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

Acta Universitatis Agriculturae Sueciae

2007: 12

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

Appendix

Papers I–VII

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

I. Gunnarsson, G., Elmberg, J., Dessborn, L., Jonzén, N., Pöysä, H. & Valkama, J. Survival estimates, mortality patterns, and population growth of Fennoscandian mallards *Anas platyrhynchos*. (Manuscript).

II. Pöysä, H., Elmberg, J., Gunnarsson, G., Nummi, P. & Sjöberg, K. 2004. Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? *Oikos 104*, 612-615.

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).

V. Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. & Nummi, P. 2006. Experimental evidence for density-dependent survival in mallard (*Anas platyrhynchos*) ducklings. *Oecologia 149*, 203-213.

VI. Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. & Nummi, P. 2004. Why are there so many empty lakes? Food limits survival of mallard ducklings. *Canadian journal of zoology 82*, 1698-1703.

VII. Elmberg, J., Gunnarsson, G., Pöysä, H., Sjöberg, K. & Nummi, P. 2005. Within-season sequential density dependence regulates breeding success in mallards *Anas platyrhynchos*. *Oikos 108*, 582-590.

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.*

$$\frac{dN}{dt} = rN \tag{1}$$

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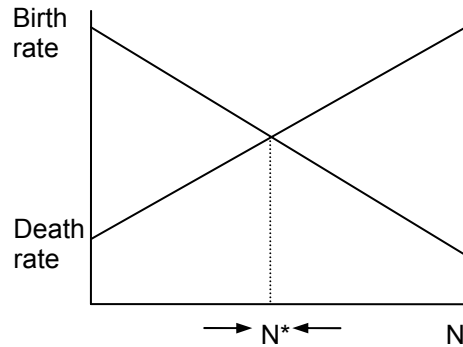
Fig. 1. Density dependence in an imagined population. In this example both birth and death rates are density-dependent; the population size (*N*) increases left of the dotted line and decreases right of it and hence goes to its equilibrium size (*N**) as indicated by arrows.

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
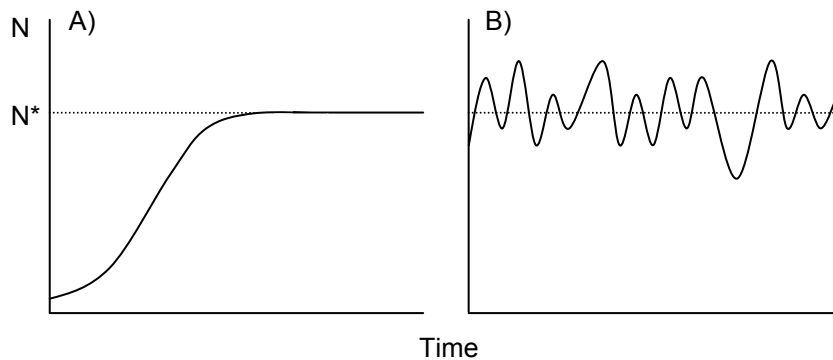
8

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.

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).

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).

11

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*

Species	Area (years)	Breeding pairs	Nest failure	Brood survival	Duckling survival	Recruitment to population	Source
Mallard *Anas platyrhynchos*	England (16)		Yes		Yes	Yes	Hill, 1984
	Sweden (13)			Yes[1]	Yes[1]		Elmberg, 2003
	Sweden (1)		No				Andrén, 1991
	Finland (16)	No		No			Pöysä, 2001
	Finland (12)	No		No	No		Elmberg *et al.*, 2003
	N.Amer. (26)					Yes	Kaminski & Gluesing, 1987
	N.Amer. (30)					Yes	Burnham & Anderson, 1984
	N. Amer (15)					Yes	Sheaffer, 1998
	N.Amer. (12)					Yes	Anderson & Burnham, 1976
	N.Amer. (11)					No	Smith & Reynolds, 1992
Wigeon *A. Penelope*	Finland (12)	Yes		Yes	Yes		Elmberg *et al.*, 2003
	Finland (17)	No		No	No		Pöysä & Pesonen, 2003
	Iceland (21)	Yes		No	No		Pöysä & Pesonen, 2003
Teal *A. crecca*	Finland (12)			Yes			Elmberg *et al.*, 2003
Blue-winged teal *A. discors*	N.Amer (13)		Yes				Weller, 1979
Grey duck *A. superciliosa*	N. Zeal. (13)					Yes	Barker, Hines & Nichols, 1991
Anatinae spp.	N.Amer (2)		Yes				Sugden & Beyersbergen, 1986[2]
	N.Amer (1)		Yes				Esler & Grand, 1993[2]
	N.Amer (1)		Yes				Larivière & Messier, 1998[2]
	N.Amer (5)		No				Ackerman, Blackmer & Eadie, 2004[2]

