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Spring phenology, latitude, and the timing of breeding in two migratory ducks: implications of climate change impacts

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We studied whether the timing of hatching in the mallard (*Anas platyrhynchos*) and the common goldeneye (*Bucephala clangula*) is associated with the timing of lake ice break-up (a local climate index) and the North Atlantic Oscillation (NAO, a large-scale climate index), and if the strength of these associations differ between southern and northern populations of the species. In both species, the date of hatching was associated with the date of ice break-up; more clearly so in northern Finland than in southern Finland. The date of hatching was neither associated with the winter NAO (December–March) nor with the spring NAO (March–May). There was no difference between southern and northern populations in terms of the annual differences (in days) between the timing of ice break-up and the timing of hatching. However, in both species, this difference decreased with increasing lateness of the spring in the north, the corresponding trend being less clear in the south.

Introduction

Global climate change has inspired an enormous amount of research on its possible impacts on the ecology of species (reviews in McCarty 2001, Walther *et al*. 2002, Parmesan & Yohe 2003, Crick 2004, Møller *et al*. 2004, Robinson *et al*. 2005). One aspect that has received considerable attention is the effect of spring climate warming on the arrival dates of migratory avian species (Lehikoinen *et al*. 2004, Jonzén *et al*. 2006, Rainio *et al*. 2006 and references therein). For example, Lehikoinen *et al*. (2004) found that a high number of Eurasian migratory species have shown earlier spring arrival towards the end of the 20th century, the average change of the first arrival date being 0.37 days/year over all species and sites studied. Similarly, Butler (2003) found that the spring arrival of birds in the northeastern United States advanced on average by 8 days from the first to the second half of the 20th century. In both of these analyses the change in spring arrival date has been coupled with global warming. An obvious question then is how well arrival date and the start of breeding are correlated. Rapidly accumulating evidence suggests that warmer springs advance breeding phenology in many species (Dunn & Winkler

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1999, Both *et al.* 2004, Pearce-Higgins *et al.* 2005, Torti & Dunn 2005) but this is not always the case and, in general, the response of different life-history parameters to climate change may be complex (Brown *et al.* 1999, Dunn 2004, Visser *et al.* 2003, Both *et al.* 2005, Weatherhead 2005, Laaksonen *et al.* 2006).

When assessing climate change impacts, surprisingly little attention has been paid to the fact that critical life-history parameters vary substantially from one breeding episode to another. For example, the breeding phenology of birds varies considerably among years (Fredga & Dow 1983, Järvinen 1993), and considering this variation, one may question the fitness consequences of relatively small long-term changes in timing due to global warming. Furthermore, the ability of individuals to respond to climate warming may vary over the geographical range of a given species, especially between southern and northern populations (Sanz 2003, Ahola *et al.* 2004, Both *et al.* 2004). To understand and to be able to predict the impacts of climate change on the demography and population dynamics of a given species we need to know the baseline annual variation and the response of critical life-history parameters to short-term climate variation in different parts of the species' range.

In this article we focus on the among-year variation in the timing of hatching in two geographically distant populations of two migratory duck species, the mallard (*Anas platyrhynchos*) and the common goldeneye (*Bucephala clangula*). Both species are short-distance migrants and relatively early breeders among boreal waterfowl but represent different nesting tactics, the mallard being a ground-nesting and the common goldeneye a cavity-nesting species. The timing of breeding is a life-history parameter that has major fitness consequences in birds (Wiggins *et al.* 1994, Verboven & Visser 1998 and references therein), including both of our study species (Dzus & Clark 1998, Milonoff *et al.* 1998). Also, nest site use plays an important role in the evolution of avian life-history traits (Martin 1995). Considering waterfowl, local ice conditions in the spring should play an important role in the timing of breeding (Väisänen 1974, Fredga & Dow 1983, Pehrsson 1984). In addition, the availability of snow-free nesting ground may constrain the start of egg laying in ground nesting ducks, as has been suggested for the oldsquaw (*Clangula hyemalis*) by Pehrsson (1986); this constraint should not apply to ducks that nest in tree cavities. During the last few decades the date of ice break-up has became earlier at many lakes around the northern hemisphere (Anderson *et al.* 1996, Magnuson *et al.* 2000, Korhonen 2005), making the study of global change impacts on duck populations particularly important. Still, almost nothing has been done with waterfowl in the context of global change. For instance, recent exhaustive reviews of studies addressing global climate change impacts on avian breeding ecology and other ecological aspects do not include a single article of waterfowl (Møller *et al.* 2004, Robinson *et al.* 2005). We are aware of two recent waterfowl studies published after these reviews. Lehikoinen *et al.* (2006) studied the effects of winter climate on subsequent breeding success in the common eider (*Somateria mollissima*) in southwestern Finland, and Sedinger *et al.* (2006) studied effects of the El Niño-Southern Oscillation on the winter distribution (Mexico) and nesting probability (Alaska) of the black brant (*Branta bernicla nigricans*).

