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Authors: Kauppinen, Jukka, and Väänänen, Veli-Matti

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Jukka Kauppinen & Veli-Matti Väänänen

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From the 1970s to the 1990s, changes in breeding waterfowl populations were monitored at 26 well-vegetated lakes in southern Finland. Extreme total population levels were found to differ by 40%, but between successive years fluctuations did not exceed 20%, the most unstable populations being garganey *Anas querquedula*, tufted duck *Aythya fuligula*, coot *Fulica atra* and pochard *Aythya ferina*. Multiple regression analysis was used to determine the effects of weather factors during wintering, spring and brood seasons on the variation in breeding waterfowl populations. The following weather factors were statistically significant in explaining fluctuations observed in four species; in garganey: spring temperature; in pintail *Anas acuta*: brood season temperature, winter severity in France and spring temperature; in goldeneye *Bucephala clangula*: winter severity in the Baltic and spring temperature; and in mallard *Anas platyrhynchos*: brood season temperature of the previous year. Mallard, teal *Anas crecca*, wigeon *Anas penelope* and goldeneye were shot in larger numbers than would be expected considering their respective proportions of the breeding waterfowl community. Hunting pressure on mallard, tufted duck and goldeneye was clearly higher in our study area than in other parts of Finland. Our results indicate that the level of hunting pressure in our study area may affect population densities of mallard.

Key words: hunting, waterfowl populations, weather factors, wetlands

Jukka Kauppinen, Kuopio Natural History Museum, Myhkyrinkatu 22, FIN-70100 Kuopio, Finland
Veli-Matti Väänänen, Department of Applied Zoology, P.O. Box 27 (Latokartanonkaari 5), FIN-00014 University of Helsinki, Finland - e-mail: veli-matti.vaananen@helsinki.fi

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During the 20th century, many waterfowl species of eutrophic lakes with a southern distribution have expanded into northern Europe (e.g. Kalela 1946, Onno 1965, Yarker & Atkinson-Willes 1971, von Haartman 1973). The expansion has been attributed to both climatic and environmental changes (e.g. Kalela 1949, von Haartman 1973). Although eutrophication of lakes has produced good habitats for many waterfowl species, the process may also have unfavourable effects on waterfowl habitats (e.g. von Haartman 1975, Nilsson 1985).

In North America, many researchers have investigated the relationship between waterfowl and environmental factors in pothole areas of northern prairies and parklands. Habitats in these areas have been shown to be unstable primarily due to climatic conditions: water level fluctuates widely both between years and during the breeding season, as do the amount of open water and mosaics of vegetation. The major reason for population and community changes has been found to be alteration and destruction of breeding habitats (e.g. Stoudt 1971, Trauger & Stoudt 1978, Boyd 1981, Leitch & Kaminski 1985, Bethke 1993). In contrast, waterfowl habitats in northern Europe may be fairly stable between years (Nummi & Pöysä 1993), and only slow changes in waterfowl communities occur (Pöysä 1989, Kauppinen 1995). Although it is evident that habitat factors can greatly affect the structure and long-term changes in waterfowl communities, other factors may play a more crucial role in the short-term dynamics of these communities (Pöysä 1984, Kauppinen 1995).

It has been suggested that weather factors may regulate short-term fluctuations of some waterfowl populations in northern Europe (e.g. von Haartman 1945, 1957, Grenquist 1965, Hildén 1966, Nilsson 1979, 1984), and these changes may also affect populations in the long term. For example, it is known that harsh weather in wintering areas can influence populations either directly by causing winter mortality or indirectly by lowering breeding success in the following season (Boyd 1964, Nilsson 1979, 1984, Andersen-Harild 1981). Spring temperatures may also prolong or shorten the spring migration period. Moreover, weather conditions in spring and summer may influence breeding success and, hence, also the breeding population in the following year.