[1]Results are not statistically independent of each other; [2]Studies 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

13

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 feed-back 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,

14

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).
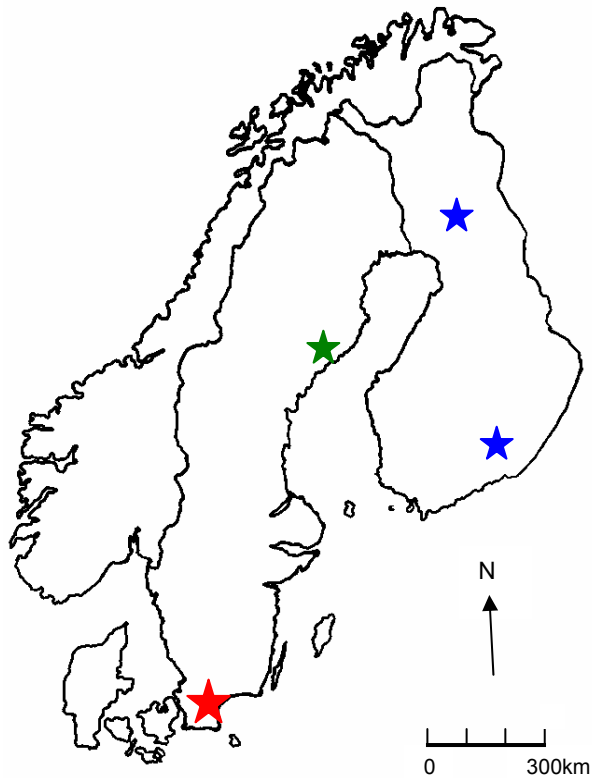
Fig. 3. Study areas in Sweden and Finland. Data for Papers III, IV & VII were collected in nemoral and boreo-nemoral sites in southern Sweden (red star), whereas the boreal region was covered in studies performed in northern Sweden (Papers V & VI; green star) and in Finland (Paper I; blue stars). Capture-recapture data analysed in the latter paper were from nationwide ringing programmes in Sweden and Finland, respectively.

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-

16

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.

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

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.

18

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 ($\hat{c}$). 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 simple 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 -2ln(*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):
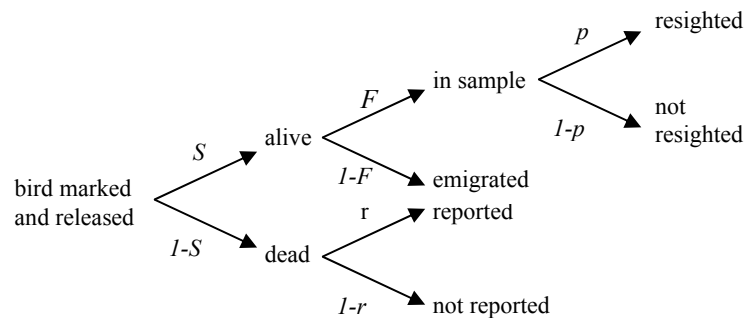
Of course this probability structure gets simpler in other model options, for example when modelling survival parameters only; it is thus known if birds are alive (*S*) or not (*1-S*). The latter 'known fate' modelling approach, which largely is based on the Kaplan-Meier method (Kaplan & Meier, 1958), 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.* Pöysa (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 affect 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; Sheaffer, 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

Ackerman, J.T., Blackmer, A.L. & Eadie, J.M. 2004. Is predation on waterfowl nests density dependent? - Tests at three spatial scales. *Oikos 107*, 128-140.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In: *Proceedings of the 2nd international symposium on information theory*. (Eds. B.N. Petran & F. Csáki). Akadémiai Kiadi, Budapest, Hungary, pp. 267-281.

Amarasekare, P. 2004. The role of density-dependent dispersal in source-sink dynamics. *Journal of theoretical biology 226*, 159-168.

Anderson, D.R. & Burnham, K.P. 1976. Population ecology of the mallard. VI. The effect of exploitation on survival. *U.S. department of the interior. Fish and wildlife service resource publication 128*, 1-66.