It has been shown that ice break-up in Scandinavian lakes is associated with the North Atlantic Oscillation (NAO; Blenckner *et al.* 2004), a large-scale climate index (*see* Hurrell *et al.* 2003 for an overview of the NAO), and a recent analysis suggests that the timing of especially early-phase spring migration in waterfowl is associated with the NAO (Rainio *et al.* 2006). The impacts of the NAO on ecological processes extend across many terrestrial and aquatic ecosystems (reviews in Ottersen *et al.* 2001, Blenckner & Hillebrand 2002, Stenseth *et al.* 2002). As there has recently been interest in exploring the relative importance of local weather variables and large-scale climate indices in explaining and predicting ecological processes (*see* Hallett *et al.* 2004, Stenseth & Mysterud 2005), we compared the performance of local weather and large-scale climate in explaining the timing of breeding in our study system. Our specific questions are: (1) How well is the timing of hatching in the two duck species associated with the timing of ice break-up (local weather) and the large-scale NAO index? (2) Does the strength of this association differ between southern and northern populations of the species? (3) Do the species, representing different nesting tactics, show differences in the association between spring phenology and the timing of hatching? Finally, we discuss the implications of our findings in terms of climate change impacts.

Material and methods

Duck data

We used data from national Finnish brood counts organized by the Finnish Game and Fisheries Research Institute between 1989 and 2006 (*see* Pöysä *et al*. 1993, Pöysä 1998). The brood counts used in the present study were carried out by two trained persons, one in southern Finland (mean latitude of census sites 62°12´N; mean number of census sites per year 45, range 17–49; brood counts started in 1989) and the other in northern Finland (mean latitude of census sites 67°12´N; mean number of census sites per year 45, range 17–59; brood counts started in 1990). The brood counts were done usually in early July in southern Finland and close to mid July in northern Finland. In the field, the census maker recorded the age class, the number of ducklings and the date of observation for each brood. The seven age classes of Pirkola and Högmander (1974; i.e., Ia-c, IIa-c, III; a combination of Gollop & Marshall 1954, and Linkola 1962) were used to estimate brood age based primarily on plumage development. The duration of each age class is 7 days in the mallard and 7.5 days in the common goldeneye (Pirkola & Högmander 1974). We used the brood-specific information to back-calculate the hatching date for each brood, assuming that all broods were of mid age within the age class when observed. For example, a Ic mallard brood observed on 1 July was estimated to have hatched 7 + 7 + 3.5 days earlier, i.e. on 14 June. Our preliminary analyses, focusing on the effect of spring phenology on the occurrence of unfledged birds at the beginning of the hunting season, supported the view that this method of estimating hatching date is appropriate for duck broods in general (Oja & Pöysä 2005, *see* also Toft *et al*. 1984, Elmberg *et al*. 2005). In line with this, Clark *et al*. (1987) found that the distribution of estimated hatching dates of mallard broods observed during routine brood counts (exact hatching date not known) in Loch Leven, Scotland, did not differ from that of the broods of radio-tagged females (exact hatching date known). Furthermore, Blais *et al*. (2001) found significant differences between male and female pintail (*Anas acuta*) ducklings in the growth of different morphometric measurements, including body mass, but not in plumage growth. These authors also concluded that plumage appearance is a valuable source of information to determine duckling age, and may allow even a more accurate determination of age than, for example, the seven age classes by Gollop and Marshall (1954). For both regions and for both species we included only years when at least five broods per species were seen in the counts (Table 1), and calculated the mean hatching date to measure the timing of breeding. Hatching dates are given as days from 1 April.

Table 1. Number of broods per year in the mallard and common goldeneye in southern and northern Finland. A hyphen (–) indicates that the sample size was not sufficient in that year (fewer than 5 broods; note that brood counts started in 1990 in northern Finland).

	Southern Finland		Northern Finland	
	Mallard	Common goldeneye	Mallard	Common goldeneye
1989	8	13	No data	No data
1990	12	15	–	13
1991	22	26	–	9
1992	16	19	–	–
1993	18	17	6	42
1994	9	11	17	44
1995	11	20	13	67
1996	15	22	9	49
1997	11	10	7	62
1998	10	19	9	59
1999	5	16	–	32
2000	10	22	8	29
2001	5	12	9	27
2002	7	12	5	25
2003	–	14	8	32
2004	12	22	–	39
2005	11	9	11	23
2006	21	11	7	23

Spring phenology and NAO data

Ice break-up dates from three lakes in southern Finland (Jääsjärvi, Simpele and Haukivesi; mean latitude 61°54´N) and three lakes in northern Finland (Unari, Kutuniva and Ounasjärvi; mean latitude 68°7´N) were used to index local spring phenology between 1989–2006. The data were obtained from the Finnish Environment Institute. Ice break-up dates from 1989 and 1990 were missing from Lake Haukivesi. We replaced the missing values with values estimated from a multiple regression model using the ice break-up dates from the nearest lake as predictor (i.e., Lake Simpele explained (r^2 = 0.673) the ice break-up date in Lake Haukivesi well). In general, the dates of ice break-up are strongly correlated between lakes within a region (Korhonen 2005), and also between distant regions in Scandinavia (Blenckner *et al*. 2004; *see* also below). By using the lake-specific values we calculated the mean ice break-up date for the two regions, i.e. the local index of spring phenology. Based on information provided by Korhonen (2005) of the relationship between latitude and the date of ice break-up (i.e., ice break-up date is delayed northward by 4 days per 100 km) we calibrated the ice break-up dates for the mean latitude of the census sites where the duck data came from. Ice break-up dates are given as days from 1 April.

