UNIVERSITY OF HELSINKI
DEPARTMENT OF APPLIED BIOLOGY
PUBLICATION no 4

NUMERICAL AND BEHAVIOURAL RESPONSES OF BREEDING DUCKS TO HUNTING AND DIFFERENT ECOLOGICAL FACTORS

by
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ACADEMIC DISSERTATION

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Lecture Room 2 of Viikki Infocenter, Viikinkaari 11, Helsinki, on April 20th, 2001, at 12 o'clock noon.

Helsinki 2001

This thesis belongs to the field of Wildlife Management

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ISBN 951-45-9909-8 (nid.)
ISBN 951-45-9924-1 (PDF)
ISSN 1457-8085
Yliopistopaino, Helsinki 2001

To my sister,
Anne Yliluoma (1957-1999)

List of original papers

The thesis is based on the following publications and manuscripts, which will be referred to in the text by their Roman numerals:

I Väänänen, V.-M. 2000. Predation risk associated with nesting in gull colonies by two *Aythya* species: observation and an experimental test. - *Journal of Avian Biology 31: 31-35.*

II Väänänen, V.-M. 2001. Message in the call - brood rearing ducks discriminate between call types of gulls. - *manuscript*

III Nummi, P. & Väänänen, V.-M. 2001. High overlap in diets of sympatric dabbling ducks - an effect of food abundance? – *Annales Zoologici Fennici (in press).*

IV Kauppinen, J. & Väänänen, V.-M. 1999. Factors affecting changes in waterfowl populations in eutrophic wetlands in the Finnish lake district. – *Wildlife Biology 5: 73-81.*

V Väänänen, V.-M. 2001. Hunting disturbance and the timing of autumn migration in Anas species. - *Wildlife Biology 7: 3-9.*

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1. Introduction

1.1. Adaptation against predation

Predation is one of the most important factors affecting the survival of birds (Lack 1968, Wiens 1989). During their life span, birds are subject to different kinds of predation and many features of their behaviour (e.g. flocking and warning behaviour, nest remaining) are adaptations against predation (Wiens 1989, Lima & Dill 1990). Evolution of cryptic coloration of breeding females is also important for making incubating females more difficult to detect by predators. For example, dabbling ducks (e.g. the mallard *Anas plathyrhynchos* and the teal *Anas crecca*) moult some upper wing coverts, tertials and some tail feathers during spring to have more cryptic coloration (Salminen 1983). However, predation on adult ducks has a rather limited impact on waterfowl populations (Owen & Black 1990). In Stoudt and Corwell's (1976) survey, predation (excluding hunting by man) represented only 0.14 % of natural mortality of adult waterfowl. Unlike predation on adult birds, nest predation is an important factor affecting reproductive success of birds (Ricklefs 1969, Owen & Black 1990, Sargeant & Raveling 1992, Martin 1993), and many adaptations against nest predation have developed (Lack 1968).

Among ducks, nest site requirements and means of avoiding predation vary between species (Owen & Black 1990). Duck species nesting in the forested boreal regions of northern Europe nest over a wide area (e.g. the mallard, the wigeon *Anas penelope*, the teal and the goldeneye *Bucephala clangula*) and their nests are difficult to detect by predators. Species nesting in eutrophic wetlands prefer certain habitat types. The pintail *Anas acuta*, the shoveler *Anas clypeata* and the garganey *Anas querquedula* prefer open shores, meadows or fields, the pochard *Aythya ferina* and the tufted duck *Aythya fuligula* floated vegetation stands and the coot *Fulica atra* dense stands of emergent vegetation from the previous year (e.g. Cramp & Simmons 1977). In wetlands and fields, corvids (especially the common crow *Corvus corone*) are the most important nest predators of birds (e.g. Hildén 1964, Gailbraith 1988, Götmark & Åhlund 1988, Bains 1990, Berg et al. 1992, Valkama et al. 1999). Crows systematically search certain habitat types and clumped nests are more vulnerable to crow predation than those on dispersed habitats (Tinbergen et al. 1967, Croze 1970). Mammalian predators may also have an important role in decreasing breeding success of birds in wetlands, fields and forests (Putaala & Hissa 1993, Viksne 1997, Virtanen et al. 1998, Pöysä 1999, Valkama et al. 1999).

It is obvious that the nest predation rates vary remarkably between areas and species. The nest predation rate of the cavity-breeding goldeneye is probably the best known of ducks in inland areas of northern Europe. Studies have shown that in central Finland about 5%, in south-east Finland 33-74% and in two areas in Sweden 10% and 38% of nests are preyed upon (Erikson 1979, Fredga & Dow 1984, Pöysä 1999, Ruusila et al 2000.

Some species nest in association with aggressive colonial breeders (e.g. larids) or close to the nests of birds of prey to avoid nest predation (Hildén 1964, Newton & Campel 1975, Götmark & Anderson 1980, Wiklund 1982, Norrdahl et al. 1995, Larsen &

Grundetjern 1997, Pius & Leberg 1998, Valle & Scarton 1999). Three hypotheses have been suggested to explain interspecific nesting associations in birds. According to the protector species hypothesis, an aggressive species defends its nesting area and all nests in this area gain protection (Hildén 1964, Newton & Cambell 1975, Wiklund 1982). According to the "information parasitism" hypothesis, individuals can exploit information of species' alarm calls (Nuechterlein 1981, Burger 1984, Pöysä 1989). Finally, it has been suggested that a mixed breeding colony can function as an information centre for food finding (Ward & Zahavi 1973). First and second hypotheses have been experimentally tested and results support the predictions of these hypotheses (Nuechterlein 1981, Götmark 1989). The information centre hypothesis has received only observational support (Krebs 1974, Emlen & Demong 1975). However, it has been pointed out that an explanation solely based on food finding seems unrealistic in a species that feed in different locations and on different foods (Lack 1968, Krebs 1974, Erwin 1979).