Andrén, H. 1991. Predation: an overrated factor for over-dispersion of birds´ nests? *Animal behaviour 41*, 1063-1069.

Arnold, T.W. & Clark, R.B. 1996. Survival and philopatry of female dabbling ducks in southcentral Saskatchewan. *Journal of wildlife management 60*, 560-568.

Åström, M., Lundberg, P. & Lundberg, S. 1996. Population dynamics with sequential density-dependence. *Oikos 75*, 174-181.

Bakken, V., Runde, O. & Tjørve, E. 2003. *Norwegian bird ringing atlas*. Stavanger Museum, Stavanger, Norway, 431 pp.

Baldassarre, G.A. & Bolen, E.G. 2006. *Waterfowl ecology and management*. 2nd edition. Krieger Publishing Company, Malabar, U.S., 567 pp.

Ball, I.J., Gilmer, D.S., Cowardin, L.M. & Riechmann, J.H. 1975. Survival of wood duck and mallard broods in north-central Minnesota. *Journal of wildlife management 39*, 776-780.

Barker, R.J., Hines, J.E. & Nichols, J. 1991. Effect of hunting on annual survival of grey ducks in New Zealand. *Journal of wildlife management 55*, 260-265.

Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A. & Krapu, G.L. 1992. *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, U.S., 635 pp.

Begon, M., Harper, J.L. & Townsend, C.R. 1996. *Ecology: individuals, populations and communities*. 3rd edition. Blackwell Science, Oxford, U.K., 1068 pp.

Bélanger, L., Reed, A. & DesGranges, J.-L. 1998. Reproductive variables of American black ducks along the St. Lawrence River Estuary, 1963-1991. *Canadian journal of zoology 76*, 1165-1173.

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

Bergan, J.F. & Smith, L.M. 1993. Survival rates of female Mallards wintering in the Playa Lakes region. *Journal of wildlife management 57*, 570-577.

Berryman, A. & Turchin, P. 1997. Detection of delayed density dependence: comment. *Ecology 78*, 318-320.

Berryman, A. & Turchin, P. 2001. Identifying the density-dependent structure underlying ecological time series. *Oikos 92*, 265-270.

Bethke, R.W. 1993. Geographical patterns of persistence in duck guilds. *Oecologia 93*, 102-108.

Boyce, M.S., Sinclair, A.R.E. & White, G.C. 1999. Seasonal compensation of predation and harvesting. *Oikos 87*, 419-426.

Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. 1985. *Statistical inference from band recovery data – a handbook*. 2nd edition. U.S. fish and wildlife service, resource publication, Washington, U.S., 156 pp.

Bulmer, M.G. 1975. The statistical analysis of density dependence. *Biometrics 31*, 901-911.

Burke, D.M., Elliott, K., Moore, L., Dunford, W., Nol, E., Phillips, J., Holmes, S. & Freemark, K. 2004. Patterns of nest predation on artificial and natural nests in forests. *Conservation biology 18*, 381-388.

Burnham, K.P. 1993. A theory for combined analysis of ring recovery and recapture data. In: *Marked individuals in the study of bird population*. (Eds. J.D. Lebreton & P.M. North). Birkhauser Verlag, Basel, Germany, pp. 199-213.

Burnham, K.P. & Anderson, D.R. 1984. Tests of compensatory vs. additive hypothesis of mortality in mallards. *Ecology 65*, 105-112.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. 2nd edition. Springer-Verlag, New York, U.S., 496 pp.

Butler, M.A. & Rotella, J.J. 1998. Validity of using artificial nests to assess duck-nest success. *Journal of wildlife management 62*, 163-171.

Cappuccino, N. & Price, P.W. 1995. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, U.S., 429 pp.

Caughley, G. & Gunn, A. 1996. Late holocene mass extinctions. In: *Conservation biology in theory and practice*. (Eds. G. Caughley & A. Gunn). Blackwell Science, Cambridge, U.K., pp. 32-46.

Caughley, G. & Sinclair, A.R.E. 1994. Wildlife harvesting. In: *Wildlife ecology and management*. (Eds. G. Caughley & A.R.E. Sinclair). Blackwell, Oxford, U.K., pp. 279-290.

Cooch, E. & White, G. 2006. Chapter 11 – combining data from multiple sources. In: *Program MARK – a gentle introduction. 5th edition*. http://www.phidot.org/software/mark/docs/book; pp. 322-336 (assessed 2-Jan-2007).

