries, were processed in Paper I, whereas Paper II synthesises earlier North American studies addressing the effect of hunting mortality on natural mortality in mallards.

All other papers (III–VII) were based on data gathered by the authors of the papers in Sweden at small to medium sized lakes (most were 1–5 ha) used by mallards as breeding sites. Different parts of Sweden were used to consider regional effects possibly influenced by nutrient status in those areas (Fig. 3). Some studies were hence conducted in the southern part of the country (‘Skåne’ and ‘Blekinge’ provinces; Papers III, IV & VII) in both oligotrophic and eutrophic lakes, while others in the north (‘Västerbotten’ and ‘Ångermanland’ provinces; Papers V & VI) using oligotrophic sites only. Breeding mallards have thus been studied in nemoral, boreo-nemoral as well as in boreal biotic regions of Sweden.

The studies were carried out on the lake level for several reasons. Lakes are important breeding sites for mallards in Fennoscandia (cf. Danell & Sjöberg, 1978) and they are the primary level of breeding site selection; nests are placed in the surrounding area, and after hatching the hen takes the brood to the lake (or watershed) where they stay until fledged. Study lakes were rather small to increase the likelihood of observing mallards under study and to be able to reliably census wild birds used as covariates in the analyses. Accordingly, only one or two census spots at the lakes were required to cover the entire lake. Further, there was a preference of choosing lakes in isolation from other ones, either to avoid the same individual predators visiting the same lakes (Papers III & IV) or to avoid that experimental hens (see below) would leave the lake for other areas (Papers V–VII). The latter is a relevant consideration since mallards are known to have the capacity of taking their brood over considerable distances within a watershed (e.g. Ball et al., 1975; Rotella & Ratti, 1992a; Dzus & Clark, 1997b). Great care was thus taken in selecting study lakes, and this was necessary for conducting successful experiments (see below).
Prior to the studies all lakes were monitored for breeding waterfowl (Koskimies & Väisänen, 1991) and only lakes that were utilised by waterfowl naturally were selected as study lakes. Lakes were characteristic for each region and nutrient status; oligotrophic lakes in boreal and boreo-nemoral regions were thus sparsely vegetated and surrounded with mostly coniferous forest while eutrophic lakes in the nemoral region usually had dense reed-beds surrounded by deciduous forests or situated in open cropland (Fig. 4).

**Experiments**

Almost all previous studies addressing density dependence in ducks have used non-experimental data, many with long-term data sets and others using only one or a few years of data (see Table 1). These studies have produced important and novel knowledge about density dependence, and many have also resulted in testable predictions for further investigation. One advantage with non-
experimental studies is that the ‘real world’ is studied. However, there are reasons to perform experiments as well. There may be strong indications for density dependence revealed by non-experimental data, but it is often difficult to separate factors from each other, density-dependent from intricate density-independent ones (Royama, 1977). This predicament makes an experimental approach necessary to establish the processes behind the patterns of density dependence (e.g. Kaminski & Gluesing, 1987; Harrison & Cappuccino, 1995; Newton, 1998; Sheaffer, 1998). Moreover, an experimental approach also has the strength of enabling replication and standardisation of conditions (i.e. lake characteristics; see above). Despite decades of descriptive research and retrospective modelling, experimental studies of density-dependent processes remain exceptionally sparse in dabbling ducks (but see nest predation studies in Table 1). However, it is a necessity to carefully plan and perform well-designed experiments. This is especially true when studying density dependence since it may occur intermittently and sequentially (Åström, Lundberg & Lundberg, 1996).

The experiments described in this thesis were carried out either during the nesting period (Papers III & IV) or brood-rearing period (Papers V–VII). Generally, density dependence in these two stages was studied by manipulating densities of nests, broods, and/or adults. Density manipulations were accomplished by using either two densities (denoted low and high) (Papers III & V), or by comparing a treatment setting with controls (Papers IV, VI & VII).

Nest predation experiments (Papers III & IV) were based on a refined principle of artificial nest, termed ‘semi-natural nests’, constructed to resemble mallards’ nests and placed close to the shoreline. Natural material found near the nest site was collected and a cup of standardised size was formed and lined with mallard down. Finally, five fertilised eggs provided by a local mallard farmer were put in the nest. The nest fate (depredated or not) was then monitored for 16 days (day 1, 2, 4, 8 and 16), and as for all experiments in this thesis, waterfowl present on the

Fig. 4. Study lakes from two biotic regions. The left lake is from the nemoral zone situated in an open agricultural landscape. Typically, oligotrophic lakes in boreo-nemoral and boreal zones (lake to the right) were surrounded by coniferous forest and were more sparsely vegetated compared to the more nutrient rich nemoral lakes.
lakes were censused and often included in the analyses as covariates (see below). In Paper III either two (low density) or eight nests (high density) were constructed at each lake, whereas the lakes in the other nest predation experiment (Paper IV) all had two nests. On half of the latter lakes two adult pairs were also introduced to study their attractive effect on predators, measured as depredation of nests. Both nest predation experiments were performed in two landscapes (forested and agricultural) and in two years for a cross-over setup; i.e. lakes subject to one treatment the first year had the other treatment the second year.