1.2. Interspecific relationships: the role of food partitioning in dabbling ducks

Resource partitioning is one of the basic aspects in community ecology when the co-occurrence of different species is considered. A species functional role in a community and its position in trophic interactions are important. Niche size, shape, location and overlap with other species will shift in response to changes in competitive pressure (Wiens 1989). Ecomorphological patterns of species, e.g. bill morphology, have been suggested to reflect resource competition. However, it is obvious that morphological structures of species are likely to reflect a compromise solution under several types of selection pressure (Wiens 1989). Species with a similar ecology will form ecological guilds. In a compact guild, the partitioning of limited food resources and/or flexibility of food use makes coexistence of species possible (Wiens 1989, 1993).

Many community ecological principles appear to be valid in waterfowl communities; for instance the species richness and especially breeding densities are highest in the most productive areas (Elmberg et al. 1993, Kauppinen & Väisänen 1993, Kauppinen 1997). Waterfowl communities also have a clear guild structure; e.g. dabbling ducks form a compact foraging guild (Pöysä 1983a, Pöysä et al. 1994). All species in the dabbling duck guild occurs together only in most productive wetlands in North Europe (Elmberg et al. 1993, Kauppinen & Väisänen 1993).

There has been long-standing debate on the importance of bill lamellar density (Nudds & Bowlby 1984, Nudds et al. 1994), neck length (Pöysä 1983b, Pöysä et al. 1994) and foraging behaviour (Pöysä 1987, Nummi 1993) as well as on the role of habitat structure in food partitioning among dabbling ducks (Nudds et al. 2000). Results from North America suggest that interspecific variation in the density of bill lamellae reflects microhabitat segregation (Nudds & Bowlby 1984, Nudds 1992, Nudds et al. 2000, see also Nudds et al. 1994). Species in North America with few lamellae, but large bodies, tend to feed in shallow, vegetated microhabitats where invertebrate prey is large. On the other hand, species with dense lamellae tend to occur in open microhabitats where prey is smaller (Nudds et al. 2000). In northern Europe, however, the evidence suggests the opposite (see Pöysä et al. 1996), indicating that it is the difference in body length that facilitates coexistence, by constraining the depths to which ducks can "up-end" to reach food in submerged vegetation (Nudds et all. 2000). However, with regard to the proposed association between bill lamellae density and prey size, our understanding of current duck community ecology is still mostly based on Nudds and Bowlby's (1984) literature survey on studies done in different parts of North America.

1.3. Weather and habitat factors affecting duck populations

During the 1900's many waterfowl species expanded into northern Europe from the south and south-east (Kalela 1946, Yarker & Atkinson-Wiles 1971, von Haartman 1972, Burton 1995, Hagemeijer & Blair 1997). Changes in distribution of species have been suggested to be mostly due to changes in habitats and/or climate (e.g. Kalela 1949, von Hartman 1973, Burton 1995, Hagemeijer & Blair 1997). During the last century, eutrophication in Finland has created favourable habitats for newcomers, and several new species (e.g. the coot, the gadwall *Anas strepera* and the pochard) have established their populations in well-vegetated wetlands.

Extremely harsh winters have affected short-term population fluctuations of waterfowl in North Europe (von Haartman 1945, Hildén 1964, Nilsson 1979, 1984). A severe winter could increase mortality on the wintering grounds, make waterfowl more vulnerable to hunters and could also indirectly (e.g. by lowering physical condition) affect breeding success of the next season (Boyd 1964, Nilsson 1979, 1984, Andersen-Harild 1981, Newton 1998). In addition, spring temperatures may shorten or lengthen migration (Siira & Eskelinen 1983), and summer temperatures may have an effect on brood production.

In North America, a high variation in population size of ducks between successive years has traditionally been associated with unpredictable changes in habitats (Evans & Black 1956, Eisenlohr 1969, Posphala et al. 1974; but see Bethke & Nudds 1995). Wetlands in pothole areas of northern prairies and parklands have been shown to be unstable due to weather factors; water level fluctuates widely both between years and during the breeding season. Changes in habitat quality (drought) also cause between-year variation in brood production (Leitch & Kaminski 1985, Sutherland 1991), and, brood production may affect the size of breeding populations in the subsequent years (Reynolds & Sayer 1991).

In northern Europe the quality of duck habitats does not vary much between or within years (Nummi & Pöysä 1993), and, hence, variation of habitat quality should not be an important determinant of population size or brood production of ducks. Unlike in North America, changes in size of waterfowl populations or structure of duck communities are usually not large during successive years (Pöysä 1989, Kauppinen 1995).

1.4. Hunting vulnerability and disturbance effect

Hunting is one of the most important mortality factors of fledged waterfowl (Stoudt & Cornwell 1976, Rogers et al. 1979, Owen & Black 1990). Mortality due to hunting in ducks is age-specific. Young ducks are shot more than adults (Anderson 1975, Kremetz et al. 1987, Nichols et al. 1990, Johnson et al. 1992, Caithness et al. 1991) and usually more males are shot than females (Anderson 1975, Reinecker 1976, Nichols et al. 1990). Furthermore, brightness of coloration (Metz & Ankney 1991), diseases (Bellrose 1959), flocking behaviour (Olson 1964, Dufour & Ankney 1995) and especially physical condition (Hepp et al. 1986, Reinecke & Shaiffer 1988, Heitmeyer et al. 1993, but see also Sheeley & Smith 1989) seem to affect vulnerability to hunting. Ducks in large flocks in good physical condition (abundant fat reserves) can avoid hunting most efficiently (Hepp et al. 1986, Reinecke & Shaiffer 1988, Heitmeyer et al. 1993, Dufour & Ankney 1995).