Coulson, T., Rohani, P. & Pascual, M. 2004. Skeletons, noise and population growth: the end of an old debate? *Trends in ecology and evolution 19*, 359-364.

Cox, R.R., Hanson, M.A., Roy, C.C., Euliss, N.H., Johnson, D.H. & Butler, M.G. 1998. Mallard duckling growth and survival in relation to aquatic invertebrates. *Journal of wildlife management 62*, 124-133.

Cramp, S., Simmons, K.E.L., Ferguson-Lees, I.J., Gillmor, R., Hollom, P.A.D., Hudson, R., Nicholson, E.M., Ogilvie, M.A., Olney, P.J.S., Voous, K.H. & Wattel, J. 1994. Tribe ANATINI dabbling ducks. In: *Handbook of the birds of Europe, the Middle East and North Africa. The birds of the western Palearctic*. (Ed. S. Cramp). Oxford University Press, Oxford, U.K., pp. 471-552.

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

Danell, K. & Sjöberg, K. 1978. Habitat selection by breeding ducks in boreal lakes in northern Sweden. *Swedish wildlife 10*, 161-190.

Davison, W.B. & Bollinger, E. 2000. Predation rates on real and artificial nests of grassland birds. *Auk 117*, 147-153.

Dennis, B. & Taper, M.L. 1994. Density dependence in time series observations of natural populations: estimations and testing. *Ecological monographs 64*, 205-224.

Durell, S.E.A. Le V. dit, Goss-Custard, J.D., Clark, R.T. & McGrorty, S. 2000. Density-dependent mortality in Oystercatchers *Haematopus ostralegus*. *Ibis 142*, 132-138.

Dzus, E.H. & Clark, R.G. 1997a. Brood size manipulation in mallard ducks: Effects on duckling survival and brood efficiency. *Ecoscience 4*, 437-445.

Dzus, E.H. & Clark, R.G. 1997b. Overland travel, food abundance, and wetland use by mallards: relationships with offspring survival. *Wilson bulletin 109*, 504-515.

Elmberg, J. 2003. Density-dependent breeding success in mallards *Anas platyrhynchos* on a eutrophic lake. *Wildlife biology 9*, 67-73.

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

Elmberg, J., Nummi, P., Pöysä, H. & Sjöberg, K. 1993. Factors affecting species number and density of dabbling duck guilds in North Europe. *Ecography 16*, 251-260.

Elmberg, J., Nummi, P., Pöysä, H. & Sjöberg, K. 2003. Breeding success of sympatric dabbling ducks in relation to population density and food resources. *Oikos 100*, 333-341.

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

Esler, D. & Grand, J.B. 1993. Factors influencing depredation of artificial duck nests. *Journal of wildlife management 57*, 244-248.

Fransson, T. & Pettersson, J. 2001. *Svensk ringmärkningsatlas* [*Swedish bird ringing atlas. In Swedish with English summary*]. Ljungföretagen Tryckeri AB, Örebro, Sweden, 190 pp.

Gardarsson, A. & Einarsson, A. 1994. Responses of breeding duck populations to changes in food supply. *Hydrobiologia 279-280*, 15-27.

Giudice, J.H. 2003. Survival and recovery of Mallards and Gadwalls banded in eastern Washington, 1981-1998. *Journal of field ornithology 74*, 1-11.

Gulland, F.M.D. 1995. The impact of infectious diseases on wild animal populations – a review. In: *Ecology of infectious diseases in natural populations*. (Eds. B.T. Grenfell & A.P. Dobson). Cambridge University Press, Cambridge, U.K., pp. 20-51.

Hagemeijer, E.J.M. & Blair, M.J. 1997. *The EBCC atlas of European breeding birds: their distribution and abundance*. T. & A.D. Poyser, London, U.K., 903 pp.

Hansen, T.F., Stenseth, N.C. & Henttonen, H. 1999. Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *American naturalist 154*, 129-139.

Hanski, I. & Woiwod, I. 1991. Delayed density-dependence. *Nature 350*, 28.

Harrison, S. & Cappuccino, N. 1995. Using density manipulation experiments to study population regulation. In: *Populations dynamics*. (Eds. N. Cappuccino & P.W. Price). Academic Press, San Diego, U.S., pp. 131-147.

Hickey, J. 1952. Survival studies of banded birds. *U.S. department of the interior. Fish and wildlife service, special scientific report. Wildlife 15*, 1-177.