Earlier studies found that the winter (December–March) NAO index is correlated both with the ice break-up date (Blenckner *et al.* 2004) and the timing of spring migration in waterfowl (Rainio *et al.* 2006). Hence, we used the winter NAO index (obtained from the website of Climate Research Unit at the University of East Anglia at http://www.cru.uea.ac.uk/data/nao.htm; same source as used by Rainio *et al.* 2006) to measure the winter time global climate. In general, negative values (< –1.0) are associated with cold winters and positive values (> 1.0) with mild winters (Hurrell 1995). Note that, differing from Hurrell (1995), the NAO indices used here are calculated as the normalized air pressure difference between Gibraltar and SW Iceland (*see* the website above for further information). The winter NAO index was calculated as the mean of the monthly values December–March provided at the website. Because ice break-up usually takes place in early May in southern Finland and in late May in northern Finland (Korhonen 2005, *see* also Blenckner *et al.* 2004), and egg laying of the mallard and common goldeneye started at about the same time or a bit later, we also calculated the corresponding NAO index for the boreal spring months March–May (spring NAO). The spring season also displays considerable NAO variability (*see* Hurrell *et al.* 2003: p. 10) and may have important consequences for ecological processes. For example, Blenckner and Chen (2003) found that the timing of ice break-up and spring phytoplankton bloom in a Swedish lake were correlated with the March value of the winter NAO index.

Statistical analyses

We used the non-parametric Kendall rank correlation (τ) to test for the association between any two variables. Many earlier studies used parametric correlation or regression to study the association between bird migration and nesting phenology and different climate variables. We prefer non-parametric correlation tests because our data did not meet all the assumptions of parametric tests. We also ran all the correlation tests by using parametric Pearson correlation; the test results (not shown here) were qualitatively similar to those derived from the Kendall rank correlation test. In cases in which there was a rather strong correlation ($P < 0.10$) between the date of ice break-up (local climate) and the two NAO indices (large-scale climate), we also calculated Kendall partial rank correlations to study whether local climate or large-scale climate independently affect the timing of hatching (Kendall partial rank correlation coefficients calculated according to Siegel & Castellan 1988). The Wilcoxon paired-sample test was used to test for differences in any variable between the two regions, southern and northern Finland. Difference between the regions in terms of the strength of association between any two variables was tested with analysis of covariance (ANCOVA) using the General Linear Model (GLM) procedure in SYSTAT 10.0 and rank-transformed data (*see* Conover & Iman 1981). Specifically, we tested whether the interaction between region and a climate variable was significant in explaining a given dependent variable. In these analyses, region was included as a categorical variable and the climate variable as a covariate (details given in the Results). All statistical analyses were conducted using SYSTAT 10.0. All significance levels are for two-tailed tests and according to Siegel and Castellan (1988) or SYSTAT.

Results

Spring phenology and NAO

The dates of ice break-up were consistently earlier in southern Finland than in northern Finland (region mean, minimum and maximum: south, 34.9, 24.0, 42.7; north, 52.5, 41.3, 66.7) but were correlated between the two regions ($\tau = 0.404$, $P = 0.019$, $n = 18$). The dates of ice break-up in the two regions did not correlate significantly with the winter NAO index; both trends, however, were negative (Table 2). A similar pattern emerged with spring NAO, except that the correlation between the date of ice break-up and the spring NAO index was stronger and significant in northern Finland. The dates of ice break-up in the two regions and the spring NAO index did not show any trend within the study period from 1989 to 2006 but the winter NAO index decreased, i.e. winters became colder towards the end of the study period (Table 2).

Timing of hatching in relation to spring phenology and NAO

The timing of hatching varied substantially in both species (Figs. 1 and 2) but did not show any trend over the study period (Table 3). In both species the timing of hatching was significantly associated with the date of ice break-up in northern Finland, the corresponding associations being weaker, and not significant for the common goldeneye in southern Finland (Table 3, Figs. 1 and 2). By contrast, the timing of hatching was not associated with the two NAO indices (winter and spring), though the correlation between the timing of hatching and the spring NAO index was rather strong in northern Finland in both species.

Partial correlation tests confirmed that the date of ice break-up was more important than the two NAO indices in explaining the timing of hatching (*see* Material and methods; mallard, southern Finland: date of ice break-up, $\tau = 0.348$, $P = 0.051$, winter NAO held constant; winter NAO, $\tau = -0.179$, $P = 0.317$, date of ice break-up held constant; mallard, northern Finland: date of ice break-up, $\tau = 0.629$, $P = 0.004$, spring NAO held constant; spring NAO, $\tau = -0.069$, $P = 0.757$, date of ice break-up held constant; common goldeneye, southern Finland: date of ice break-up, $\tau = 0.276$, $P = 0.110$, winter NAO held constant; winter NAO, $\tau = -0.014$, $P = 0.936$, date of ice break-up held constant; common goldeneye, northern Finland: date of ice break-up, $\tau = 0.409$, $P = 0.027$, spring NAO held constant; spring NAO, $\tau = -0.136$, $P = 0.465$, date of ice break-up held constant). The strength of the association between the timing of hatching and the date of ice break-up (*see* above) did not differ significantly between southern and northern Finland (*see* Material and methods; ANCOVA: interaction term region × ice

Table 2. Kendall rank-order correlation coefficients (τ) among ice break-up dates, NAO indices and year in 1989–2006. Variables are explained in the Material and methods.