The mortality of waterfowl varies from year to year and, in theory, mortality due to hunting can be compensated to certain degree by a decrease in mortality due to other causes (Anderson & Burnham 1976, Patterson 1979, Rogers et al. 1979, Nichols et al. 1984). However, compensation of mortality due to hunting is possible only if other mortality factors are density dependent (Newton 1998). The timing of hunting is crucial in the compensation process; mortality due to hunting during autumn is more easily compensated for than that occurring in winter (Mc Gowan 1975, Kokko & Lindström 1998, Kokko et al. 1998, Newton 1998). In geese mortality due to hunting has been additive, and therefore, increased the total yearly mortality rate; after hunting limitation geese populations have increased rapidly (Owen & Black 1990, Newton 1998).

Natal philopatry and age-specific reproductive success are important factors in management of waterfowl populations. Local hunting can have a direct effect on population size in later years if the harvesting rate is too high, because of natal and breeding site philopatry of female ducks (Greenwood 1980, Clarke et al. 1997, Ruusila 1999). Therefore, the most valuable individuals in waterfowl populations are experienced females which produce the largest clutches and broods, more recruits and, in particular, nest in the same area year after year (Mihelsons et al 1986, Sæther 1990, Forslund & Larsson 1992, Rohwer 1992, Forslund & Pärt 1995, Milonoff et al. 1998, Ruusila et al. 2000).

In addition to mortality, hunting also has a disturbing effect on waterfowl (see reviews of Davidson & Rothwell 1993, Madsen & Fox 1995). Hunting disturbance has been shown to affect waterfowl behaviour, such as increase escape-flight distance, modify diurnal activity and decrease daily foraging time (Owen & Williams 1976, Owens 1977, Gerbes & Repmeyer 1983, Madsen 1985, 1998a, Mayhew 1988). There are differences between species in sensitivity to disturbance and in wintering/staging areas. The most sensitive species are those which stay close to the coast or inland waters and are concentrated in relatively large flocks (Madsen et al. 1998). Periods of lowest nutrient reserves and/or increased energy expenditure are most critical to hunting disturbance (Madsen & Fox 1995, Dehorter & Tamisier 1998).

Hunting disturbance may cause a local and also a large-scale regional redistribution of ducks (Lorentsen 1988, Madsen & Jepsen 1992, Follestad 1994, Madsen 1998b). Our knowledge of the large-scale effects of hunting disturbance on waterfowl distribution is scarce. Most studies on the disturbance effects of hunting, have been carried out in staging or wintering areas (Madsen & Fox 1995).

1.5. Finland as a waterfowl breeding and harvesting area

Within Europe, Finland is one of the most important duck breeding areas. For instance, a central part of the European population of the following species breed in Finland: the goldeneye (about 60% of the European population), the goosander *Mergus merganser* (45%), the red-brested merganser *Mergus serrator* (39%), the wigeon (23%), the eider *Somateria mollisima* (21%), the teal (15%), the pintail (10%) and the shoveler (10%), (Hagemeijer & Blair 1997, Väänänen 2000). Hence, conservation and management of waterfowl habitats in Finland is very important for European waterfowl populations.

In Europe, waterfowl hunting is a popular recreational activity, especially in staging and wintering areas, but also in breeding areas such as Finland. The hunting bag of waterfowl in Europe has been increasing and about 11 million ducks and geese are shot annually by approximately 3.2 million hunters (Scott 1982, Owen & Black 1990). The annual hunting bag in Finland has been almost one million ducks (Ermala 1992, Suomen Virallinen Tilasto 1997, see also Suomen Virallinen Tilasto 2000).

In the course of a year, waterfowl are distributed in an exceptionally large area as compared with other game birds. The distances between the breeding and wintering areas may be thousands of kilometres (Cramp & Simmons 1977, Owen & Black 1990). The most important wintering areas for ducks breeding in Finland are the southern Baltic and north-west Europe, the southernmost wintering areas being in Africa (Väänänen 1999, Finnish Museum of Natural History unpubl. data).

Thus, the waterfowl populations are common for large areas across Europe. The population estimates of most waterfowl species in wintering areas of Europe have shown increasing trends. However, the populations of the pochard and the pintail have decreased (Monval & Pirot 1989, Rose & Scott 1997). It has been suggested that hunting has not caused the decrease of these two species (Layndry 1990).

1.6. Aims of this thesis

In this thesis, I examine numerical and behavioural responses of waterfowl to different biotic and abiotic factors at individual, population and community levels. In paper I and II, I studied breeding association between ducks and small colonial larids, i.e. the common tern *Sterna hirundo*, the black-headed gull *Larus ridibundus* and the little gull *Larus minutus*. In paper I, I focused on nest predation risk in the pochard and the tufted duck and tested the hypothesis that gull colonies protect ducks against nest predation. In paper II, I focused on the association between ducks and gull colonies during the brood period.

In paper III, I focused on the size distributions of invertebrates in the diets of dabbling ducks, and on the proposed association between bill lamellae density and mean prey size in the diet of ducks. I directly compared the feeding niches of six dabbling duck species from the same lakes from which the prey availability data were collected. I briefly discussed the role of food in limiting numbers of ducks in eutrophic wetlands.

