

# Climate forcing on avian life history

Alexi Lehikoinen



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Academic dissertation

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This thesis is based on the following articles, which are referred to in the text by their Roman numerals:

- I Lehikoinen, A., Kilpi, M. & Öst, M. 2006. Winter climate affects subsequent breeding success of common eiders. – *Global Change Biology* 12: 1355–1365.
- II Lehikoinen, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Korpimäki, E., Pietiäinen, H. & Henttonen, H. Reproduction of the common buzzard at its northern range margin under climatic change. – *Oikos* (in press).
- III Lehikoinen, A., Ranta, E., Byholm, P., Saurola, P., Valkama, J., Pietiäinen, H., Huitu, O., Henttonen, H. & Korpimäki, E. The impact of climate and cyclic food abundance on the timing of breeding and brood size in four boreal owl species. – Submitted to *Oikos*.
- IV Lehikoinen, A., Ranta, E., Byholm, P., Saurola, S., Valkama, J., Kaitala, V. & Lindén, H. Impact of climate change and prey abundance on nesting success of a top-predator, the goshawk. – To be resubmitted to *Oecologia*.
- V Lehikoinen, A., Saurola, P., Byholm, P., Lindén, A. & Valkama, J. Life cycle of Eurasian sparrowhawk in a changing climate. – To be resubmitted to *Global Change Biology*.

## Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV	V
Original idea	MK, AL	ER, AL	AL, ER	ER, AL	AL
Materials	MK, MÖ, AL	PS, JV, HH, HP, EK	PS, JV, HH, OH, HP, EK	PS, JV, HL	AL, PS, JV
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## Abstract

In the 21<sup>st</sup> century, human-induced global climate change has been highlighted as one of the most serious threats to ecosystems worldwide. According to global climate scenarios, the mean temperature in Finland is expected to increase by 1.8–4.0°C by the end of the century. The regional and seasonal change in temperature has predicted to be spatially and temporally asymmetric, where the High-Arctic and Antarctic areas and winter and spring seasons have been projected to face the highest temperature increase. To understand how species respond to the ongoing climate change, we need to study how climate affects species in different phases of their life cycle. The impact of climate on breeding and migration of eight large-sized bird species was studied in this thesis, taking food availability into account. The findings show that climatic variables have considerable impact on the life-history traits of large-sized birds in northern Europe. The magnitude of climatic effects on migration and breeding was comparable with that of food supply, conventionally regarded as the main factor affecting these life-history traits. Based on the results of this thesis and the current climate scenarios, the following not mutually exclusive responses are possible in the near future. Firstly, asymmetric climate change may result in a mistiming of breeding because mild winters and early spring may lead to earlier breeding, whereas offspring are hatching into colder conditions which elevate mortality. Secondly, climate induced responses can differ between species with different breeding tactics (income vs. capital breeding), so that especially capital breeders can gain advantage on global warming as they can sustain higher energy resources. Thirdly, increasing precipitation has the potential to reduce the breeding success of many species by exposing nestlings to more severe post-hatching conditions and hampering the hunting conditions of parents. Fourthly, decreasing ice cover and earlier ice-break in the Baltic Sea will allow earlier spring migration in waterfowl. In eiders, this can potentially lead to more productive breeding. Fifthly, warming temperatures can favour parents preparing for breeding and increase nestling survival. Lastly, the climate-induced phenological changes in life history events will likely continue. Furthermore, interactions between climate and food resources can be complex and interact with each other. Eiders provide an illustrative example of this complexity, being caught in the crossfire between more benign ice conditions and lower salinity negatively affecting their prime food resource. The general conclusion is that climate is controlling not only the phenology of the species but also their reproductive output, thus affecting the entire population dynamics.

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## Summary

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### SUMMARY

#### 1. Introduction

In the 21<sup>st</sup> century, human induced global climate change has been highlighted as one of the most serious threats not only to wildlife, but also to mankind (Thomas et al. 2004, CNAC 2007, IPCC 2007). Based on different scenarios the expected increase of the mean global surface temperature will be 1.8–4.0°C by the end of the century (IPCC 2007). It is also fundamental to our understanding that the regional and seasonal change in temperature is asymmetric. Especially the high Arctic areas and Antarctica have been predicted to warm more rapidly than other areas (e.g. IPCC 2007).