The last three papers in the thesis describe experiments performed during the brood-rearing period. In Papers V & VI, broods (of standardised size) with attending hens were introduced, whereas adult pairs without broods were released onto each treatment lake in Paper VII (Fig. 5). Two breeders were contracted to supply the mallards, one in boreal Sweden (Papers V & VI) and one in the south (Paper VII). Wild strain mallards were used and hens in Papers V & VI were the true mothers of her ducklings which were hatched outdoors in an environment similar to the breeding habitat of local wild mallards. The flight feathers from one wing were cut in introduced adult birds, and this was done for two reasons; 1) to enable accurate identification of introduced mallards easily separated from wild ones, and 2) mallards unable to fly were less likely to leave the lake onto which they were released facilitating successful introductions. Introduced mallards behaved naturally in most of the cases when released, i.e. ducklings stayed close to their hen and usually started to forage immediately. Hens were also typically very

Fig. 5. Introduction of adult mallards in southern Sweden (Paper VII). Birds were wild strain mallards raised in captivity. By cutting flight feathers from one wing ducks were unable to fly, which was a prerequisite for successful introductions, i.e. mallards staying on the lake.
vigilant and silently hid in protecting vegetation when for example humans and predators were sighted.

Density dependence was studied in Paper V by introducing either one hen with brood (low density) or four hens with broods (high density). In the study described in Paper VI only one hen and her brood were introduced on each of the study lakes, and to study the effect of food limitation on the survival of ducklings extra food (barley and pellets) were added *ad libitum* to half of the lakes whereas the rest were controls. The fate of ducklings and hens were followed for 24 days in both studies, daily until day 12 and then every third day.

The last paper including the introduction of adult pairs addressed density dependence by using half of the study lakes as treatment lakes (two pairs introduced; Fig. 5) and the remaining half as controls. Dependent variables were habitat use and duckling production in wild mallards recorded for 14 weeks. Data on invertebrate abundance (see below) were also collected and analysed for impact on reproductive output. The study in Paper VI was run for one year only, whereas those in Papers V & VII for two years enabling a cross-over approach.

**Analysing survival**

Survival is the main dependent variable used in my thesis, and such data were collected for nests (Papers III & IV), ducklings and adults (Papers I, V–VII). How to analyse survival patterns is, however, not always straight-forward. For example, traditional statistical tests are often based on assumptions violated by *e.g.* longitudinal data, such as those in this thesis. Other problems are related to inter-dependencies such as between individuals within the same breeding lake; *i.e.* the survival of ducklings among and between broods cannot be assumed to be independent of each other. Moreover, Dennis & Taper (1994) found either type I or type II errors in several tests often used for analysing data for density dependence (*e.g.* Morris, 1959; Varley & Gradwell, 1963; Bulmer, 1975; Slade, 1977).

Except for Paper VII (and Paper II reviewing other studies) a capture-recapture modelling approach was instead used to analyse survival data (*e.g.* Brownie *et al.*, 1985; Lebreton *et al*., 1992; White & Burnham, 1999; Burnham & Anderson, 2002). This is totally different from statistical testing based on confirmation or falsification of hypotheses by using a certain level of significance. Alternatively, with a modelling approach, *a priori* models including different variables are instead considered as to how well they fit data. Program MARK (White & Burnham, 1999) was used, partly due to the possibility of controlling for overdispersion by adjusting the variation inflation factor (*c*). In this context overdispersion means extra binomial variation not explained by the variables included in the models (*i.e.* noise). Program MARK thus works with binomial data defining survival in encounter histories either as 1 or 0 depending on status (alive or missing), even though covariates with continuous values, like the waterfowl presence data described above, also can be added in design matrices by using a...
logit link function. The latter are, however, standardised to fall in between 0 and 1 to conform to the model structure.

Models are ranked using the Akaike’s Information Criterion (\( AIC \)) (Akaike, 1973) adjusted for low sample size (\( AIC_c \)). The formulation is calculated as

\[
AIC_c = -2 \ln(L) + 2K + \frac{2K(K+1)}{n-K-1}
\] (3)

where \( L \) is the model likelihood, \( K \) the number of parameters, and \( n \) the sample size (see Burnham & Anderson, 2002). Alternatively, if data are overdispersed and \( \hat{c} \) thus is adjusted, the quasi-likelihood Akaike’s Information Criterion (\( QAIC_c \)) is used instead. (Burnham & Anderson, 2002). The expression in eq. 3 is then slightly modified by dividing \(-2\ln(L)\) in the first step with \( \hat{c} \), i.e.

\[
QAIC_c = -\left[ \frac{2 \ln(L)}{\hat{c}} \right] + 2K + \frac{2K(K+1)}{n-K-1}
\] (4)

The lower the \( AIC_c \) (or \( QAIC_c \)) value the higher the rank, and a model with two or more \( AIC_c \) (or \( QAIC_c \)) units lower than subsequent models is generally considered superior to those (Burnham & Anderson, 2002).