In the last two papers I studied factors affecting changes in waterfowl populations breeding in Finnish inland lake area. In paper IV I examined recent changes in the breeding numbers in relation to weather factors and hunting pressure in the northern part of the Finnish inland lake area. In paper V I studied hunting disturbance, refuge use and timing of autumn migration of dabbling ducks. In addition, I examined hunting bag (wing data) in relation to breeding and autumn populations, to give a more detailed picture on hunting pressure of waterfowl in the studied sites.

2. Study area, material and methods

Data were gathered from central and southern Finland from the period 1970-2000. The study areas in central Finland consist of both richly vegetated lakes surrounded by cultivated fields or usually a narrow forest line on a shore and shores of more urban sites. Dominant vegetation stands in eutrophic wetlands consist of horsetail *Equisetum fluviatile*, reed *Phragmites australis*, bullrush *Schoenoplectus lacustris* and sedges *Carex* spp., whereas reed and sedges are common on urban shores. The most important study wetlands are located in Maaninka (63°N, 27°E), in northern part of the Finnish inland lake area (Fig 1). Data from southern Finland are from lakes and shores of the Helsinki area (60°N, 20°E) and from more oligotrophic lakes and ponds in the Nuuksio lake area. Stands of reed are dominant in the Helsinki area and sedges in the Nuuksio lake area.

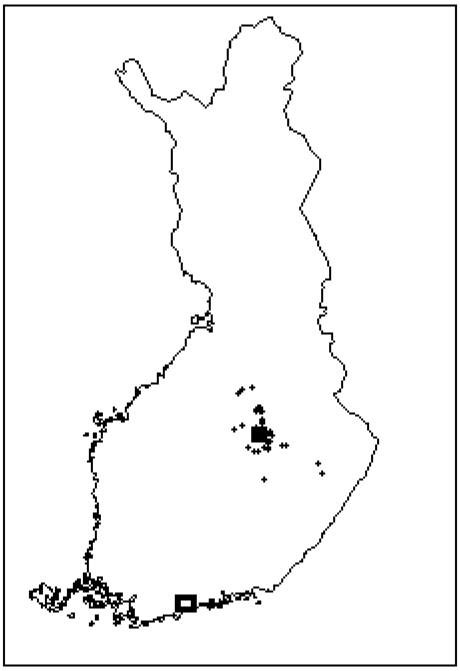

Figure 1. Distribution of study areas. Most important study area is marked as black square (include ten study wetlands). Study areas in southern Finland (Helsinki area and Nuuksio lake area) are marked as open square.

Data on pochard and tufted duck nests were gathered in Maaninka between 1985 and 1996 (I). The nest predation experiment was carried out in Maaninka and Lapinlahti (63°N, 27°E) in 1998. In the experiment artificial nests were placed within a gull colony (ten nests with one hen *Gallus domesticus* egg in each) and an equal number of control nests well outside the defence area of the colony on the same lake or nearest suitable wetland (I). The experiment included six replicates.

Distribution of duck broods (within or outside gull colony) was observed between 1998 and 2000 and data were summarised as broods within or outside the defence area of a gull colony (II). Shorelines of study lakes with a colony were calculated using the Mapinfo program (Mapinfo Professional Version 5.0.1, copyright 1985-199 Mapinfo Corporation). The playback experiment was conducted in 1999 and 2000. Alarm and basic (as a control) calls of black-headed gulls were played to each female duck with brood. The experiment tested whether a brood rearing female duck distinguishes between alarm and basic calls of gulls (II).

Data for paper III were collected in Maaninka. The esophagi of dabbling ducks were removed after the ducks were shot and preserved in alcohol pending analysis for diets between 1992 and 1998 (Swanson & Bartonek 1970). Food availability data were collected using activity traps and corer (see Nudds & Bowlby 1984, Nummi 1993, Nummi et al. 1995). Data were summarised and analysed according to methods used by Nudds and Bowlby (1984) to allow direct comparisons.

Data on the breeding pairs (IV) were obtained from the northern part of Finnish inland lake area from the period 1970-1998. Data on the effect on hunting disturbance (V) were obtained from northern part of Finnish inland lake area from 1995 to 1999. Duck ringing data are from the period 1970-1991 (IV). Wing data are gathered in the Maaninka area between 1985 and 1989 and data include about 30% of annual bag (IV).

To give a clearer picture of hunting pressure in eutrophic wetlands in central Finland, wing data from the most important study lakes (four lakes, total area 2.92 km^2) gathered from 1985 to 1998 were analysed. The wing data comprise about 40% of annual bag. The estimate is based on numbers of hunters and bag statistics of local hunting association in the study area. In this area the annual bag was compared with breeding and autumn numbers of dabbling ducks. The age and sex of each bird was determined from the wing sample according to Salminen (1983). The development status of juveniles (primaries full grown or undeveloped) and moulting phase of adult ducks (wing moulting not yet started, primaries were growing or have already changed) was determined. The census of the dabbling ducks in each wetland was taken just before the opening of the hunting season, i.e. between 17 and 19 August (mostly 18 or 19 August), (V, this study). The timing of the autumn migration was observed in two wetlands from the middle of July to the end of ice-free period over the 1995-1998 period (V).