		τ	n	P
Ice break-up, south *vs.*	winter NAO	–0.304	18	0.078
	spring NAO	–0.277	18	0.107
	year	0.079	18	0.646
Ice break-up, north *vs.*	winter NAO	–0.131	18	0.447
	spring NAO	–0.420	18	0.015
	year	–0.013	18	0.936
Winter NAO *vs.*	year	–0.464	18	0.007
Spring NAO *vs.*	year	–0.216	18	0.211

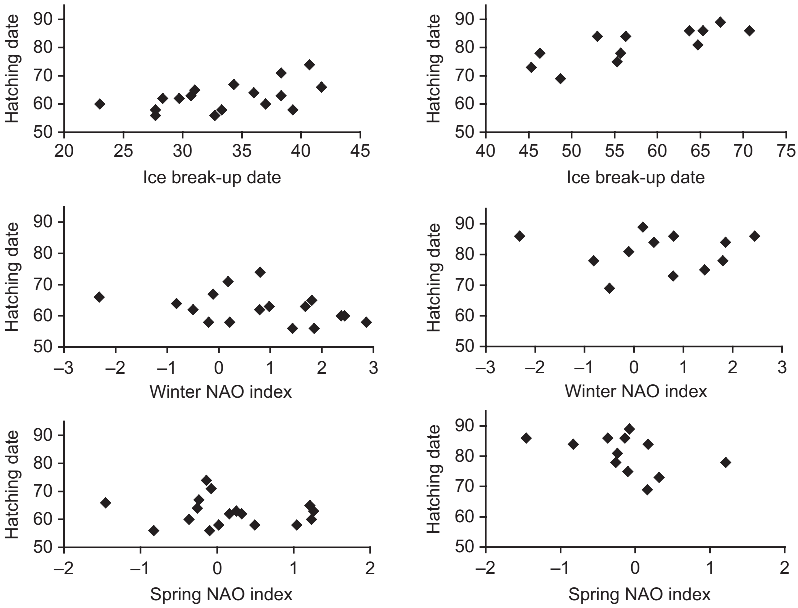

Fig. 1. Hatching date of the mallard in relation to ice break-up date, winter NAO index and spring NAO index in southern (left column) and in northern (right column) Finland. Corresponding test statistics are given in Table 3 and in the text. Dates are given as days from 1 April. Variables are explained in the Material and methods.

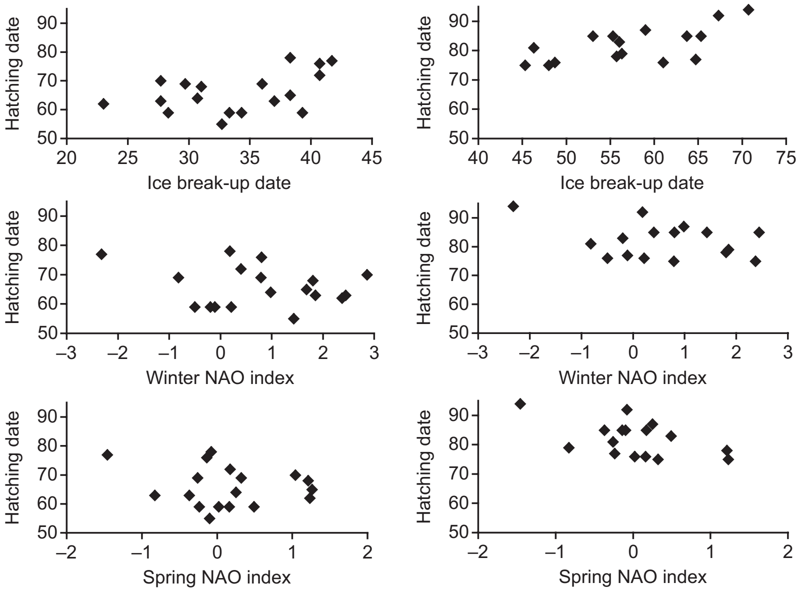

Fig. 2. Hatching date of the common goldeneye in relation to ice break-up date, winter NAO index and spring NAO index in southern (left column) and in northern (right column) Finland. Corresponding test statistics are given in Table 3 and in the text. Dates are given as days from 1 April. Variables are explained in the Material and methods.

break-up date; mallard, $F_{1,25} = 0.839$, $P = 0.368$; common goldeneye, $F_{1,30} = 0.156$, $P = 0.695$).

The timing of hatching was earlier in southern Finland than in northern Finland in both species (Table 4) but the hatching dates tended to correlate between the two regions (mallard: $\tau = 0.404$, $P = 0.084$, $n = 11$; common goldeneye: $\tau = 0.366$, $P = 0.048$, $n = 16$). Considering the annual difference (in days) between the timing of ice break-up and the timing of hatching, there was no statistically significant difference between southern and northern Finland in the timing of hatching in relation to spring phenology (Table 4: difference between hatching date and ice break-up date). However, in both species the annual difference between the date of ice break-up and the date of hatching decreased with increasing lateness of the spring (i.e., date of ice break-up) in northern Finland (mallard: $\tau = -0.462$, $P = 0.037$, $n = 12$; common goldeneye: $\tau = -0.504$, $P = 0.007$, $n = 16$), the corresponding trend being similar but not significant in southern Finland (mallard: $\tau = -0.307$, $P = 0.085$, $n = 17$; common goldeneye: $\tau = -0.192$, $P = 0.267$, $n = 18$). The difference in the strength of this trend was not statistically significant between southern and northern Finland (*see* Material and methods; ANCOVA: interaction term region × ice break-up date; mallard: $F_{1,25} = 1.018$, $P = 0.323$; common goldeneye: $F_{1,30} = 1.312$, $P = 0.261$).