Apart from weather factors, hunting may be the most important mortality factor affecting fledged waterfowl populations (e.g. Stoudt & Cornwell 1976, Rogers, Nichols, Martin, Kimball & Posphala 1979). Caithness, Williams & Nichols (1991) reported age-specific mortality in ducks; more young than old individuals are shot. Other studies have shown that the survival rates of ducks vary between years, and in theory, the increase in hunting mortality appears to be compensated for by a decrease in non-hunting mortality (Anderson & Burnham 1976, Rogers et al. 1979). However, few studies have focused on the role of hunting mortality in regulating waterfowl populations, especially waterfowl populations in Europe.

In this study, we investigate recent changes in the breeding waterfowl populations in the wetlands of the Finnish lake district, and examine the role of weather factors and hunting in explaining changes in waterfowl populations.

Study area, material and methods

Data were gathered from richly vegetated lakes in northern Savo, (63°N, 27°E) at the northern border of the Finnish lake district. Breeding waterfowl populations were censused in 26 lakes covering a total area of 22.4 km^2, once at the beginning of the 1970s (1972-1975), and then again at the beginning of the 1980s (1983-1985). Eleven of these lakes, in total covering 9.46 km^2, were monitored for waterfowl yearly during 1984-1995.

The area of the 11 lakes ranged within 18-226 ha, with most lakes comprising <100 ha (mean = 94.6 ha). Emergent vegetation covered 25-90% (mean = 54.1%) of the total lake area. Stands of sedge *Carex* sp. and horsetail *Equisetum fluviatile* were dominant, though reed *Phragmites australis* and bullrush *Schoenoplectus lacustris* were sometimes also found. Maximum water depth varied within 1-8 m, with depths of 1-2 m predominating (mean = 2.8 m). Transparency of the water usually varied between 0.5 and 1.5 m, and the pH-value of the water ranged within 6.0-7.0. Both the characteristics of the lake types examined and the methods used to measure the environmental parameters of the lakes are described in more detail in Kauppinen & Väisänen (1993).

Censuses of breeding waterfowl were conducted using the 'round count' method (Kauppinen 1980, 1983, Kauppinen, Koskimies & Väisänen 1991). Lakes were censused twice during the breeding season, i.e. 10-15 and 25-30 May. The criteria used to determine whether pairs were breeding or not are described in Kauppinen & Väisänen (1993). All censuses were performed by the authors, with the same lake always being monitored by the same person. When calculating coefficient of variation there may be more inherent stochastic variation in small samples than in large samples and therefore the results may only reflect natural noise (Helle & Mönkkönen 1986, see also Wiens 1981). To minimise this problem, coefficient of variation of densities (CV%) was not calculated for less abundant species, i.e. for species with mean densities of <1.5 pairs/km^2.

Wing and ringing data were used to indicate the hunting pressure on waterfowl in our study area. Species, age and sex composition of the annual hunting bag were determined from wing data using criteria described by Salminen (1983). Wing data accounting for ca 30% of the annual bag were obtained annually from hunters in a restricted area in the municipality of Maaninka in 1985-1989. In the area

Table 1. Indices of winter severity expressed as maximum ice cover in the Baltic Sea (%), mean temperatures in December - January in northern France, and mean temperatures (°C) in northern Savo in spring (pair season) and at the beginning of summer (brood season) during 1983-1995.

Winter severity	1983/84	84/85	85/86	86/87	87/88	88/89	89/90	90/91	91/92	92/93	93/94	94/95	
Baltic sea ice cover	45	85	80	96	35	12	16	29	16	17	49	16	
Mean temperature in northern France	4.1	0.9	4.6	1.5	5.5	5.3	4.9	3.5	2.8	5.4	5.9	5.5	
Mean temperatures in northern Savo	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995
15 April - 24 May	8.0	7.9	3.9	6.8	5.3	5.2	8.7	8.4	4.3	4.9	9.8	5.9	4.8
1 June - 10 July	15.1	14.4	14.0	17.1	14.1	17.2	17.1	14.5	14.7	15.3	11.8	14.7	

where the wings were collected, the breeding population of tufted duck was smaller than that observed for the whole study area, whereas populations of shoveler *Anas clypeata* and pintail were somewhat larger. Waterfowl ringing data covering 1970-1991 were obtained from the Finnish Museum of Natural History. Ringing data which were used to compare the recovery rate of young ducks (see hunting mortality, Table 6) in northern Savo with those in other parts of Finland were available for the years 1980-1991.