Other valuable information that program MARK provides are beta estimates for parameters (i.e. how each variable is related to the intercept), as well as real estimates. The latter are especially useful when analysing bird ringing data, for example to estimate annual survival rates (Paper I).

Depending on what your data look like and how they were collected, there are several model options to choose among in program MARK. In Paper I both dead (recoveries) and live (recaptures and resightings) encounters were used and hence also the model option developed by Burnham (1993), which includes parameters of survival (\( S \)), recapture (\( p \)), reporting (\( r \)), and fidelity (\( F \)). Model fitting using this approach is based on the following probability structure (cf. Cooch & White, 2006):

![Diagram showing the probability structure of bird marking and release data](image)
Of course this probability structure gets simpler in other model options, for example when modelling survival parameters only; it is thus known if birds are alive ($S$) or not ($1-S$). The latter ‘known fate’ modelling approach, which largely is based on the Kaplan-Meier method (Kaplan & Meier, 1958), was used for the experimental data in Papers III–VI.

Invertebrate sampling

One weakness in many observational studies addressing density dependence is that they do not measure birth and death rates related to prey units, but plain density solely (i.e. individuals per area unit). Moreover, the interpretation of White (2001), arguing for the necessity of identifying the key-resource (see above), is that density should be a measure relative to its most limiting resource (see also Newton, 1998; Lindström et al., 2005). Breeding is a period of high energetic demands and food is therefore a likely key-resource candidate for many animal species.

Most experiments in the thesis had a cross-over design (see above) to control for possible lake effects such as prey availability. Even if there may have been some variations in food supply between years, I still argue that the experimental setups to a large extent controlled for such differences. This is based on the assumption that variation in food abundance between years should be synchronous in each study area, respectively, and not specifically for single lakes. Nevertheless, in one study (Paper VII) data on invertebrates were collected and included in the analysis of density dependence. In each lake eight to ten submerged activity traps of one litre volume and with small entrance funnels (cf. Murkin, Abbott & Kadlec, 1983) were placed horizontally below the surface at 10–40 cm depth for 48 hours in or close to vegetation in the littoral zone. Benthic, nektonic as well as hatching invertebrates were caught and classified in size classes and identified to taxonomic groups largely adhering to Nudds & Bowlby (1984). Because small ducklings are restricted to invertebrate prey of small size, invertebrates larger than 12.5 mm were excluded from this analysis. In addition, to control for varying invertebrate size, the mid-value of each size class was multiplied by the total number of prey in each size class, and partial sums were then summed and standardised per 100 traps days enabling comparison with other studies (e.g. Nummi & Pöysä, 1995; Elmberg et al., 2003).

Results and discussion

Mallard mortality and population growth (Paper I)

More than 90 years of ringing data from Finland and Sweden were analysed, and one striking result was that 86.3–93.9% of recovered mallards had died due to hunting. In fact, adding other human-induced mortality causes such as traffic collisions, oil spill etc., indicated that humans stood for 95.2% and 97.0% of the deaths in Finnish and Swedish birds, respectively. Natural mortality, with
predation as the most common cause, was thus responsible for 3.0–4.8% of the deaths in birds from the two countries. One can easily understand that the ultimate fate of mallards to a great extent is affected by man, and that mortality is largely decided by hunting pressure and variation thereof. This conclusion is confirmed by other European studies (e.g. Wernham et al., 2002; Bakken, Runde & Tjørve, 2003; see also Bentz, 1985; Fransson & Pettersson, 2001). However, the situation in North America seems to be somewhat different, with more equal shares of human-induced and natural mortality reported (Bergan & Smith, 1993; Baldassare & Bolen, 2006). That hunting is an important cause of mortality is also clear when analysing recoveries by season; most were from the hunting season (August–December) in both Sweden (83.5%) and Finland (73.7%).

Acknowledging the fact that quite many of the recoveries were not sexed, more males than females were recovered in both Sweden and Finland. Other studies from Sweden, as well as from other countries, have found the same pattern (e.g. Bentz, 1985; Soutiere, 1989; Smith & Reynolds, 1992; Johnson & Moore, 1996; Giudice, 2003). To identify the reason behind the pattern further studies and testing are needed. A suggestion may be that a potential skewed sex ratio in the population is responsible.

One should keep in mind that conclusions based on recovery data may be biased in the sense that they do not give a true picture of mallards in general, but of recovered ones only. It is hazardous to equal a record that was once ringed and later on recovered, with a ringed bird that leaves the sample (i.e. not encountered again). In other words, a recovered bird does not necessarily have to die under the same circumstances as a bird not being recovered. For example, one cannot claim that 90% of all mallards will be harvested (cf. above), simply because shot birds previously ringed are also very likely to be reported. Further, it is likely that few birds that die naturally will be encountered and hence reported.