Hill, D.A. 1983. Compensatory mortality in the mallard. *Game conservancy annual review 14*, 87-92.

Hill, D.A. 1984. Population regulation in the mallard (*Anas platyrhynchos*). *Journal of animal ecology 53*, 191-202.

Hill, D., Wright, R. & Street, M. 1987. Survival of Mallard ducklings *Anas platyrhynchos* and competition with fish for invertebrates on a flooded gravel quarry in England. *Ibis 129*, 159-167.

Johnson, D.H. & Shaffer, T.L. 1987. Are mallards declining in North America? *Wildlife society bulletin 15,* 340-345.

Johnson, F.A., Kendall, W.L. & Dubovsky, J.A. 2002. Conditions and limitations on learning in the adaptive management of mallard harvests. *Wildlife society bulletin 30*, 176-185.

Johnson, F.A. & Moore, C.T. 1996. Harvesting multiple stocks of ducks. *Journal of wildlife management 60*, 551-559.

Johnson, F.A., Williams, B.K., Nichols, J.D., Hines, J.E., Kendall, W.L., Smith, G.W. & Caithhamer, D.F. 1993. Developing an adaptive management strategy for harvesting waterfowl in North America. *Transactions of the North American wildlife and natural resources conference 58*, 565-583.

Jonzén, N. & Lundberg, P. 1999. Temporally structured density-dependence and population management. *Annales zoologici Fennici 36*, 39-44.

Kaminski, R.M. & Gluesing, E.A. 1987. Density- and habitat-related recruitment in mallards. *Journal of wildlife management 51*, 141-148.

Kaplan, E.L. & Meier, P. 1958. Nonparametric estimation from incomplete observations. *Journal of American statistical association 53*, 457-481.

Kjellander, P., Hewison, A.J.M., Liberg, O., Angibault, J.-M., Bideau, E. & Cargnelutti, B. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. *Oecologia 139*, 478-485.

Kokko, H., Pöysä, H., Lindström, J. & Ranta, E. 1998. Assesing the impact of spring hunting on waterfowl populations. *Annales zoologici Fennici 35*, 195-204.

Koskimies, J. 1956. Heinäsorsakantamme verotus meillä ja muualla [Harvest of our Mallard population here and abroad. In Finnish]. *Suomen riista 10*, 18-25.

Koskimies, P. & Väisänen, R. 1991. *Monitoring bird populations*. Zoological Museum, Finnish Museum of Natural History, Helsinki, Finland, 144 pp.

32

Krapu, G.L., Greenwood, R.J., Dwyer, C.P., Kraft, K.M. & Cowardin, L.M. 1997. Wetland use, settling patterns and recruitment in mallards. *Journal of wildlife management 61*, 736-746.

Krebs, C.J. 1978. A review of the Chitty Hypothesis of population regulation. *Canadian journal of zoology 56*, 2463-2480.

Krebs, C.J. 1994. *Ecology: the experimental analysis of distribution and abundance.* 4th edition. HarperCollins College Publishers, New York, U.S., 801 pp.

Krebs, J.R. 1970. Regulation of numbers in the Great tit (Aves: Passeriformes). *Journal of zoology 162*, 317-333.

Lake, B.C., Walker, J. & Lindberg, M.S. 2006. Survival of ducks banded in the boreal forest of Alaska. *Journal of wildlife management 70*, 443-449.

Larivière, S. & Messier, F. 1998. Effect of density and nearest neighbours on simulated waterfowl nests: can predators recognize high-density nesting patches? *Oikos 83*, 12-20.

Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs 62*, 67-118.

Liebezeit, J.R. & George, T.L. 2002. Nest predators, nest-site selection, and nesting success of the Dusky flycatcher in a managed Ponderosa pine forest. *Condor 104*, 507-517.

Lindström, J., Enemar, A., Andersson, G., von Proschwitz, T. & Nyholm, N.E.I. 2005. Density-dependent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos 110*, 155-163.

Marcström, V. 1966. Mallard ducklings (*Anas platyrhynchos* L.) during the first days after hatching. *Swedish wildlife 4*, 343-368.

Miller, M.W. 2000. Modeling annual mallard production in the prairie-parkland region. *Journal of wildlife management 64*, 561-575.

Morris, R.F. 1959. Single factor analysis in population dynamics. *Ecology 40*, 580-588.

Murdoch, W.W. 1994. Population regulation in theory and practice. *Ecology 75*, 271-287.