Maximum ice cover in the Baltic Sea, which is an important wintering area for mallard, tufted duck, goldeneye and coot, and the mean temperatures for December and January in northern France, which is an important wintering area for all other species, were used as indices of winter severity in the wintering areas of the waterfowl studied (Finnish Marine Research Institute, Météo-France). Mean temperatures in spring, i.e. 15 April - 24 May, were used as indices for determining the timing of spring, and mean temperatures in the beginning of the summer, i.e. between 1 June and 10 July, were used to indicate the conditions of the brood season (Kuopio Meteorological Station). Indices describing weather conditions are presented in Table 1. Winter severity indices and spring and summer temperature indices were uncorrelated (in all cases $R_s < 0.463$, $P > 0.05$), as were the indices indicating winter severity in the Baltic sea area and in France ($R_s = -0.366$, $P > 0.05$).

Multiple regression analysis was used to study if and how weather factors affect waterfowl populations. Indices of spring and summer temperatures of the previous year and winter severity were used as independent variables. The statistical significance of the models was tested using an analysis of variance. Goldeneye data were analysed without brood season temperature; as the goldeneye starts breeding at the age of 2-4 years (Dow & Fredga 1984), offspring

Table 2. Numbers of pairs of 12 waterfowl species occurring in 26 lakes covering a total area of 22.5 km^2 in southern Finland in the beginning of 1970s and 1980s. Differences in pair numbers was tested using G-test; level of significance: *** P < 0.001, ** = P < 0.01, * = P < 0.05.

Species	1970s	1980s	Level of significance
Great crested grebe	36	44	
Slavonian grebe	15	15	
Wigeon	59	108	**
Teal	125	193	***
Mallard	94	78	
Pintail	41	51	
Shoveler	24	48	*
Garganey	32	27	
Pochard	26	24	
Tufted duck	132	197	***
Goldeneye	39	61	*
Coot	11	42	***
Total	634	893	***

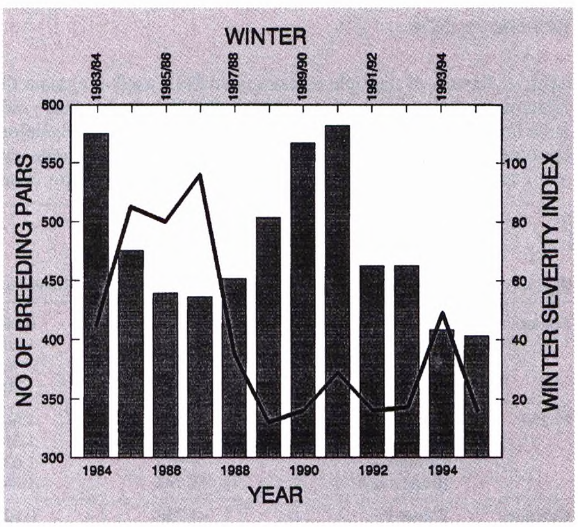

Figure 1. Total number of breeding pairs in the waterfowl population in 11 eutrophic wetlands of northern Savo, Finland, during 1984-1995. The solid line indicates the winter severity index for the Baltic Sea during the winters of 1983/84-1994/95.

Table 3. Densities of 14 waterfowl species expressed as pairs/km^2 (range, mean and standard deviation), coefficients of variations in densities (CV%) and Spearman rank correlations (R_s) of densities and year in 11 wetlands covering a total area of 9.46 km^2 during 1984-1995. Level of significance: ***P < 0.001, **P < 0.01, *P < 0.05.