Modelling capture-recapture data for Finnish mallards over 33 years gave annual survival rates ranging from 0.66 to 0.81 for most groups. These groups were different combinations of sex (females, males, and unknown sex) and age (pulli, juvenile, adult, and unknown age). Distinctive groups with relatively low survival rates were juvenile females (0.46) and pulli, among the latter especially those that were not sexed (0.21). Sexed pulli had higher rates of survival (females: 0.45; males: 0.56) probably because such birds were quite old ducklings in which sex identification was possible. That very young mallards are more vulnerable than older ones was also indicated by relatively high recovery rates for pulli (cf. Batt et al., 1992). Even though survival rates differed depending on sex and age, estimates based on the Finnish data set are rather high compared to many previous studies, both from Scandinavia (Koskimies, 1956; Olsson, 1960; Bentz, 1985) and North America (e.g. Batt et al., 1992; Arnold & Clark, 1996; Giudice, 2003). However, the relatively high survival rates in Paper I may be a true and so far little acknowledged latitudinal effect; boreal mallards in North America also seem to have higher survival rates than birds in more southern areas (Lake, Walker & Lindberg, 2006).
Simulating population growth for a Finnish sub-population of mallards, using the survival rates from the preceding analysis and also data about breeding population size and fledgling production from ten years (study areas are blue stars in Fig. 3), resulted in a somewhat overestimated annual population size (two years fell outside the 95% confidence interval limits). However, census data turned out to be very interesting as fledgling production seemed to be clearly density-dependent; i.e. the number of fledglings per breeding pair was negatively related to the number of breeding pairs. A speculation is therefore that a large-scale source-sink dynamic system caused by density-dependent processes force surplus mallards to disperse from native grounds.

Density dependence in nesting mallards (Papers III & IV)

Density dependence was evident in the nesting period in several ways. Nest predation rates were higher for the high density treatment compared to the low density treatment in Paper III, and this result was consistent in the two study years and also for both landscape types (agricultural and forested). Even though the use of artificial nests has been criticised (e.g. Butler & Rotella, 1998; Wilson, Brittingham & Goodrich, 1998; Davison & Bollinger, 2000; Pärt & Wretenberg, 2002; Burke et al., 2004) most previous studies on nest predation have used such nests for reasons of simplicity and the possibility of conducting experiments. Accordingly, most of the studies in Table 1, addressing nest predation explicitly, used artificial nests. Some of those (Weller, 1979; Hill, 1984; Sugden & Beyersbergen, 1986; Esler & Grand, 1993; Larivière & Messier, 1998) indicate that depredation rates indeed are positively related to nest density. Nevertheless, the study in Paper III is the first to show density-dependent nest predation consistent in two different landscapes types within the same years and region. This finding may have wide implications since it highlights the significance and generality of density-dependent nest predation. The landscape types investigated in both studies are indeed representative for vast areas important as breeding areas for mallard. Similar regions to the ‘agricultural landscape’ can be found in Central Europe, eastern and central North America (cf. Sugden & Beyersbergen, 1986; Larivière & Messier, 1998; Ackerman, Blackmer & Eadie, 2004), whereas the ‘forested landscape’ is typical for large areas of boreal regions in Europe and North America (cf. Esler & Grand, 1993).

The results in Paper IV were not as clear-cut as those in Paper III. There was some support for depredation rates being affected by the introduction of adult pairs on the lakes (i.e. increasing the density of waterfowl). However, this effect was only negative, i.e. lower nest survival with higher waterfowl density, at lakes in the forested landscape. Contrary to expectations the effect was the opposite in agricultural landscape lakes. This remarkable result may be caused by different composition of the predator communities in the two landscape types. In fact, it was found that more avian (e.g. crows Corvidae spp. and gulls Laridae spp.) than mammal predators (e.g. red fox, badger, American mink) robbed the nests in agricultural landscape, whereas the opposite scenario was the case at forest lakes. Mammal predators may be more capable of responding to increased waterfowl density and adjust depredation rates thereafter, whereas avian predators may be
less efficient in assessing such densities. An alternate explanation may be that the increase in duck density on the agricultural lakes was not large enough to induce density-dependent predation.

It was very clear that nest survival differed between landscapes; predation rates were higher in agricultural landscape compared to the forested. Both nest predation studies corroborate this landscape effect, thus emphasising its generality. There are two likely explanations for the outcome. The first relates to different predator communities in terms of species richness and abundance, both of which are higher in the agricultural setting. Secondly, even though nests were constructed in the same way in both landscape types, conspicuousness of nests was lower in the forest landscape. Earlier studies on waterfowl as well as on other birds have indeed showed that nest fate is related to concealment and vegetation cover (e.g. Sugden & Beyersbergen, 1986; Willms & Crawford, 1989; Bélanger, Reed & DesGranges, 1998; Liebezeit & George, 2002).

The main result from the nest predation experiments is thus that nest predation may be density-dependent, and related to both the density of nests and waterfowl on the lakes. The predators do certainly respond to increased densities, but how? Is it a functional (increase of individual predatory efficiency) or a numerical (increase in predator numbers) response? The experiments were not designed to explicitly answer this question, even though it is a relevant one. However, in the forest landscape, where most nests seem to be robbed by mammalian predators, a functional response is probably most likely because the density of such predators is rather low. Moreover, several species (e.g. red fox and badger) are territorial and forage solitarily. In the agricultural landscape, avian predators are often very numerous, which should enable a functional response as well.