Table 3. Kendall rank-order correlation coefficients (τ) between hatching date and other variables in the mallard and common goldeneye in southern and northern Finland. Corresponding data, except for the relationships hatching dates *vs.* year, are depicted in Figs. 1 and 2. Years included in the analyses are given in Table 1. Variables are explained in the Material and methods.

		τ	n	P
Mallard				
Hatching date, south *vs.*	ice break-up, south	0.403	17	0.024
	winter NAO	–0.279	17	0.119
	spring NAO	–0.053	17	0.764
	year	0.219	17	0.222
Hatching date, north vs.	ice break-up, north	0.678	12	0.002
	winter NAO	0.110	12	0.617
	spring NAO	–0.331	12	0.134
	year	–0.173	12	0.435
Common goldeneye				
Hatching date, south *vs.*	ice break-up, south	0.285	18	0.099
	winter NAO	–0.074	18	0.667
	spring NAO	–0.060	18	0.726
	year	–0.007	18	0.968
Hatching date, north *vs.*	ice break-up, north	0.483	16	0.009
	winter NAO	–0.104	16	0.575
	spring NAO	–0.311	16	0.093
	year	–0.035	16	0.849

Table 4. Timing of breeding (as days from 1 April) and the difference (in days) between hatching date and ice break-up date in the mallard and common goldeneye in southern and northern Finland. Wilcoxon paired-sample test statistics (T) are also given for the comparisons between the south and the north. Note that because samples from the two regions were matched by year (n gives the number of years), actual sample sizes used in the tests (column n) were smaller than the maximum in the whole data (row n). Variables are explained in the Material and methods.

		Southern Finland	Northern Finland	T	n	P
Mallard						
Hatching date	Median	62.0	82.5	0	11	< 0.001
	Range	56–74	69–89			
	n	17	12			
Difference between hatching date and ice break-up date	Median	29.3	26.0	21	11	0.285
	Range	17.7–36.0	19.3–35.7			
	n	17	12			
Common goldeneye						
Hatching date	Median	64.5	82.0	0	16	< 0.001
	Range	55–78	75–94			
	n	18	16			
Difference between hatching date and ice break-up date	Median	32.2	29.8	42.5	16	0.182
	Range	18.7–41.3	16.3–38.7			
	n	17	16			

Discussion

Our study revealed two patterns that in particular are of general interest in the context of global climate change impacts and ecological processes. First, the timing of hatching in the two migratory duck species was determined by local weather conditions (indexed by the date of ice break-up) but not by large-scale climate (indexed by NAO). Second, although the timing of hatching was associated with local weather conditions, the time interval between the hatching date and the date of ice break-up decreased with increasing lateness of the spring. The first result suggests that the association between the timing of spring migration and the winter NAO index found by Rainio *et al.* (2006) in waterfowl may not translate to the start of breeding in this species group, at least not in the mallard and the common goldeneye. Interestingly, Lehikoinen *et al.* (2006) found that the timing of spring migration in the common eider was associated with the timing of ice break-up at Jussarö, Gulf of Finland, but not with the winter NAO. In addition, they found that neither the winter NAO nor the timing of ice break-up were correlated with mean laying date in common eiders. The latter result (i.e. winter NAO did not affect the timing of egg laying) is particularly interesting considering the fact that the common eider is a pure 'capital' breeder (*sensu* Drent & Daan 1980; *see* also Lehikoinen *et al.* 2006) and the mallard and common goldeneye are 'income' breeders. Based on this fundamental difference between the species in terms of resource acquisition for egg production we might expect that winter climate affects the timing of breeding more in common eiders than in mallards and common goldeneyes. Notwithstanding, similarity between the mallard and common goldeneye in the response to the climate variables studied here may be due to the fact that they both are 'income' breeders.

It has been found in a passerine long-distance migrant, the pied flycatcher (*Ficedula hypoleuca*), that both the arrival period and the time interval between arrival and start of breeding (laying date) extended in southwestern Finland between 1970 and 2002 (Ahola *et al.* 2004). The authors suggested that spring temperatures, affecting the timing of migration, raised only during a short period at the time when the early migrants pass northern central Europe, i.e., early migrants arrived earlier but waited longer to start breeding after arrival. The mallard and the common goldeneye are short-distance migrants, and it is difficult to say if this type of climate-driven uncoupling has taken place between migration and breeding schedules in these species (*see* also below). It can be concluded, however, that the winter NAO as such cannot be used to explain both the timing of migration and the timing of breeding in waterfowl. Interestingly, Ahola *et al.* (2004) also found that the effect of NAO on median arrival date of the pied flycatcher was overridden by the local weather conditions of relevant time periods and sites during spring migration.