Species	Range	Mean	SD	CV%	R_s	Level of significance
Great crested grebe	3.9 - 5.6	4.55	0.52	11.4	-0.413	
Slavonian grebe	0.1 - 0.5	0.26	0.12	-	0.116	
Red-necked grebe	0.0 - 0.1	-	-	-	-	
Whooper swan	0.1 - 0.5	0.24	0.15	-	0.921	**
Wigeon	3.2 - 8.0	5.87	1.19	20.3	0.031	
Teal	5.9 - 13.0	8.63	2.36	27.4	-0.529	
Mallard	3.5 - 5.9	4.52	0.91	20.1	-0.172	
Pintail	2.0 - 5.2	3.63	1.01	27.8	0.350	
Shoveler	2.7 - 5.3	3.79	0.67	17.7	0.305	
Garganey	1.0 - 2.6	1.62	0.57	35.2	-0.299	
Pochard	0.8 - 2.8	1.81	0.59	32.6	-0.902	***
Tufted duck	2.7 - 10.5	6.52	2.24	34.4	-0.867	**
Goldeneye	2.3 - 4.4	3.43	0.70	20.4	0.712	*
Coot	3.6 - 9.2	5.86	1.97	33.6	0.322	

production does not affect breeding numbers until after two or more years, therefore, the results for goldeneye consist of breeding females only.

Results

Changes in waterfowl populations

In the beginning of the 1980s, the total waterfowl population was ca 40% higher than at the beginning of the 1970s (Table 2). Populations of most species increased during this decade; the increase was significant for six species (see Table 2). Differences between extreme population levels during the 1980s and 1990s was 30%, and between successive years not above 20%.

We chose data from 12 successive years (1984-1995) for a more detailed analysis. During this period the wintering conditions of waterfowl clearly varied, but most of the winters in the Baltic Sea area were milder than average (Finnish Marine Research Institute). After the severe winter of 1984/85 followed by a cool spring, the total population decreased by 16%, and by 26% from the highest level recorded in 1984 to the lowest level recorded in 1986. The winter of 1986/87 was also severe, thus causing the total population to remain at a low level within our study area. The situation did not improve until spring 1989; the mean brood size of the previous summer was high (V-M. Väänänen, unpubl. data), and the previous winter was mild (Fig. 1, see Table 1).

Table 4. Results of multiple regression analysis used to explain the importance of weather factors (wintering, spring and brood seasons) affecting variation in breeding mallard, pintail, garganey and goldeneye populations during 1985-1995. The final model has been calculated including only significant independent variables. Explanations: Winter B = winter severity index in the Baltic Sea, Winter Fr = winter severity index in northern France, Spring x = spring temperature in year x, Spring x-1 = Spring temperature in year x-1, Brood s. x-1 = brood season temperature in year x-1 (see Methods for details).

							Final Model			
							Analysis of variance			
Species	Variable	DF	Parameter estimate	Standard error	T	P	DF	F-value	P	Adjusted R^2
Mallard	Winter B	1	-0.075	0.065	-1.244	0.254	1	11.384	0.007	0.486
	Spring x	1	0.290	1.102	0.263	0.800				
	Spring x-1	1	1.414	0.963	1.468	0.185				
	Brood s. x-1	1	4.012	1.300	3.089	0.018				
Pintail	Winter Fr	1	5.565	1.667	3.338	0.012	3	3.278	0.080	0.383
	Spring x	1	-4.136	1.519	-2.723	0.030				
	Spring x-1	1	1.955	1.039	1.881	0.102				
	Brood s. x-1	1	5.787	1.686	3.432	0.011				
Garganey	Winter Fr	1	-1.250	0.627	-1.994	0.086	1	20.178	0.001	0.636
	Spring x	1	2.616	0.571	4.580	0.003				
	Spring x-1	1	-0.673	0.391	-1.723	0.129				
	Brood s. x-1	1	0.297	0.634	0.469	0.654				
Goldeneye	Winter B	1	-0.190	0.044	-4.320	0.002	2	10.169	0.005	0.625
	Spring x	1	-1.919	0.685	-2.812	0.020				

Table 5. Proportions (%) of 10 waterfowl species of the total breeding population, and their respective proportions (%) of the hunting bag in August, September-November and in total during 1985-1989. The proportion of juveniles in the bag is given separately and the total number of observations is given in parenthesis.