Murkin, H.R., Abbott, P.G. & Kadlec, J.A. 1983. A comparison of activity traps and sweep nets for sampling nektonic invertebrates in wetlands. *Freshwater invertebrate biology 2*, 99-106.

Murray Jr., B.G. 1994. On density dependence. *Oikos 69*, 520-523.

Newton, I. 1998. *Population limitation in birds*. Academic Press, San Diego, U.S., 597 pp.

Nichols, J.D. 1991. Responses of North American duck populations to exploitation. In: *Bird population studies: relevance to conservation and management*. (Eds. C.M. Perrins, J.-D. Lebreton & G.J.M. Hirons). Oxford University Press, Oxford, U.K., pp. 498-525.

Nichols, J.D. 2000. Evolution of harvest management for North American waterfowl: selective pressures and preadaptations for adaptive harvest management. *Transactions of the North American wildlife and natural resources conference 65*, 65-108.

Nichols, J.D., Conroy, M.J., Anderson, D.R. & Burnham, K.P. 1984. Compensatory mortality in waterfowl populations: a review of the evidence and implications for research and management. *Transactions of the North American wildlife and natural resources conference 49*, 535-554.

Nichols, J.D., Johnson, F.A. & Williams, B.K. 1995. Managing North American waterfowl in the face of uncertainty. *Annual review of ecology and systematics 26*, 177-199.

Nicholson, A.J. 1933. The balance of animal populations. *Journal of animal ecology 2*, 132-178.

Nordström, M., Högmander, J., Nummelin, J., Laine, J., Laanetu, N. & Korpmäki, E. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. *Ecography 25*, 385-394.

Nudds, T.D. & Bowlby, J.N. 1984. Predator-prey size relationships in North American dabbling ducks. *Canadian journal of zoology 62*, 2002-2008.

Nummi, P., Elmberg, J., Pöysä, H. & Sjöberg, K. 1995. Occurrence and density of mallard and green-winged teal in relation to prey size distribution and food abundance. *Annales zoologici Fennici 32*, 385-390.

Nummi, P. & Pöysä, H. 1995. Breeding success of ducks in relation to different habitat factors. *Ibis 137*, 145-150.

Nummi, P., Pöysä, H., Elmberg, J. & Sjöberg, K. 1994. Habitat distribution of the mallard in relation to vegetation structure, food, and population density. *Hydrobiologia 279-280*, 247-252.

Nummi, P., Sjöberg, K., Pöysä, H. & Elmberg, J. 2000. Individual foraging behaviour indicates resource limitation: an experiment with mallard ducklings. *Canadian journal of zoology 78*, 1891-1895.

Olsen, B., Munster, V.J., Wallensten, A., Waldenström, J., Osterhaus, A.D.M.E. & Fouchier, R.A.M. 2006. Global patterns of influensa A virus in wild birds. *Science 312*, 384-388.

Olsson, V. 1960. Märkningar och återfynd av svenska gräsänder, *Anas platyrhynchos* L [Recoveries of marked Swedish Mallards *Anas platyrhynchos* L. In Swedish with English summary]. *Swedish wildlife 2*, 87-152.

Orthmeyer, D.L. & Ball, I.J. 1990. Survival of mallard broods on Benton Lake National Wildlife Refuge in northcentral Montana. *Journal of wildlife management 54*, 62-66.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. 2002. Exploring density-dependent relationships in demographic parameters in populations of birds at a large spatial scale. *Oikos 97*, 293-307.

Pärt, T. & Wretenberg, J. 2002. Do artificial nests reveal relative nest predation risk for real nests? *Journal of avian biology 33*, 39-46.

Pehrsson, O. 1984. Relationships of food to spatial and temporal breeding strategies of mallards in Sweden. *Journal of wildlife management 48*, 322-339.

Pietz, P.J., Krapu, G.L., Brandt, D.A. & Cox Jr., R.R. 2003. Factors affecting gadwall brood and duckling survival in prairie pothole landscapes. *Journal of wildlife management 67*, 564-575.

Pöysä, H. 1998. Monitoring waterfowl production in Finland. *Acta zoologica Lituanica ornithologia 8*, 52-55.

Pöysä, H. 2001. Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. *Oikos 94*, 365-373.

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

Pöysä, H., Lammi, E., Väisänen, R.A. & Wikman, M. 1993. Monitoring of waterbirds in the breeding season: the programme used in Finland in 1986-92. *IWRB special publication 26*, 7-12.