3. Main results and discussion

3.1. The gull colony: a “protective umbrella” for breeding ducks

Gull colonies have an important role in the nesting success of ducks (I). I found that aggressive gulls protect nests within their colony area as the protector-species hypotheses predicts (I, Götmark 1989, see also Larssen & Molsvor 1992, Norrdahl et al. 1995, Larssen & Grundetjern 1997, Pius & Leberg 1998). The predation rate of pochard and tufted duck nests within colony was less than 10 %, whereas outside the gull colonies it was about 48% and 40 %, respectively (I). Experimental testing with artificial nests also showed that a higher proportion of nests was preyed upon outside than within the colonies (0.98 and 0.13, respectively) (I). The predation rate of pochard and tufted duck nests was high (I), but even higher predation rates among ducks and geese have been reported (e.g. Summers & Underhill 1987, Pöysä 1999).

Götmark (1989) suggested that the timing of nesting may be an important factor in the evolution of nesting association between ducks and larids as well as between birds and their predators (Wiklund 1982, Norrdahl et al. 1995, Larssen & Grundetjern 1997). Within the gull colony nests were protected when the laying period of ducks began at the same time or after that of the larids (Götmark 1989). However, extremely late clutches may be left without protection when fledged gulls leave the colony area. Pochard and tufted duck lay their eggs later than black-headed gull, so, my results support Götmark's (1989) suggestion. However, it is obvious that there may be other factors, such as nest site requirements, affecting the evolution of the nesting associations. My results show that the tufted duck nested more often within colonies than the pochard. I found that the pochard favour smaller floated vegetation stands than the tufted duck (I). Because black-headed gulls mostly start laying before pochards, it is possible that small vegetated islands are colonised first by gulls, and hence, pochards may nest more often outside a colony even though the nesting success rate within the colony area is better. Therefore, the nest site requirements may explain differences in the nesting association with gulls between pochards and tufted ducks (I).

Gull colonies are also important for ducks during the brooding season (II). Broods of most duck species are prevalent in the defence area of colonies and only the territorial goldeneye do not clump within a colony (II). Nuehterlein (1981) showed that grebes can utilise terns' alarm calls, and furthermore, Burger (1984) found that grebes nesting within gull colonies had better survival rates than grebes nesting outside the colonies. These findings indicate that grebes can exploit the warning behaviour of terns, and hence, reduce predation. Among ducks, foraging teals have been found to respond to alarm calls of the black-headed gull (Pöysä 1988). My "playback" experiment confirmed the ability of ducks to distinguish information of black-headed gull calls without using visual cues (II, see Neuchterlein 1981). It may also suggest that female ducks can use the visual cues of attacking and mobbing larids, and it is probable that by using this information for early warning, broods can avoid predation.

As a whole, gull colonies are important for breeding ducks, especially during the nesting phase (I). During first weeks of the brooding season, when broods are the most vulnerable to loosing ducklings (Ortmeyer & Ball 1990, Savard et al. 1991, Talent et al. 1983, Mauser et al. 1994, Pöysä & Virtanen 1994), larids may also have an important role as protector species and act as early warners to ducks (II).

3.2 The role of food resources in eutrophic wetlands

I found a high overlap in food use among the dabbling ducks in eutrophic wetlands. I suggested that the overlap of food in the dabbling duck guild may not be exceptional (III). High diet overlap is usually associated with "fat" times with abundant food, and low diet overlap with “lean” times (Smith et al. 1978, Rotenberry 1980, Rosenberg et al. 1982, Schoener 1986, Wiens 1989). The high diet overlap seen in my study may thus indicate low food competition between dabbling ducks. This can be seen in the diet patterns of teal and mallard (the smallest and largest species in the dabbling duck guild). In my study the diets of mallard and teal overlapped considerably, whereas in another study based on data from oligotrophic lakes the diets of the two species clearly differed (Nummi 1993).

Unlike in more oligotrophic wetlands (see Nummi et al. 2000, Sjöberg et al. 2000), food abundance hardly limited breeding densities or composition of duck communities in eutrophic wetlands (III). North European dabbling ducks coexist only in eutrophic wetlands (with abundant food), and some species, i.e. the shoveler and the garganey, do not even breed outside lush wetlands (e.g. Kauppinen 1993, Hagemeijer & Blair 1997, Väisänen et al. 1998). It seems possible that an abundant food supply enabled a high overlap in food use, and that resource competition may not be an important factor in affecting breeding densities or brood production in eutrophic wetlands.

3.3. Do weather factors cause changes in waterfowl populations?

There was a 40 % difference between maximum and minimum of the total waterfowl population in our study area. However, between successive years fluctuations did not exceed 20 % (IV). The most unstable species were the garganey, the tufted duck, the coot and the pochard (IV). It has been suggested that weather factors may cause short-term fluctuations of waterfowl populations in northern Europe (von Haartman 1945, 1957, Greenquist 1965, Hildén 1966, Nilsson 1979, 1984). In particular, a hard winter may be associated with population fluctuations by causing direct winter mortality or by indirectly lowering the breeding success in the following summer (e.g. Boyd 1964, Nilsson 1979, 1984, Andersen-Harild 1981). In my analyses, the following weather factors appeared to be associated with population fluctuations of the species; in the garganey: spring temperature; in the pintail: brood season temperature, winter severity in France and spring temperature; in the goldeneye: winter severity in the Baltic and spring temperature; and in the mallard: brood season temperature in the previous year (IV).

Some species seem to be sensitive to spring temperatures which has been suggested to cause fluctuations in southern/northern species at the limit of their distribution area (IV, Siira & Eskelinen 1983). The garganey is perhaps the best-known example being more numerous after warmer than average springs (IV, Siira & Eskelinen 1983). Abnormal climatic conditions during spring should affect more first-time breeders than older females that are nest site philopatric. Hence, we found some support for the idea that weather factors may affect short-term fluctuation of waterfowl populations but, in general, climatic factors seem not to play an important role in population fluctuations (IV).