Density dependence in brood rearing mallards (Papers V–VII)

In Paper I, non-experimental data on breeding pairs and fledgling production revealed a clear indication of density dependence (see above). Preceding this observation, predictions explicitly addressing density dependence or limitation of reproductive output were studied in Papers V–VII. In Papers V & VII, evidence for density dependence was demonstrated; in the former in duckling survival rate and in the latter in the number of observed wild broods. The experimental approaches were quite different in these two studies, one concerning the response of the introduced mallards (Paper V), and the other in wild ones (Paper VII). Direct comparisons of results should therefore not be done. However, density dependence was indeed detected in both studies, which once again underlines the generality of such processes, especially considering that the research was carried out in two very different landscapes, with lakes of different nutrient status, situated in distantly separated regions in Sweden.

The main result from the northern study of oligotrophic lakes was lower survival rate for ducklings in the high density treatment as compared to the low density treatment. However, there was also support for a year effect since the outcome was more pronounced in one of the two years. This ‘year effect’ seemed not to be
a weather effect, since the latter was included as a covariate in the analyses. Some other variable, possibly stochasticity or environmental noise (cf. Coulson, Rohani & Pascual, 2004; Saether & Engen, 2004), must thus have been involved and overriding the effect of density. In contrast to ducklings, hens did not respond to the density of introduced birds. This is probably explained by the fact that young ducklings, compared to older ones, are very vulnerable the first weeks of life (Hill, Wright & Street, 1987; Orthmeyer & Ball, 1990; Rotella & Ratti, 1992b; Sargeant & Raveling, 1992; Pietz et al., 2003) and therefore more likely respond to variation in crucial environmental variables.

Besides the fact that the study in Paper VII was carried out in a different region and at lakes of higher productivity than the study in Paper V, another aspect of interest is that density dependence was apparent also when studying the response in wild mallards. However, only the number of observed wild broods was negatively affected by the introductions of adult pairs, and not the number of almost fledged ducklings. In other words, only studying the reproductive output in late breeding season would not have revealed any regulatory mechanisms. In agreement with Åström, Lundberg & Lundberg (1996) and Jonzén & Lundberg (1999) it is thus necessary to study population dynamics at the right temporal scale, since density dependence may operate sequentially. A parallel can be drawn to the previous study in Paper V showing that the density-dependent effect was year dependent; the process may apparently vary in strength and occurrence in short-term (within year) as well as in long-term (between years) perspectives. Density dependence may consequently be overlooked if it is masked sporadically by stochastic episodes. Maybe this is why e.g. Pöysä (2001) and Elmberg et al. (2003), both studies using non-experimental data from Finland, did not find any indication of density-dependent breeding success in mallards.

One reason why there is a long-lasting controversy about the importance of density dependence (see Introduction) may be that the latter sometimes is overridden by abiotic factors (or stochasticity and environmental noise; see above), and that previous non-experimental studies have failed to separate regulative factors from intriguing non-regulative ones. Experimental studies which have the capacity to make such distinctions, indeed remain rare, making the interpretations and conclusions about density dependence in this thesis novel and important, especially so as they confirm prior suggestions of regulation in breeding dabbling ducks (Weller, 1979; Hill, 1984; Kaminski & Gluesing, 1987; Elmberg, 2003; Elmberg et al., 2003; see also Table 1). In one way or another, density dependence was detected in all studies included in this thesis, which entails that such processes surely exist, and also that they may be general and important for dabbling ducks.

Density dependence in mallard ducklings was hence detected in both nemoral and boreal regions of Sweden. Of course a relevant question concerns the underlying factor(s) behind the pattern. The experiments were not designed to specifically identify such factors. However, food abundance has earlier been recognised as a limiting resource for mallard ducklings (Street, 1977; but see e.g. Elmberg et al., 2003) and it is therefore a likely candidate. Accordingly, the study
in the nemoral setting (Paper VII) also included sampling of invertebrates (see Materials and methods). Prey abundance was, though, not correlated to any of the dependent variables and did hence not explain the density-dependent response. Given the fact the those lakes were very productive, reflected in e.g. high abundances of prey, it is likely that food was too abundant to have limiting consequences for ducklings (cf. Danell & Sjöberg, 1977; Hill, Wright & Street, 1987; Sedinger, 1992; Cox et al., 1998; Nummi et al., 2000). Some other factor, possibly predation and/or hens deserting the lakes, may instead be more likely to have produced a density-dependent pattern in this system. In contrast to the study in Paper VII, food abundance was not collected in the study in Paper V. However, food as a limiting factor was studied in a separate study (Paper VI) in the same system and also partially using the same lakes as in Paper V. It was evident that food was an important limiting factor for duckling survival since it increased dramatically on the lakes where food was added. The study is the first to give experimental evidence for food limitation in a precocial bird in natural conditions (but see Swennen, 1989). Identifying food limitation in oligotrophic lakes may explain earlier non-experimental studies showing that the number of breeding pairs is negatively correlated to food abundance in boreal lakes (Elmberg et al., 1993, Gardarsson & Einarsson, 1994; Nummi et al., 1994; Nummi et al., 1995). In fact, starvation is a common cause of mortality in young ducklings (cf. Solman, 1945; Talent, Jarvis & Krapu, 1983; Cox et al., 1998). It is likely, though, that predation further increased the mortality rates of the ducklings in the control group as they showed higher mortality rates than in Marcström (1966) in which starvation solely, without predation events, was studied in mallard ducklings. The two factors may of course not be mutually exclusive since starved ducklings are more likely to be predated than those in good condition; e.g. hungry ducklings spend much time on foraging and thus expose themselves to predators.