Pöysä, H. & Pesonen, M. 2003. Density dependence, regulation and open-closed populations: insights from the wigeon, *Anas penelope. Oikos 102*, 358-366.

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*, 502-510.

Pulliam, H.R. & Caraco, T. 1984. Living in groups: is there an optimal group size. In: *Behavioural ecology: an evolutionary approach*. (Eds. J.R. Krebs & N.B. Davis). Blackwell Scientific Publications, Oxford, U.K., pp. 122-147.

Pulliam, H.R. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American naturalist 137*, 50-66.

Ray, C. & Hastings, A. 1996. Density dependence: are we searching at the wrong spatial scale? *Journal of animal ecology 65*, 556-566.

Reynolds, R.E. & Sauer, J.R. 1991. Changes in Mallard breeding populations in relation to production and harvest rates. *Journal of wildlife management 55*, 483-487.

Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology 78*, 2025-2042.

Rogers, J.P., Nichols, J.D., Martin, F.W., Kimball, C.F. & Pospahala, R.S. 1979. An examination of harvest and survival rates of ducks in relation to hunting. *Transactions of the North American wildlife and natural resources conference 44*, 114-126.

Rotella, J.J. & Ratti, J.T. 1992a. Mallard brood movements and wetland selection in southwestern Manitoba. *Journal of wildlife management 56*, 508-515.

Rotella, J.J. & Ratti, J.T. 1992b. Mallard brood survival and wetland habitat conditions in southwestern Manitoba. *Journal of wildlife management 56*, 499-507.

Royama, T. 1977. Population persistence and density dependence. *Ecological monographs 47*, 1-35.

Saether, B.-E. & Engen, S. 2004. Stochastic population theory faces reality in the laboratory. *Trends in ecology and evolution 19*, 351-353.

Sargeant, A.B. & Raveling, D.G. 1992. Mortality during the breeding season. In: *Ecology and management of breeding waterfowl*. (Eds. B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu). University of Minnesota Press, Minneapolis, U.S., pp. 396-422.

Sedinger, J.S. 1992. Ecology of pre-fledgling waterfowl. In: *Ecology and management of breeding waterfowl*. (Eds. B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu). University of Minnesota Press, Minneapolis, U.S., pp. 109-127.

Sheaffer, S.E. 1998. Recruitment models for mallards in eastern North Amercia. *Auk 115*, 988-997.

Shenk, T.M., White, G.C. & Burnham, K.P. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological monographs 68*, 445-463.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Pagel, M. 2005. On the regulation of populations of mammals, birds, fish, and insects. *Science 309*, 607-610.

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*, 329-335.

Slade, N.A. 1977. Statistical detection of density dependence from a series of sequential censuses. *Ecology 58*, 1094-1102.

Smith, G.W. & Reynolds, R.E. 1992. Hunting and mallard survival, 1979-88. *Journal of wildlife management 56*, 306-316.

Solman, V.E.F. 1945. The ecological relations of pike (*Esox lucius* L.) and waterfowl. *Ecology 26*, 157-170.

Soutiere, E.C. 1989. Survival of hand-reared mallards released in 2 private farms. *Journal of wildlife management 53*, 114-118.

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

Sugden, L.G. & Beyersbergen, G.W. 1986. Effect of density and concealment on American crow predation of simulated duck nests. *Journal of wildlife management 50*, 9-14.

Swennen, C. 1989. Gull predation upon eider *Somateria mollissima* ducklings – destruction or elimination of the unfit. *Ardea 77*, 21-45.

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

Trost, R., Dickson, K. & Zavaleta, D. 1993. Harvesting waterfowl on a sustainable yield basis: the North American perspective. *IWRB special publication 26*, 106-112.

Turchin, P. 1990. Rarity of density-dependence or population regulation with lags? *Nature 344*, 660-663.

Turchin, P. 1995. Population regulation: old arguments and a new synthesis. In: *Population dynamics: new approaches and synthesis*. (Eds. N. Cappuccino & P.W. Price). Academic Press, San Diego, U.S., pp. 19-40.

Turchin, P. 1999. Population regulation: a synthetic view. *Oikos 84*, 153-159.

Varley, G.C. & Gradwell, G.R. 1963. Predatory insects as density dependent mortality factors. *Proceeding of the XVI international congress of zoology, Washington 1*, 240.

Wauters, L.A., Matthysen, E., Adriaensen, F. & Tosi, G. 2004. Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *Journal of animal ecology 73*, 11-25.