3.4. Hunting pressure of waterfowl in Finland

Information of duck reproduction in Finland and in other parts of northern Europe is scarce. In their study from the oligotrophic Evo area in southern Finland Nummi and Pöysä (1997) reported the following numbers of young per breeding pair: the teal 1.5, the mallard 1.4 and the goldeneye 1.3. It is obvious that in eutrophic wetlands offspring production is higher (see Nummi & Pöysä 1997), even though nest predation rates may also be higher at these sites (I). In Finland, the annual waterfowl bag has been almost one million birds (Ermala 1992, Suomen Virallinen Tilasto 1997, see also Suomen Virallinen Tilasto 2000). The total bag of waterfowl in Finland in relation to the breeding population or brood production (Nummi & Pöysä 1997, Väisänen et al. 1998) seems to be high (bagged waterfowl/breeding pair in hunting season 1994/95: the bean goose *Anser fabalis* 3.9, the greylag goose *Anser anser* 1.5, the mallard 1.8, the teal 1.0 and the goldeneye 0.9; Väänänen 2000). According to Finnish ringing data (ducks ringed as young) most of the recoveries of shot ducks are found in Finland, in particular, near natal areas (Väänänen 1996). However, we lack the knowledge of the respective sites of origin of waterfowl in the bag. Moreover, it is obvious that a lot of waterfowl shot in Finland migrate from Russia.

The breeding population of the goldeneye has been studied intensively since 1984, in my study area all hatched ducklings have been ringed in an area of about 280 km^2 (Pöysä et al. 1997). The proportion of ringed goldeneyes (own population) in the bag in 1985-1998 has been over 30% at the beginning of the hunting season and still clearly over 20% in the middle of September (Fig 2). This result shows that the proportion of the local goldeneye population bagged is high in eutrophic wetlands. The recovery data of the goldeneye show that even at the beginning of the hunting season some juvenile goldeneyes have regularly been found far from their natal area, whereas recoveries of mallards have been made only in their natal area (Väänänen 1992, Runko unpubl. data). This implies that, at the beginning of the open season, fledged juvenile mallards may be more numerous in their respective natal area than goldeneyes (see also phenology of autumn migration of mallard in V), and, hence, mallards may face more serious losses due to local hunting in natal areas.

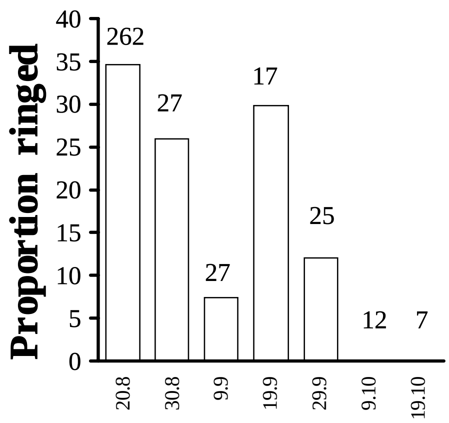

Figure 2. Proportion of ringed goldeneyes (n=108 ringed goldeneyes) in the hunting bag in four study wetlands in the 1985-1998 period. Results are shown in 10-day periods, and the first day of each period is given under the bar and the total number of observations in the top of the bar. Data consist only for those ringed goldeneyes which are collected from hunters during wing sample survey. The total number of bagged goldeneye is 377.

Eutrophic wetlands are the most popular duck hunting areas. In my eutrophic study wetlands hunting pressure for ducks is high when comparing the hunting bag to breeding and/or autumn populations (Fig 3A and 3B) or checking recovery data of e.g. goldeneye and mallard (IV, Väänänen 1992, Runko unpubl. data).

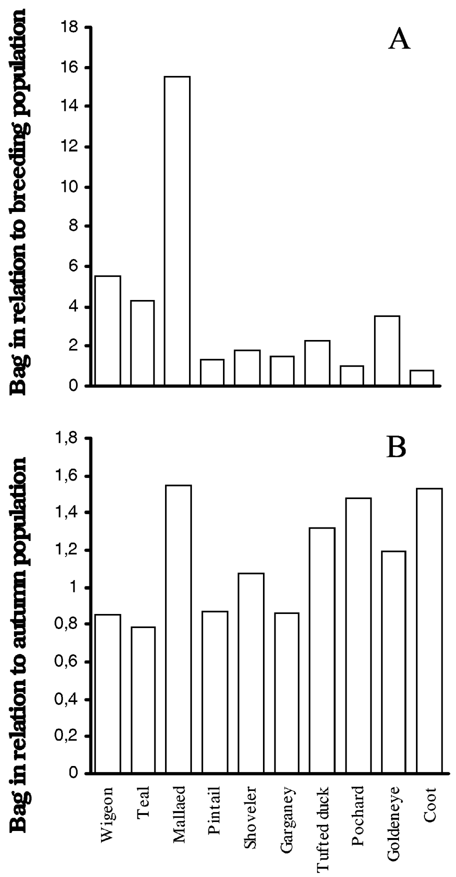

Figure 3. The bag in relation to breeding population in the 1988-1998 period (A) and in relation to autumn population (census taken just before the opening the season) in the 1988-1998 period (B) in four study wetlands in Maaninka. The bag was calculated from wing data by assuming that wing data are 40% of the total bag.

The timing of autumn migration of waterfowl is an important factor affecting the level of local hunting. My results indicate that in the Finnish inland lake area early and late migrating dabbling ducks face differing local hunting pressure (V). The numbers of late migrants, i. e. the mallard, the teal and the wigeon, increased steadily towards opening of the hunting season, whereas numbers of early migrants, i.e. the garganey, the pintail and the shoveler, already peaked at the beginning of August (V). At the beginning of the hunting season only late broods of pintails and shovelers were present in the natal area (Väänänen 1996). In general hunting pressure in northern Savo seemed to be higher than on average in Finland (IV). Local hunting pressure may limit the population size of mallard in my study area (IV).