In conclusion, ducklings responded in terms of survival or habitat utilisation to increased densities of broods and/or adults in experiments in two biotic regions. Food abundance was probably the main factor responsible in the oligotrophic lakes in the boreal zone whereas no such effect was evident in the more productive lakes in the nemoral zone, in which predation instead is the most likely agent behind the pattern. That the impact of food may vary corroborates earlier conclusions that ducklings indeed respond to different nutrient status of lakes (Nummi et al., 2000; Sjöberg et al., 2000).

Harvest and management implications

To perform successful management, it is of crucial significance that theory about population dynamics are anchored in real data, especially so for harvested species (Murdoch, 1994; Turchin, 1995, 1999). Waterfowl management has a long tradition in North America (Nichols, 1991; Nichols, Johnson & Williams, 1995), and knowledge from prior ecological research has led to the development of adaptive harvest management plans (Johnson et al., 1993; Williams, Johnson &
Wilkins, 1996; Williams, Koneff & Smith, 1999; Nichols, 2000; Johnson, Kendall & Dubovsky, 2002). In Europe, no such organised actions have been taken yet, even though nationwide monitoring of waterfowl in Finland is run annually (Pöysä et al., 1993; Pöysä, 1998).

Whether hunting mortality is compensatory or additive to natural mortality is of critical concern for the management of harvested species. If hunting mortality turns out to be additive in a declining population (cf. Johnson & Shaffer, 1987), then it is necessary to initiate restrictions on hunting bags to allow the population to recover. Until the mid 70s it was indeed believed that hunting mortality in North American mallards was additive to natural mortality. However, ever since the rigorous study by Anderson & Burnham (1976), giving convincing support for hunting mortality being compensatory, this has been the prevailing view. In Paper II of the thesis it is discussed whether more recent studies of this topic instead support the additive mortality hypothesis. Reviewing eight studies that together comprise mallard harvest and recruitment data from almost 30 years (1961–1988) actually shows that there is a significant temporal trend of a change from compensatory mortality to additive. Almost 20 years have past since the last year of data was analysed (Smith & Reynolds, 1992), and of course much can have happened since. The take-home message is that there is no ultimate answer how hunting affects harvested mallards; to be able to do valid analyses on the impact of hunting on harvested species, updated data on recruitment and harvest rate must be used (cf. Elmberg et al. 2006).

Because no accurate data on harvest or recruitment are available for Europe (but see Pöysä et al., 1993; Pöysä, 1998), I cannot say if hunting mortality of European mallards is compensatory or additive. Yet, I can say something about density dependence on breeding mallards, being a prerequisite for compensatory natality (Boyce, Sinclair & White, 1999). Firstly, the process is generally occurring in both nesting and brood rearing mallards, and also in different biotic regions and lakes of different productivity. In other words, the number of birds surviving the preceding hunting season comprising the population in early breeding season is of importance to per capita breeding success. This was evident on a local scale, but may also be evident on a larger scale since it was found that predicted population sizes were somewhat overestimated for a Finnish sub-population. This is a probable scenario, since fledgling production in the same sub-population was density-dependent. A second major conclusion for management purposes is that the strength of density dependence often varies on a temporal scale, i.e. both within and between years. For example, studying survival in separate sequences during breeding (e.g. nest success, duckling survival and fledgling survival) may detect regulatory mechanisms that possibly would not have been detected if compiling data from longer time periods (cf. Pöysä & Pöysä, 2002; Wauters et al., 2004). A relevant example in this context is that many previous mallard population models (e.g. Kaminski & Gluesing, 1987; Reynolds & Sauer, 1991; Shaffer, 1998; Miller, 2000) are based on the proportion of juveniles in autumn harvest as a measure of recruitment. If using such data, valuable information may be missed; the final outcome (i.e. proportion of juvenile in harvest) not showing any density dependence may be due to counteracting density-dependent processes
in different sequences of the preceding breeding season. Kaminski & Gluesing (1987) and Sheaffer (1998) did indeed find density dependence, but others did not. It is thus possible that density dependence was occurring in early season in the latter studies as well, but that such effects were masked due to the choice of temporal scale.