	Mallard	Teal	Wigeon	Shoveler	Pintail	Garganey	Tufted duck	Pochard	Goldeneye	Coot
Breeding population	10.3 (232)	20.2 (454)	12.5 (280)	7.8 (174)	7.1 (159)	3.5 (79)	19.0 (427)	4.6 (103)	6.4 (144)	8.5 (191)
Hunting bag										
August	23.6 (393)	30.8 (504)	13.4 (223)	4.9 (82)	5.0 (84)	2.8 (47)	4.3 (72)	2.0 (33)	10.3 (172)	2.2 (36)
September-November	41.2 (361)	14.7 (129)	19.5 (171)	2.2 (19)	2.0 (17)	0.1 (1)	5.5 (48)	2.1 (18)	6.8 (60)	5.9 (52)
Total	29.8 (754)	25.0 (633)	15.5 (394)	4.0 (101)	4.0 (101)	1.9 (48)	4.7 (120)	2.0 (51)	9.2 (232)	3.5 (88)
Juveniles (%)	86.7	80.9	87.5	95.0	89.0	91.7	90.0	100.0	98.3	-

Populations of whooper swan *Cygnus cygnus* and goldeneye showed a statistically significant increasing trend, whereas populations of pochard and tufted duck showed decreasing trends (Table 3). Populations of garganey, tufted duck, coot and pochard were found to be the most unstable (see coefficients of variation in Table 3).

Weather factors affecting species populations

Our multiple regression model examining the relationship between the number of pairs and weather factors during wintering, spring and brood seasons was statistically significant for garganey, mallard and goldeneye and almost significant for pintail (Table 4), but not significant for all other species.

In garganey, spring temperatures explained most of the fluctuation: in warm springs numbers of garganey were highest. In mallard, cold brood seasons negatively affected the population and explained most of the fluctuations (see Table 4). In goldeneye, both severe winters in the Baltic and warm springs had negative effects on breeding numbers. Both winter severity in France and cold brood seasons in our study area had negative effects on the numbers of pintail. In cold springs pintails were found to be most abundant.

Hunting

Mallard, teal, wigeon and goldeneye were shot in higher numbers than would be expected considering their respective proportion of the breeding communities (Table 5). All in all, a statistically significant difference was observed between proportions in the breeding duck community and in the hunting bag (G-test, $G = 706.9$, $P < 0.001$).

For the most hunted duck species, i.e. mallard, teal and wigeon, 81-87% of the hunting bag consisted of young individuals (see Table 5). The corresponding figures for other duck species were 90-100 %. The proportion of bagged adults was larger in dabbling ducks (14 %) than in diving ducks (<4%) ($G = 35.8$, $P < 0.001$). Only a small proportion (<2%) of the hunting bag consisted of adult goldeneyes.

The hunting pressure on mallard, tufted duck and goldeneye was clearly higher in our study area than elsewhere in Finland (Table 6). According to Finnish ringing data (young ringed), 77.5% of the mallards shot during 1970-1991 originated from Finland.

Discussion

Weather factors affecting populations

Fluctuations in total population levels may be related to weather factors, especially through the wintering success of the species wintering in the North. In Europe, there was a period of mild winters in the beginning of the 1970s; at that time, the wintering

Table 6. Recovery rates of young wigeons, mallards, pintails, shovelers, tufted ducks and goldeneyes banded in northern Savo and 'Other parts of Finland' during 1980-1991, and subsequently shot in Finland. Differences in recovery rates between northern Savo and 'Other parts of Finland' (mallard, tufted duck, goldeneye and total) were tested using G-test; *** P < 0.001.

	Northern Savo		Other parts of Finland		
Species	Nos ringed	Nos recovered	Nos ringed	Nos recovered	G-test
Wigeon	55	7 (12.7%)	110	5 (4.6%)	
Mallard	79	21 (26.6%)	528	32 (6.1%)	G = 20.8 ***
Pintail	71	7 (9.9%)	41	3 (7.3%)	
Shoveler	63	8 (12.7%)	47	2 (4.3%)	
Tufted duck	184	36 (19.8%)	954	17 (1.8%)	G = 62.0 ***
Goldeneye	3364	489 (14.5%)	3148	115 (3.7%)	G = 207.5***
Total	3816	568 (14.9%)	4828	174 (3.6%)	G = 298.3***

populations of many waterfowl species increased (e.g. Rüger, Prentice & Owen 1986, Monval & Pirot 1989).