Our second main finding was that, in both species, the time interval between the hatching date and the date of ice break-up decreased with increasing lateness of the spring. This suggests that, provided that resource phenology in lakes closely tracks ice phenology, there is a potential for a 'mismatch' between hatching phenology and resource phenology also in ducks, as has been found for example in the great tit (*Parus major*) (Visser *et al.* 1998), the pied flycatcher (Laaksonen *et al.* 2006) and the black grouse (*Tetrao tetrix*) (Ludwig *et al.* 2006). In addition, even though differences between southern and northern Finland in the strength of the association between the timing of hatching and the timing of ice break-up turned out not to be significant, all four comparisons (i.e. two species, hatching date and time interval between hatching date and ice break-up date vs. ice break-up date) based on Kendall rank correlations indicated the timing of ice break-up to be more influential in the north. Furthermore, in both species breeding started 2–3 weeks later in the north. These results together suggest that the timing of ice break-up may constrain the timing of breeding of the two duck species more in the north than in the south. This makes intuitive sense because the time available for breeding is much shorter in the north than in the south (i.e., later ice break-up and shorter interval between ice break-up and ice freeze, *see* also Pöysä 1989, Blenckner *et al.* 2004). This finding has important implications in the context of global climate change impacts. Ice break-up dates have advanced at several lakes around the northern hemisphere (Anderson *et al.* 1996, Magnuson *et al.* 2000, Korhonen 2005), and the long-term trends in lake and river ice phenologies have been taken as evidence that freshwater ecosystems are responding to warming trends during the last 150 years (Magnuson *et al.* 2000). Considering the high inter-annual variation of ice break-up dates and the response of the breeding phenology of the two duck species to that variation, it is difficult to say if the long-term change in ice phenology has had any effect on waterfowl populations. Nevertheless, if this trend continues and even accelerates, we expect the direct impact of advanced ice break-up dates on the timing of hatching and, subsequently, on other individual and population level processes, to be more pronounced in northern than in southern breeding areas of waterfowl. It would be particularly important to study whether there is a 'mismatch' between hatching phenology and resource phenology (*see* above) and if its occurrence differs between southern and northern breeding areas. For comparison, Sanz (2003) found that climate change, indexed by the winter NAO, does not act uniformly among breeding populations of the pied flycatcher over western Europe; the rate of change in laying date was greater at more northern and western populations (*see* also Ahola *et al.* 2004).

We did not find statistically significant associations between the date of ice break-up and the winter NAO index, although the association was negative in both regions and was rather strong in the south, i.e., warm winters, as indicated by high positive values of the winter NAO, mean earlier ice break-up, especially in the south. This trend is in agreement with Blenckner and Chen (2003) and Blenckner *et al.* (2004) who used longer time series and found significant negative correlations between the date of ice break-up and the winter NAO index, the association being stronger in southern regions both in Sweden and in Finland. These authors also found that, in general, even though the large-scale NAO influenced lake ice phenology, regional atmospheric circulation was more powerful in explaining the among-year variation in the timing of ice break-up. Blenckner *et al.* (2004) concluded that the influence of the NAO on local climate is less pronounced north of 65°N. Furthermore, it has been found that the impact of the winter NAO on the timing of ice break-up is not stationary over time (*see* Blenckner & Chen 2003, Blenckner *et al.* 2004 and references therein).

In conclusion, the timing of hatching in the two duck species did not show any trend during the study period, from 1989 to 2006, so we are here dealing with normal inter-annual variation in this critical life history variable. Local ice phenology clearly affected duck hatching phenology. Because the among-year variation in the timing of hatching was substantial in both species, representing a fundamental difference in nest site use, climate-induced long-term changes in the timing of hatching and in other fitness-related traits may be difficult to recognize in ducks. We urgently need more research on the influence of local ice phenology and other climate factors on the breeding ecology of ducks around the northern hemisphere to be able to understand and predict global climate change impacts on duck populations. An important management implication of our results is that, if global warming advances the breeding chronology of ducks, the vulnerability of ducklings and moulting females to hunting may decrease under the fixed hunting season opening date currently used in Finland (20 August). Our preliminary analysis revealed that, especially in northern Finland, the proportion of unfledged mallard and common goldeneye ducklings at the beginning of the hunting season decreases with the earliness of the spring (Oja & Pöysä 2005). These findings call for more research on the impacts of global warming and spring phenology on the age and sex composition of duck bag. As a more general conclusion, we would like to join the opinion of Blenckner and Hillebrand (2002) that to enhance our understanding of climate-driven responses of ecosystems, and to be able to get an unbiased assessment how much large-scale climate indices like the NAO can add to that understanding, it is desirable to report also non-significant results with respect to the NAO. There is no doubt that NAO is an important large-scale climatic factor affecting ecological processes in many systems around the northern hemisphere (examples in Ottersen *et al.* 2001, Blenckner & Hillebrand 2002, Hallet *et al.* 2004). Future research should focus on identifying why large-scale climate indices are better predictors of ecological processes in some systems than in others.

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References

Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehikoinen, E. 2004: Variation in climate warming along the migration route uncouples arrival and breeding dates. — *Global Change Biol.* 10: 1610–1617.

Anderson, W. L., Robertson, D. M. & Magnuson, J. J. 1996: Evidence of recent warming and El Niño-related variations in ice breakup of Wisconsin lakes. — *Limnol. Oceanogr.* 41: 815–821.