Conclusions and future perspectives

Density dependence was found to be important in several phases of the breeding period and also using different response variables. The results are important for several reasons and some major conclusions appear. Firstly, results are experimental, meeting the call in several studies that experiments are necessary to properly understand patterns and processes of density dependence (e.g. Kaminski & Gluesing, 1987; Harrison & Cappuccino, 1995; Newton, 1998; Sheaffer, 1998). Secondly, the process turned out to be general, which underlines its prevalence and importance in mallards, but probably also so in other species and taxa. Thirdly, the strength of density dependence varies on both spatial and temporal scales, the former influenced by e.g. regional conditions such as predator communities and lake nutrient status and the latter both within and between years. Lastly, detecting density dependence for harvested species needs special consideration in the management of populations. Although the conclusion needs further challenging and testing, density dependence in breeding dabbling ducks may compensate hunting mortality and allow for adaptive harvesting provided that breeding output and harvest are monitored correctly and regularly.

Some of the studies (Papers V & VI) were performed in areas where waterfowl density is very low; only single pairs typically breed on a given oligotrophic lake. That these lakes were poor was confirmed by high rates of mortality, being evident even though duck density was low. One relevant question is why birds use poor habitats at all, if they in most cases are doomed to fail. This is possibly what happens in species affected by source-sink dynamics, assuming ‘ideal preemptive distribution’ and not ‘ideal free distribution’ taking place (Pulliam & Danielson, 1991). Good habitats (i.e. productive lakes) may be occupied first by the earliest arriving and/or dominant individuals (cf. Elmberg et al., 2005). To have a chance of producing offspring at all, others are forced to disperse to patches of poorer quality. This is not unlikely as iteroparous species, like the mallard, have a fair opportunity to breed in several years. Breeding success does vary between years (Paper V), and in years with good conditions it may be worth using sinks as well. Compared to sources, sinks should reasonably be easier to defend as a territory, and predation rates may be lower which also should justify why poor habitats are utilised. It is thus indeed possible that density-dependent processes acting on a local scale may have consequences, in terms of habitat choice and population dynamics, on a larger scale too (Pulliam & Danielson, 1991; Amarasekare, 2004).
Although my thesis has produced interesting results for management and further testing, many new questions have arisen for future studies. The experimental studies were performed on small lakes, i.e. on a small local level. That the spatial scale needs to be considered when studying density dependence is nothing new in ecology (e.g. Newton, 1998; see also above discussion about source-sink dynamics), a fact that calls for population level studies of dabbling ducks in Europe. Due to the experimental design of the studies in this thesis, mallards have been regarded in a more or less closed system. However, density dependence may not be of the same magnitude in open populations (Pöysä & Pesonen, 2003) which calls for more large-scale studies. How such studies should be designed, e.g. if experiments are feasible or not, remains to be solved. Nonetheless, large-scale studies of open populations are needed to either confirm density dependence, or in concordance with others (Ray & Hastings, 1996; Rodenhouse, Sherry & Holmes, 1997), suggest that density dependence on such scales is of minor importance.

Moreover, the thesis’ studies have to a large extent only considered the actual process of density dependence, and not the underlying factors driving it. Although the role of food availability and predation was studied in some papers (III, IV & VI), their relative contribution to survival, habitat utilisation and other fitness-related parameters should be considered more thoroughly. A field that has received relatively little attention concerns possible interactions between fish and waterfowl (but see e.g. Solman, 1945; Pehrsson, 1984; Hill, Wright & Street, 1987; Pöysä, 2004). This topic is especially interesting since fish may act both as competitors for food (invertebrates) and as predators (mainly pike *Esox lucius*). Performing such community level studies may possibly shed new light on the understanding of waterfowl population dynamics. In addition, there are other factors not addressed at all in this thesis and barely in other studies either, which need to be included in future experiments. One obvious example is disease, and for waterfowl especially so avian influenza that has received much attention recently (Olsen et al., 2006).

Finally, experiments addressing density dependence should be performed on staging and wintering waterfowl as well. In terms of compensatory and additive mortality the traditional view is how survival on wintering populations is affected. Relevant and interesting studies would be those scrutinising the relative impact of compensatory mortality and natality within the same season. It is equally important to consider processes acting over time in a greater context, as it is considering seasonally stages separately. Not until all pieces are identified can the jig-saw puzzle be laid out and the big picture understood; i.e. if populations follow their ‘equilibrium size’ or not.
References


Acknowledgements

There are many kinds of supervisors; very bad, bad, less bad, and pretty good ones. Johan Elmberg is in his own category. He is a good friend, ambitious, efficient, always answering his phone, a good researcher, and he has a good nose for tasty wines and food. For me Johan has not only been an excellent supervisor, he also meets the criteria for being a true mentor of mine. I am not sure a supervisor can be much better. Johan, I am very grateful to you and I hope we will write many more papers together, with or without Dr. Akaike.