In the beginning of the 1980s, the total breeding waterfowl population in our study area was ca 40% higher than in the beginning of the 1970s. Our census results for the 1970s were obtained before the effects of mild winters could be seen in populations. The second census was performed mainly during the population peak of the 1980s. After the severe winters of the 1980s, the total population decreased by ca 30%.

In our study, we analysed population fluctuations of different waterfowl species in the 1980s and 1990s in more detail. With the exception of several winters in the 1980s, winters were generally mild in Europe during this period. Nevertheless, winter temperature explained population fluctuations in the goldeneye.

Spring temperature is known to cause population fluctuations in southern/northern species at the limit of their distribution area (in waterfowl, see e.g. Siira & Eskelinen 1983). In our study area, the annual breeding populations of garganey and pintail are primarily affected by spring temperatures, with southern garganey being found to be most abundant in warm springs and northern pintail in cold springs.

Early onset of spring may be important to waterfowl populations. After late springs, local hunting of early-arriving autumn migrants such as shoveler, pintail, garganey and wigeon may be more intense and larger proportions of ducklings may be less developed when the hunting season begins. In our study area, only late broods of pintail and shoveler were observed to be in their natal area at the beginning of the hunting season on 20 August (Väänänen 1996). These results indicate that after late springs ducks may be more vulnerable to local hunting.

In North America, the most important waterfowl production areas are very unstable (Evans & Black 1956, Eiserlohr 1969, Posphala, Anders & Henny 1974). In these areas, brood production is significantly correlated with the size of the following year's breeding population (Reynolds & Sauer 1991). Variation in the quality, and especially in the number of August wetlands of brood production areas are known to bring about a strong annual fluctuation in the brood production (Leitch & Kaminski 1985, Sutherland 1991). In contrast, the quality of wetlands in northern Europe does not change dramatically, neither within nor between successive years (e.g. Nummi & Pöysä 1993), and thus are not very likely to cause considerable variation in brood production. Brood production may also occasionally play an important role in the fluctuations of populations in our study area but, unfortunately, we do not have the data to examine this in detail.

Hunting

The total effect of hunting (compensatory or additive mortality) on breeding populations is difficult to evaluate, because waterfowl hunting occurs in the breeding, gathering, migrating and wintering areas. Mortality due to hunting also fluctuates between years (Rogers et al. 1979); for example, in severe winters, the hunting pressure may be high, because the ice cover forces ducks to move to areas with limited open water, thus making them more vulnerable to hunting (e.g. Grenquist 1965, Ogilvie 1981).

In our study area, the hunting pressure was most heavy on mallards (see also Pirkola & Lindén 1972, V-M. Väänänen, unpubl. data) and might have had adverse effects on breeding numbers. For example, in 1986-1988, the densities of the mallard populations in our study area were clearly below those observed in other parts of Finland, such as Satakunta, Päijät-Häme, southeastern Finland and southern Lapland (E. Lammi & R.A. Väisänen, unpubl. data). However, densities of the southern duck species, garganey and shoveler, were higher in our study area than in other parts of Finland (E. Lammi & R.A. Väisänen, unpubl. data). Thus, the quality of the habitats does not explain the low mallard densities in our study area.

Furthermore, in our study area, unlike in other areas of Finland, the rapid increase in the waterfowl populations during 1987-1991 was not observed for mallard (Spearman $R_s = 0.100$, $P > 0.1$) even though an overall increase in total waterfowl numbers was evident (see Fig. 1). Conversely, during the same period in the Päijät-Häme area of southern Finland (E. Lammi, unpubl. data), the mallard population showed a steady increase (Spearman $R_s = 1.000$, $P < 0.001$). Similar increasing trends for mallards were also observed by H. Pöysä (unpubl. data) in southeastern Finland (Spearman $R_s = 0.670$, $P < 0.1$), and are further corroborated by the findings of the nationwide monitoring program of breeding waterfowl in Finland showing an increasing trend in mallard numbers during the same period (Pöysä, Lammi, Väisänen & Wikman 1993). During 1987-1991, the annual bag of mallard in our study area increased (Spearman $R_s = 0.900$, $P = 0.072$); this result, however, was only marginally significant possibly due to a study period of only five years. These findings seem to indicate that local hunting could have had a remarkably adverse effect on the densities of mallard breeding populations in our study area.