To understand how species are able to cope with the ongoing warming, we need to study how climate affects species in different phases of their life cycle. For example migratory species, like most bird species, may have to face climatic changes not only in the breeding areas, but also during migration or at the wintering grounds (e.g. Baele et al. 2006, Newton 2008). Migratory bird populations can be limited by the amount of breeding habitat and survival habitat, the latter of which can be exploited by the species, but breeding is not possible (*sensu* Alerstam & Högstedt 1982). The survival of adults is mainly affected during periods spent in survival habitats, whereas annual breeding success, including early mortality of fledglings, is a function of time spent in breeding habitats. Annual survival is especially important for long-lived species with a low annual reproductive potential, although repeated breeding

failure will ultimately drive a species to extinction no matter how high the adult survival (Newton 1998, Begon et al. 2006).

This thesis is about how climate affects life history events, especially breeding, in birds. In northern latitudes, arrival and breeding dates are often strongly forced by climate. By forcing I mean here e.g. that birds are forced to breed late enough, since otherwise parents would have difficulties to acquire resources for breeding, and young would be hatching into circumstances were cold weather and lack of food could decrease survival of offspring. Incubating during cold periods is also energetically highly demanding (e.g. Smyth & Boag 1984, Piersma et al. 2003), even though some species are capable of doing this. On the other hand, birds are trying to arrive and start breeding as early as possible, since early birds get the best territories and have higher breeding success than later-arriving ones (e.g. Newton 2008). Nevertheless, local climate often dictates whether the species is able to breed at all, the possible time frame for breeding, and the realized breeding success (Böhning-Gaese & Lemoine 2004, Dunn 2004).

Climate, defined as the average weather conditions during a certain period of time, is more stable than daily variation in weather. However, climate also varies between years, decades and longer periods, depending on the time scale that is used. When studying how climate affects the breeding of birds, the relevant time window is each breeding attempt, e.g. the annual breeding period. If annual climatic variables are explaining breeding events, it can be projected how

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changing climate is changing the average reproductive performance. Global warming will likely affect not only temperature, but also precipitation levels, snow and ice conditions, which are often crucial for many species (e.g. Rodriguez & Bustamante 2003, Murphy et al. 2007, I, II, III, IV), and increase extreme weather conditions, that can be more catastrophic than small changes in mean weather (see e.g. Newton 1998). In general, changing weather conditions have been considered to complicate the migration of birds, since optimal weather circumstances occur only rarely throughout the migration season (Alerstam 1990). This is likely the case also during breeding periods.

Species range margins have been expected to shift polewards or altitudinally upwards due to climate change, and such shifts have already been documented (Böhning-Gaese & Lemoine 2004, Brommer 2004, Hickling et al. 2006, Parmesan 2006). One mechanism that can enhance range shifts is that breeding success may increase at the poleward side of the species distribution and, correspondingly, decrease at the equatorial side of the range limit (Smith et al. 1999, Gaston et al. 2005). However, there is fairly little population-level evidence from the Northern Hemisphere showing that the breeding success of northern edge populations would actually have improved with the ongoing warming (but see Gaston et al. 2005; IV), and there is an urgent need for large-scale studies investigating how the reproductive performance is affected by climate throughout the species range (Dunn 2004).

### *1.1. Climate and avian breeding*

Climate may affect birds in many ways, and these effects may be especially prominent at northern latitudes. On the one hand, a warming climate has been predicted to reduce ice cover and thus directly advance arrival and breeding dates of waterfowl (Meier 2002, Rainio et al. 2006, I). On the other hand, climate change may affect the magnitude and timing of food peaks, which can have consequences at the population level (Hörnfeldt et al. 2005, Both et al. 2006, Ludwig et al. 2006). Nevertheless, the relative importance of food abundance and climatic conditions has rarely been examined simultaneously in avian studies.

Climate may affect the breeding of species directly or indirectly. By direct effects, I mean here that a climatic factor is a proxy signal or limiting variable affecting the arrival or start of breeding. For example, earlier ice-break can enable earlier migration in waterfowl (I). Furthermore, direct breeding consequences may include increasing or decreasing survival of offspring due to changing stress caused by weather conditions. Young birds are more vulnerable to harsh weather conditions than adults because it takes some time for the thermoregulation of young birds to build up to the level of full-grown birds (e.g. Newton 1998). For example in Northern Europe, increasing temperatures and decreasing precipitation during brooding can enhance the survival of nestlings, because nestlings are facing smaller risk of hypothermia or improved parental feeding conditions, leading to higher

## Summary

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reproductive output (e.g. Newton 1986, Kostrzewa & Kostrzewa 1990, II, IV).