I have been privileged working in a group with experienced and friendly European duck researchers. Johan Elmberg, Hannu Pöysä, Petri Nummi, Kjell Sjöberg, and the last year also Lisa Dessborn: our regular meetings every half a year in Finland or Sweden have been great. Thanks for all productive meetings including ducky discussions, good food, Finnish beers, Finnish sauna, ‘sauna makkara’, and headache. Kjell Sjöberg and Per Lundberg have been my co-supervisors for which I am grateful. Céline Arzel and Matthieu Guillema from France are also acknowledged, not only for duck matters, but also for stinky cheese and dark chocolate.

My position as a PhD-student has been a bit ambivalent; I have been employed by Kristianstad University, but have received my education at SLU in Umeå. Thanks to that I have met twice as many nice people as an ordinary PhD-student, and I would like to thank all my colleagues at my two departments. In Umeå I especially would like to thank Lars Edenius who together with Carin Magnhagen arranged the fantastic trip to Borneo and also the other students joining that adventure. I wish all students would be as lucky as me having the opportunity to take part of such excursions. At my department in Kristianstad I especially would like to thank the biology group. Thank you Kristina for being a great roommate, and Urban for the many conversations about bees, honey and house construction. There are quite many graduate students at the department now (Pär, Betty, Lisa, Urban, Lena L., Lena H., Ola et al.) and I wish you all good luck with your theses. Your PhD-project is probably the funniest thing you will ever do!

Other people or institutions that have been involved in my project are mallard breeders (Göran Karlsson and Frenne Lindell), statistical guides (Per-Erik Isberg and Gary White), field assistants/slaves (Per Wedholm, Eric Andersson, Åke Nordström, Thomas Trygg, Céline Arzel, Jessica Bengtsson, Helena Schnabel, Ebba Trolle Gunnarsson, Sten Forsberg and Kelly Squires), data providers (Bengt-Olov Stolt and Bo Sällström at the Bird Ringing Centre at the Swedish Museum of Natural History, Hans Cronert and David Stühlberg at the Scania County Administration Board), all landowners for lake access (sorry, I do not have your names), co-authors (Johan Elmberg, Hannu Pöysä, Kjell Sjöberg, Petri Nummi, Lisa Dessborn, Niclas Jonzén and Jari Valkama), people giving valuable comments on manuscripts (Bob Clark, Jim Nichols, Scott Petrie, Pertti Saurola, Hannu Pöysä and several anonymous persons), and the Swedish Environmental Protection Agency (Naturvårdsverket) for financing my project. I am grateful to
you all; it would not have been possible to construct all those nests and ‘take the life of the many innocent mallard ducklings’ without your help.

In my professional network there is one guy that is especially acknowledged and that is a man I have never met in person. Paul Flint, you have never hesitated to answer the questions about program MARK in my e-mails. I have at several occasions invited you for co-authorship, and you have always replied that it is not necessary. The numerous, and often very long, e-mails from you can probably be reviewed to be a pretty good MARK manual as a complement to the existing one. At the next duck symposium I wish we could have a chat over a beer or two.

Tack!

Nu till tacken som inte direkt har med jobbet att göra (även om många av personerna nedan är delaktiga/ansvariga för att jag disputerar i biologi) och då kännas det bättre att uttrycka sig på svenska.


Några personer har varit speciellt viktiga när det gäller mitt intresse för biologi och fåglar. Bror Olof är i högsta grad delaktiv. Han lät köpa in Mörbylånga Fältbiologers första (enda och sista) tubkikare som jag och brosna använde flitigt när vi stod på vallen i Kalvhagen i Mörbylånga och blickade ut över Södra Viken och de många änder som låg där (på den tiden tyckte jag nog att de var rätt tråkiga). Även om jag inte betecknade mig som ornitolog på den tiden (dvs < 13 år gammal) grundlades ett naturintresse, mycket tack vare min bror Olof. Det pedagogiska med att berätta spökhistorier för den då 8-årige lillebrodern som, efter mycket tjat på föräldrarna, fick följa med och tävla på gravfältet i Ottenby har jag dock aldrig förstått. Tur att syster Johanna var med som övertygade mig att allt var påhittat, och tur att vi nästa dag längs fyrvägen såg rödhalsad gås; min första ”tunga” art.

avhandlingens framsida. Ami och Bo Mörnerud har betytt mycket för mig och ni kommer alltid att vara min extramama och extrapappa. Och Frida, du är som en syster.


"The dudes” med långa kikarremmar i Club Durango är mina allierade och jag är evigt tacksam att jag har så fina vänner; Oskar, Niklas, Jonas, Olof H., Olof G., Richard, Emil, Martin, Andreas, Sten och Patrik. Salig Sigfrid ler nog i sin himmel.

Andra personer som har varit och är centrala i mitt liv och som jag vill tacka är svärmor Margareta, Gustav och Tezz (med Helga, Bo, och Hans), Kajsa och Henrik, Jonas och Emelie (med Hedda), Ingrid och Sören, kusin Andreas, Sara och Jonas (med Hedvig), Sara-Felicia och Pär (med Flora, Mandel och Isidor), Ia och Fredrik (med Alice och Arvid).


Jaha, de va de de……