Siira and Eskelinen (1983) reported that local hunting explained 76 % of the population fluctuations of the shoveler, even though most of the recoveries were found in wintering areas (Merilä et al. 1977, Siira & Eskelinen 1983). My results indicate the opposite: local hunting could not have a significant effect on populations of early migrants, such as the pintail and the shoveler, because most of the local pintails and shovelers had already migrated before the open season (V, Väänänen 1996).

The age structure of hunted ducks is also important, because it is more reasonable to shoot juveniles than experienced adult individuals. The shooting of juveniles is profitable in a species with a delayed maturity, such as goose, goldeneye and goosander because shooting of breeding females decrease next year offspring production (Owen & Black 1990). In Finland the bag mostly consists of juveniles (IV, Pirkola & Lindén 1972), whereas in Denmark the proportion of adults in the bag is much higher (e.g. Clausager 1987, 1988, 1989).

Table 1. The proportion of bagged adult duck females of different species in relation to breeding population (A) and percentage of females in different moulting phase (B-E) in wing data during 1985-1998 in four wetlands in Maaninka. The bag was calculated from wing data by assuming that wing data are 40% of the total annual bag in the study area. Moulting phase of adult females (analyzed from wing samples) was divided into four categories: B = wing moulting has not yet started, C = primaries growing, D = primaries full grown, but base of primaries are still soft, E = primaries are fully developed. Total numbers of bagged adult females (wing samples) are shown in column F.

Species	A	B	C	D	E	F
Wigeon	0.93	6.5	47.7	4.7	41.1	107
Teal	0.80	4.4	41.3	11.5	42.9	182
Mallard	2.00	5.2	37.0	8.1	49.6	135
Pintail	0.25	11.5	57.7	15.4	15.4	26
Shoveler	0.08	16.7	58.3	8.3	16.7	12
Garganey	0.13	-	83.3	-	16.7	6
Pochard	0.03	100.0	-	-	-	1
Tufted duck	0.20	47.1	23.5	5.9	23.5	17
Goldeneye	0.03	-	100.0	-	-	1
Total		7.4	42.7	8.9	40.9	487

In Finland the proportion of bagged adults in relation to the breeding population can be high, particularly in my study area where adult females of mallard, teal and wigeon are shot in great numbers (Table 1). The timing of moulting and moulting strategy of successful breeders is extremely critical. The breeding dabbling duck females face local hunting in breeding areas by moulting near their breeding areas, whereas goldeneyes and pochards avoid local hunting by migrating to moulting grounds (see Salminen 1983). It is obvious that in the beginning of the hunting season the adult dabbling duck females belong to a local population (mostly moulting) whereas most of the females bagged late in autumn, originated outside the study area.

In the total annual bag in the studied area, half of the adult duck females had growing or old primaries (Table 1). Breeding females begin their wing moulting after or slightly before (renester) juveniles are fledged, whereas the unsuccessful breeders already have new primaries at the beginning of hunting season. In my study area, the first broods of mallard and wigeon are fledged usually in the last week of July or at the beginning of August. It takes about one month to moult primaries, and females are flightless for about 2/3 of the moulting period (see Salminen 1983). Therefore, successful breeders of mallard and wigeon have not enough time to finish wing moulting before the opening of the hunting season. My results indicate that successful breeders in particular are vulnerable to hunting.

This is unfavourable, because those females are the most valuable part of waterfowl population (see Sather 1990, Forslund & Larsson 1992, Rohwer 1992, Forslund & Pärt 1995, Milonoff et al. 1998, Ruusila et al. 2000).

3.5. Hunting disturbance and distribution of ducks

About 200 000 duck hunters participate in the first day of the open season for ducks in Finland (Ermala & Leinonen 1995). It is well known that hunting has strong disturbance effects on waterbirds (see reviews by Davidson & Rothwell 1993, Madsen & Fox 1995). I found that immediately after the opening of the hunting season the numbers of dabbling ducks collapsed and hunting caused a clear local redistribution (V).

In Finland there are no large-scale data available for estimating the effect of hunting disturbance on the regional/ national distribution of ducks. However, because local-scale disturbance effects seem to be common at least in the inland lake district, it seems that regional changes in the distribution of dabbling ducks are also possible (V). In general, knowledge of large-scale redistribution caused by hunting is scarce (Madsen & Fox 1995). However, the early mass departure of pink-footed geese *Anser brachyrhynchus* in Denmark and greylag geese in Norway have been ascribed to the disturbance caused by hunting (Lorentsen 1988, Madsen & Jespen 1992, Follestad 1994).

Waterfowl have been reported to seek shelter in refuge areas. Furthermore, in Denmark numbers in quarry dabbling ducks increase 4 to 50-fold after reserve was established (Madsen & Fox 1995, Madsen 1998a). My results indicate that the redistribution pattern between hunting and refuge areas is also the same in my study areas. After the beginning of the hunting season, ducks use reserves more than hunting areas (V).

4. Management implications

Many functional characteristics of a species - i.e. adaptations against predation, morphological feeding structures, foraging and flocking behaviour - may reflect compromise solutions under several types of selective pressure (Lack 1968, Wiens 1989). The selective forces may operate either in evolutionary or ecological time scale. Also, in widely ranging species the patterns that we see locally may reflect selection pressures that are promoted elsewhere. For example, waterfowl use several kinds of habitats within year and during life-span they have diverse intra- and interspesific interactions. These factors may shape both duck population fluctuations and waterfowl communities and have different effects on population fluctuation of waterfowl. In waterfowl management, it is crucially important to have large-scale knowledge of species' ecology.