Blais, S., Guillemain, M., Durant, D., Fritz, H. & Guillon, N. 2001: Growth and plumage development of pintail ducklings. — *Wildfowl* 52: 69–86.

Blenckner, T. & Hillebrand, H. 2002: North Atlantic Oscilation signatures in aquatic and terrestrial ecosystems — a meta-analysis. — *Global Change Biol.* 8: 203–212.

Blenckner, T. & Chen, D. 2003: Comparison of the impact of regional and North Atlantic atmospheric circulation on an aquatic ecosystem. — *Climate Res.* 23: 131–136.

Blenckner, T., Järvinen, M. & Weyhenmeyer, G. A. 2004: Atmospheric circulation and its impact on ice phenology in Scandinavia. — *Boreal Env. Res.* 9: 371–380.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Järvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P.-A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Török, J., Winkel, W., Wright, J., Zang, H. & Visser, M. E. 2004: Large-scale geographical variation confirms that climate change causes birds to lay earlier. — *Proc. R. Soc. Lond. B* 271: 1657–1662.

Both, C., Bijlsma, R. G. & Visser, M. E. 2005: Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. — *J. Avian Biol.* 36: 368–373.

Brown, J. L., Shou-Hsien, L. & Bhagabati, N. 1999: Long-term trend toward earlier breeding in an American bird: A response to global warming? — *Proc. Natl. Acad. Sci. USA* 96: 5565–5569.

Butler, C. J. 2003: The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. — *Ibis* 145: 484–495.

Clark, N. A., Varley, T. A., Evans, J. & Wright, G. A. 1987: Breeding success of mallard *Anas platyrhynchos* at Loch Leven national nature reserve. — *Bird Study* 34: 129–134.

Conover, W. J. & Iman, R. L. 1981: Rank transformations as a bridge between parametric and nonparametric statistics. — *Am. Stat.* 35: 124–129.

Crick, H. Q. P. 2004: The impact of climate change on birds. — *Ibis* 146 (Suppl.1): 48–56.

Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — *Ardea* 68: 225–252.

Dunn, P. 2004: Breeding dates and reproductive performance. — *Adv. Ecol. Res.* 35: 69–87.

Dunn, P. O. & Winkler, D. W. 1999: Climate change has affected the breeding date of tree swallows throughout North America. — *Proc. R. Soc. Lond. B* 266: 2487–2490.

Dzus, E. H. & Clark, R. G. 1998: Brood survival and recruitment of mallards in relation to wetland density and hatching date. — *Auk* 115: 311–318.

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. — *Ann. Zool. Fennici* 42: 37–43.

Fredga, S. & Dow, H. 1983: Annual variation in the reproductive performance of goldeneyes. — *Wildfowl* 34: 120–126.

Gollop, J. B. & Marshall, W. H. 1954: *A guide to ageing duck broods in the field*. — Mississippi Flyway Council Technical Section Report.

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M. & Grenfell, B. T. 2004: Why large-scale climate indices seem to predict ecological processes better than local weather. — *Nature* 430: 71–75.

Hurrell, J. W. 1995: Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. — *Science* 269: 676–679.

Hurrell, J. W., Kushnir, Y., Ottersen, G. & Visbeck, M. 2003: An overview of the North Atlantic Oscillation. — *Geophysical Monograph Series* 134: 1–35.

Järvinen, A. 1993: Spatial and temporal variation in reproductive traits of adjacent northern pied flycatcher *Ficedula hypoleuca* populations. — *Ornis Scand.* 24: 33–40.

Jonzén, N., Lindén, A., Ergon, T., Knudsen, E., Vik, J. O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenström, J., Lehikoinen, A., Edvardson, E., Solvang, R. & Stenseth, N. C. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. — *Science* 312: 1959–1961.

Korhonen, J. 2005: *Suomen vesistöjen jääolot* [*Ice conditions in lakes and rivers in Finland*]. — Suomen ympäristö 751, Finnish Environment Institute. [In Finnish with English summary].

Laaksonen, T., Ahola M., Eeva, T., Väisänen, R. A. & Lehikoinen, E. 2006: Climate change, migratory connectivity and changes in laying date and clutch size of the pied flycatcher. — *Oikos* 114: 277–290.

Lehikoinen, A., Kilpi, M. & Öst, M. 2006: Winter climate affects subsequent breeding success of common eiders. — *Global Change Biol.* 12: 1355–1365.

Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. 2004: Arrival and departure dates. — *Adv. Ecol. Res.* 35: 1–31.

Linkola, P. 1962: Havaintoja sorsalintujen lisääntymistuloksesta Keski-Hämeessä [Notes on the breeding success of ducks in central Häme]. — *Suomen Riista* 15: 157–174. [In Finnish with English summary].

Ludwig, G. X., Alatalo, R. V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006: Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. — *Proc. R. Soc. Lond. B* 273: 2009–2016.

Magnuson, J. J., Robertson, D. M., Benson, B. J., Wynne, R. H., Livingstone, D. M., Arai, T., Assel, R. A., Barry, R. G., Card, V., Kuusisto, E., Granin, N. G., Prowse, T. D., Stewart, K. M. & Vuglinski, V. S. 2000: Historical trends in lake and river ice cover in the Northern Hemisphere. — *Science* 289: 1743–1746.

Martin, T. E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. — *Ecol. Monogr.* 65: 101–127.