The proportion of adult females bagged in our study area is, except for teal, smaller than that reported in Denmark (Clausager 1987, 1988, 1989). In Denmark, most hunting of adult diving ducks is concentrated in wintering areas, where the proportion of, for example, adult goldeneye in the bag may exceed 50% (Clausager 1987, 1988, 1989), whereas in our study area adult goldeneye accounted for less than 2% of the bag. The survival of breeding females is very important because experienced breeders have considerably higher breeding success than first-time breeders (e.g. Owen & Black 1990).

Even though large numbers of goldeneye were shot, the breeding population of this duck species seemed to increase. During our study, the bag of goldeneye mainly consisted of young ducks (see Table 5). This is due to the fact that adult females migrate to the Finnish sea area in order to moult prior to the opening of the Finnish hunting season (Runko & Väänänen 1989), and that males typically leave the breeding areas before the middle of June.

Goldeneye start breeding at the age of 3-5 years (Fredga & Dow 1984). Because of this late breeding age, survival of old females is crucial for the stability of the population. In Sweden, an annual survival rate of 71.8% has been reported for adult goldeneye females (Fredga & Dow 1984); in our study area approximately 81% of breeding females have been observed to breed again (Runko & Väänänen 1989). Thus, the exceptionally high survival rate of breeding females evidently contributed to the increase in the goldeneye population.

Our ringing data indicate that the hunting pressure on mallard, tufted duck and goldeneye is stronger in our study area than in other parts of Finland. In many cases, hunting is likely to have an adverse effect only in years when weather conditions are unfavourable (e.g. late springs and severe winters).

Garganey, shoveler and pintail are early autumn migrants, as demonstrated by the banding and bag data (Mihelsons, Mednis & Blums 1986, Clausager 1987, 1988, 1989, Väänänen 1996, V-M. Väänänen, unpubl. data). In contrast to the findings of Siira & Eskelinen (1983) from the Liminka Bay wetland in western Finland, our data suggest that local hunting hardly affects the breeding populations of these early migrating species in our study area.

Concluding remarks

In summary, fluctuations of waterfowl populations appear to reflect many interacting factors. Weather is an important factor affecting breeding numbers. In pothole areas of Northern America, habitat alteration and destruction are crucial factors influencing fluctuations. In northern Europe, the conditions of habitats do not generally change so dramatically.

Expansion of tall vegetation, such as *Salix* and *Phragmites*, into open sedge stands and shore meadows affects populations of certain wetland species (e.g. von Haartman 1975, Soikkeli & Salo 1979). Most dabbling ducks have been shown to favour open habitats in our study area (Kauppinen 1993). These species have not shown parallel population trends that can be easily explained by such habitat alterations. In our study area the shores of many eutrophic lakes are still pastured, with cultivated fields in the near vicinity, so the features of landscape are still open. In contrast, the shores of many mixotrophic lakes have never been pastured, and their habitat structure has remained fairly stable for a long time.

Predation, especially nest predation, is an important factor affecting the production of offspring in birds (e.g. Lack 1968, Wiens 1989). In our study area, nest predation of *Aythya* species is high outside gull colonies, whereas inside colonies gulls successfully protect all nests (Väänänen in press). Decreasing numbers of breeding black-headed gulls *Larus ridibundus* may play an important role also in the decreasing population trends of tufted duck and pochard (J. Kauppinen & V-M. Väänänen, unpubl. data).

In our study area, the total population of all waterfowl species was in a phase of increase during the 1970s, and reached its peak level at the beginning of the 1990s. Nevertheless, the mallard population level was lower in the 1990s. We suggest that hunting has had a negative effect on the densities of the breeding mallard population.

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