My results suggest that gull colonies may increase breeding success of ducks, especially by providing safe nesting sites. It is important that habitat requirements of small colonial larids are taken into account in the conservation and restoration of wetlands. This is even more timely because numbers of black-headed gull, the most important protector species of ducks, have decreased in many parts of Finland (Väisänen et al. 1998, Ruokolainen et al. 1999).

Habitat quality, especially as measured by food abundance and availability, is an important factor affecting the density of breeding duck pairs and broods (e.g. Nummi & Pöysä 1993, Nummi et al. 2000, Sjöberg et al. 2000). If the food availability is below the resource-limitation level (see Wiens 1993) food resources may affect the population density and community structure of ducks. However, the extensive food overlap of dabbling ducks in the wetlands of my study indicates that food resources may not limit duck populations in eutrophic wetlands. Other factors, such as hunting, may keep some duck populations (e.g. mallard) under carrying capacity. Therefore, in eutrophic wetlands there is no need to manage food resources.

At least in eutrophic wetlands of central Finland hunting pressure of waterfowl seems to be high. Most of the hunting of the Finnish ducks population is done near natal areas, not in staging or wintering areas, though there are differences in harvesting rates between different species and different areas. It seems evident that early migrants are heavily hunted much in wintering areas, whereas late migrating species, except the teal, are harvested mostly in Finland (see Väänänen 1996). However, in general, duck populations have tolerated hunting in Finland surprisingly well. We are responsible for the management of especially those species in which most of the European population breeds in Finland, e.g. common goldeneye and goosander.

In Finland we have a lot of shores and wetlands within towns and villages where hunting is not allowed because of human settlement and recreational activity. However, we lack refuges of high quality feeding and moulting habitats for waterfowl. In Finland, there is a need to establish a network of reserves for waterfowl in eutrophic wetlands, as has been done in Denmark (Madsen & Fox 1997, Madsen et al. 1998). The main functions of such a network are: (i) to provide undisturbed high quality moulting areas for breeding female ducks, (ii) to provide high quality undisturbed feeding habitats, and (iii) to prevent the early mass departure of waterfowl due to hunting disturbance. Co-operation in the management of waterfowl populations between breeding, staging or wintering area is of crucial importance.

Acknowledgements

My interest in waterfowl is originated from my childhood. I observed the wildlife of wetland habitats when I was trapping muskrats on my "home lake" *Valkeinen* with my father. Later *Jukka Kauppinen* and *Matti K. Pirkola* awoke my interest in waterfowl to a more scientific direction.

During recent years, the most important person for my work has been my excellent supervisor *Hannu Pöysä*. *Hannu* has patiently commented on my writings (and ideas) and even though he was very busy, he always has sent his comments back very quickly – on many occasions with the statement*: I stole time from other work and red your manuscript first*. *Hannu* has encouraged me and his guidance has been invaluable during recent years. *Petri Nummi* was an other important person during this process. He has patiently commented on all my writings. Co-operation with *Petri* has always been comfortable (e.g. in writing or planning "torpedo" during coffee break or with beer on a terrace). With *Pentti Runko* I have felt wet, chill and heat during bird ringing journeys many times. These fine moments have enormously increased my knowledge of wetlands habitats. *Pentti* has collected unique ringing data from goldeneyes and this data has been very valuable for my thesis. Meetings of the duck group in *Evo Game Research Station* have been very important - late hour discussions of life and science as well as the body and bouquet of wines with *Hannu, Pentti, Petri , Markku Milonoff, Antti Paasi-vaara, Vesa Ruusila* and *Juha Virtanen* have been unforgettable.

I had the honour to co-operate with *Jukka Kauppinen*, the grand old man of waterfowl monitoring. I began to count waterfowl in the middle of 1980, after reading *Jukkas* work in *Siiveкäs*. The process of writing and publishing our paper in WB (paper IV in this thesis) has been very valuable and educational experience for me. Many people have commented on my manuscripts and always during the reviewing process my writings have been improved enormously. *Mikael Kilpi* and *Erkki Korpimäki* reviewed the thesis and *Alisdair Mclean* checked the English. *Matti K. Pirkola* and *Arno Salminen* brought me up on the secrets of age and sex determination of ducks.

During study period I had many co-operators in *Maaninka*. My dear family: parents *Eeva* and *Veli*, my brothers *Juha-Pekka* and *Jarmo* and my late sister *Anne*, supported me all the time. Especially the parts played by *Juha-Pekka* and *Rellu* (a German fire-haired pointer) has been invaluable. Patiently *J-P* has helped me during whole study period and without his field assistance a considerable part of my data has been impossible to collect. In addition, many of my friends have given a valuable field assistance for me. *Esa Pienmunne* and *Jani Pellikka* has guided me to the awe-inspiring world of computers – a world of frustrating, never-ending movements of systems. I have worked in the *Department of Applied Zoology*. The spirit of our department has been engaging and exhilarating. Professor *Kari Heliövaara* has given me excellent opportunities to study ducks.

During last two years *Kaisu Husu* has lightening my life. She has always supported me - by encouraging me, giving field assistance…. This time has been unforgettable for me and was also a crucial importance for my thesis.

I can not mention all of you. *You* who have helped me for so many years. Here I want to express my warmest gratitude to all of *you*. I never forgot your support and assistance!!!

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