McCarty, J. P. 2001: Ecological consequences of recent climate change. — *Conserv. Biol.* 15: 320–331.

Milonoff, M., Pöysä, H. & Runko, P. 1998: Factors affecting clutch size and duckling survival in the common goldeneye *Bucephala clangula*. — *Wildl. Biol.* 4: 73–80.

Møller, A. P., Fiedler, W. & Berthold, P. (eds.) 2004: *Birds and climate change. Adv. Ecol. Res.* 35. — Elsevier Science, London.

Oja, H. & Pöysä, H. 2005: Kevään ajoittumisen vaikutus sinisorsan ja telkän pesimäaikatauluun ja poikasten lentokykyyn metsästyskauden alkaessa [The effect of spring chronology on the timing of breeding and on the occurrence of unfledged birds at the beginning of the hunting season in mallard and common goldeneye populations]. — *Suomen Riista* 51: 7–15. [In Finnish with English summary].

Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. 2001: Ecological effects of the North Atlantic Oscillation. — *Oecologia* 128: 1–14.

Parmesan, C. & Yohe, G. 2003: A globally coherent fingerprint of climate change impacts across natural systems. — *Nature* 421: 37–42.

Pearce-Higgins, J. W., Yalden, D. W. & Whittingham, M. J. 2005: Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). — *Oecologia* 143: 470–476.

Pehrsson, O. 1984: Relationships of food to spatial and temporal breeding strategies of mallards in Sweden. — *J. Wildl. Manage.* 48: 322–339.

Pehrsson, O. 1986: Duckling production of the oldsquaw in relation to spring weather and small-rodent fluctuations. — *Can. J. Zool.* 64: 1835–1841.

Pirkola, M. K. & Högmander, J. 1974: Sorsapoikueiden iänmääritys [The age determination of duck broods in the field]. — *Suomen Riista* 25: 50–55. [In Finnish with English summary].

Pöysä, H. 1989: Vesilintuyhteisöjen vakauden alueellisista eroista Suomessa [Geographical gradients in the stability of waterfowl communities in Finland]. — *Suomen Riista* 35: 7–16. [In Finnish with English summary].

Pöysä, H. 1998: Monitoring waterfowl production in Finland. — *Acta Zoologica Lituanica, Ornithologica* 8: 52–56.

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 Spec. Publ.* 26: 7–12.

Rainio, K., Laaksonen, T., Ahola, M., Vähätalo, A. V. & Lehikoinen, E. 2006: Climatic responses in spring migration of boreal and arctic birds in relation to wintering area and taxonomy. — *J. Avian Biol.* 37: 507–515.

Robinson, R. A., Learmonth, J. A., Hutson, A. M., Macleod, C. D., Sparks, T. H., Leech, D. I., Pierce, G. J., Rehfisch, M. M. & Crick, H. Q. P. 2005: *Climate change and migratory species*. — BTO Research Report 414.

Sanz, J. J. 2003: Large-scale effect of climate change on breeding parameters of pied flycatchers in Western Europe. — *Ecography* 26: 45–50.

Sedinger, J. S., Ward, D. H., Schamber, J. L., Butler, W. I., Eldridge, W. D., Conant, B., Voelzer, J. F., Chelgren, N. D. & Herzog, M. P. 2006: Effects of El Niño on distribution and reproductive performance of black brant. — *Ecology* 87: 151–159.

Siegel, S. & Castellan, N. J. Jr. 1988: *Nonparametric statistics for the behavioral sciences*. — McGraw-Hill, New York.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. 2002: Ecological effects of climate fluctuations. — *Science* 297: 1292–1296.

Stenseth, N. C. & Mysterud, A. 2005: Weather packages: finding the right scale and composition of climate in ecology. — *J. Anim. Ecol.* 74: 1195–1198.

Toft, C. A., Trauger, D. L. & Murdy, H. W. 1984: Seosonal decline in brood size of sympatric waterfowl (*Anas* and *Aythya*, Anatidae) and a proposed evolutionary explanation. — *J. Anim. Ecol.* 53: 75–82.

Torti, V. M. & Dunn, P. O. 2005: Variable effects of climate change on six species of North American birds. — *Oecologia* 145: 486–495.

Väisänen, R. A. 1974: Timing of waterfowl breeding on the Krunnit Islands, Gulf of Bothnia. — *Ornis Fennica* 51: 61–84.

Verboven, N. & Visser, M. E. 1998: Seasonal variation in local recruitment of great tits: the importance of being early. — *Oikos* 81: 511–524.

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M. 1998: Warmer springs lead to mistimed reproduction in great tits (*Parus major*). — *Proc. R. Soc. Lond. B* 265: 1867–1870.

Visser, M. E., Adriaensen, F., van Balen, J. H., Blondel, J., Dhondt, A. A., van Dongen, S., du Feu, C., Ivankina, E. V., Kerimov, A. B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D. L. 2003: Variable responses to large-scale climate change in European *Parus* populations. — *Proc. R. Soc. Lond. B* 270: 367–372.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002: Ecological responses to recent climate change. — *Nature* 416: 389–395.

Weatherhead, P. J. 2005: Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. — *Oecologia* 144: 168–175.

Wiggins, D. A., Pärt, T. & Gustafsson, L. 1994: Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. — *Oikos* 70: 359–364.