Weller, M.W. 1979. Density and habitat relationships of blue-winged teal nesting in northwestern Iowa. *Journal of wildlife management 43*, 367-374.Verhulst, P.-F. 1838. Notice sur la loi que la population suit dans son accroissement. *Correspondance mathématique et physique 10*, 113-121.

Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. 2002. In: *The migration atlas: movements of the birds of Britain and Ireland*. T. & A.D. Poyser, London, U.K., 884 pp.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird study (supplement) 46*, 120-139.

White, T.C.R. 2001. Opposing paradigms: regulation or limitation of populations? *Oikos 93*, 148-152.

Williams, B.K., Johnson, F.A. & Wilkins, K. 1996. Uncertainty and the adaptive management of waterfowl harvests. *Journal of wildlife management 60*, 223-232.

Williams, B.K., Koneff, M.D. & Smith, D.A. 1999. Evaluation of waterfowl conservation under the North American waterfowl management plan. *Journal of wildlife management 63*, 417-440.

Williams, B.K., Nichols, J.D. & Conroy, M.J. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, U.S., 817 pp.

Willms, M.A. & Crawford, R.D. 1989. Use of earthen islands by nesting ducks in North Dakota. *Journal of wildlife management 53*, 411-417.

Wilson, G.R., Brittingham, M.C. & Goodrich, L.J. 1998. How well do artificial nests estimate success of real nests? *Condor 100*, 357-364.

Wobeser, G.A. 1997. *Diseases of wild waterfowl*. 2nd edition. Plenum Press, New York, U.S., 324 pp.

Woiwod, I.P. & Hanski, I. 1992. Patterns of density dependence in moths and aphids. *Journal of animal ecology 61*, 619-629.

36

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 Guillemain 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, Cèline 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 Ståhlberg 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 känns det bättre att uttrycka sig på svenska.

Mamma Lena och pappa Birger. Tack för att ni inte tröttnade efter alla dessa barn utan också satte mig till världen. Mamma, du har aldrig i skrift tackats för de hundratusentals bullar du bakat genom åren så jag passar på att göra det nu. Och tack mamma för så mycket mer. Du är en fin mor. Pappa, vårt gemensamma intresse för natur och jakt har ofta varit förekommande i våra samtal, och de har varit en glädje. Syskonen Tomas, Johanna, Olof, Anna, Karin, Per och Mats (med alla respektive och alla dessa otaliga syskonbarn!): ni har alltid en central plats för mig och ni betyder mycket.

Några personer har varit speciellt viktiga när det gäller mitt intresse för biologi och fåglar. Bror Olof är i högsta grad delaktig. Han lät köpa in Mörbylånga Fältbiologers första (enda och sista) tubkikare som jag och brorsan 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 tälta 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.

Oskar Mörnerud med familj flyttade till Mörbylånga 1990 och började i min parallellklass i åttonde klass. Det gick inte många dagar förrän vi fann varandra och snart var vi som lång och lerhalm. Du är en mycket, mycket fin vän som jag har väldigt mycket att tacka för, bl.a. alla dessa oräkneliga dagar i Södra Viken som följdes av rituellt hamrande på Facit-skrivmaskinen då vi angav vad vi sett. Det är av Oskar, brodern Niklas, och pappa Bo som jag har lärt mig det mesta om artbestämning av fåglar. Niklas är tillsammans med Oskar mina bonusbröder och ni tackas speciellt för alla stunder i fält, på boulebanan, i fjällen, och i äppelträdet på Västerlånggatan. Tack Oskar också för den söta döda ällingen som pryder

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

Under studietiden i Lund lärde jag känna underbara människor som jag speciellt vill tacka: Olof och Lotta, Jonas och Kajsa, Sten, Ebba L., Kristina, Sofie och Per, Mirja och Christian, Martin och Anna, Helena, Jenny, Richard och Helene, Daniel m.fl. Tack också alla lärare under grundutbildningen.

"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).

Ebba, det största tacket går till dig. Du har i allra största grad bidragit till min avhandling. Du är min bästa vän och bättre hälft, och jag älskar dig. Tack för att du älskar mig. Tack för att du står ut med mig och med att jag varit borta under långa perioder under dessa år. Jag beundrar dig för att du alltid är så leende positiv och för att du alltid får mig på fötter när det känns motigt. Tack Axel och Otto för att vi har er och tack för era skratt och påhitt.

Jaha, de va de de……