In contrast to direct consequences, indirect climatic effects are mediated through the habitat or the food chain affecting the amount of prey or the incidence of predators and parasites (Newton 1998, Both et al. 2006, Pounds et al. 2006). Warming may for example prolong the growing season and increase overall primary production, which may in turn improve feeding conditions, enabling the production of multiple clutches per breeding season instead of only one (Halupka et al. 2008). On the other hand, increasing temperatures or decreasing precipitation may, especially in arid areas, lead to drying of wetlands or a decrease in plant production, thus hampering feeding conditions (Newton 1998, Acquarone et al. 2003, Chase et al. 2005). According to Martin (2007), most effects of climate change will likely be manifested through the food chain. As both direct and indirect effects are plausible, it is important to investigate the relative importance of climatic conditions *per se* (direct effect) and food abundance (indirect effect) for breeding success.

### 1.2. Effects of asymmetric climate change: mismatches

Changes in the climate are not projected to be symmetric. According to this hypothesis of asymmetric climate change, polar regions are predicted to face higher temperature increase than areas near the equator (IPCC 2007). The changes are also occurring asymmetrically within a year and e.g. in North Europe winter and spring

temperatures have been predicted to increase more rapidly than summer and autumn temperatures (e.g. Jylhä et al. 2004). Since the rate of global warming shows seasonal variation and species' phenology often depends on season-specific temperature profiles, asymmetric climate change may produce mismatches between the timing of highest food demand of a predator and the availability of its prey (Visser et al. 2004, Visser & Both 2005, Moline et al. 2008, Post et al. 2008, Both et al. 2009).

Mismatches have been documented in phytoplankton-zooplankton interactions in aquatic systems as well as in plant-herbivore and insects-insectivore interactions (Visser & Both 2005). Responses are usually species- and population-specific. For example, the phytoplankton bloom of *Asterionella* sp. was advanced nearly by one month during four decades in Lake Washington. However, of the two grazing zooplankton species, only one showed an advance in its occurrence (*Keratella* sp. 21 days), whereas the other one (*Daphnia* sp.) did not shift its phenology. This led to poorer feeding conditions (Winder & Schindler 2004). In another invertebrate example, the hatching of winter moth eggs has clearly advanced in the Netherlands, but since the bud burst date of oaks, the main diet of caterpillars, has not shifted as much, the caterpillars are hatching too early in relation to available food resources (Visser & Holleman 2001).

A well-known example of a mismatch between avian predators and their prey concerns western European songbirds. Early spring warming has advanced the occurrence of caterpillars,

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which are the main food for nestlings. However, since pied flycatchers *Ficedula hypoleuca* in the Netherlands have not advanced their breeding as much as the occurrence of caterpillars has advanced, the brooding conditions have deteriorated leading to the decline of late-breeding populations (Both et al. 2006). Mismatches between the breeding schedule and climatic conditions are not solely restricted to passerines, however. Finnish black grouse *Tetrao tetrix* have advanced their timing of breeding due to warmer April temperatures. However, since early summer temperatures have not increased, the chicks are hatching in colder conditions, where prey abundance of chicks (insects) is reduced. Colder post-hatching conditions increase the mortality of grouse chicks, thus contributing to the declining population trend of the black grouse (Ludwig et al. 2006). Mismatches have traditionally been considered to deal with predators and the peak in their temporarily limited food resource (Visser & Both 2005).

Arrival and breeding initiation (e.g. Leikoinen et al. 2004, Dunn et al. 2004; I, II, V) may advance faster than changes in weather conditions during the latter part of the breeding season (e.g. Ludwig et al. 2006; II; Table 1). Therefore, asymmetric climate change may also produce mismatches such as increased hypothermia-induced offspring mortality due to excessively advanced breeding schedules (Fig. 1).

### 1.3. Future directions of climate change research

Global warming has induced the invasion

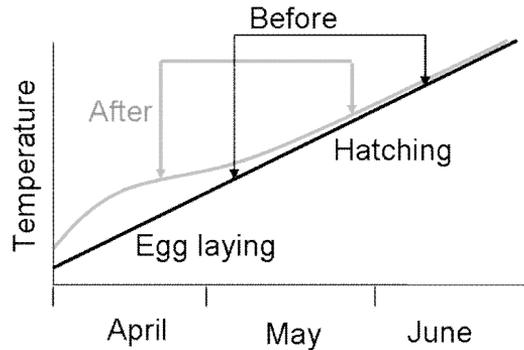


Fig. 1. Simplified illustration of how asymmetric warming may affect egg laying dates and thereby also post-hatching temperatures. The situation before asymmetric warming is shown in black and circumstances after the warming are shown in grey.

of lethal diseases, which has already contributed to extinctions of tropical amphibians (Pounds et al. 2006). However, climate change is obviously not the only factor which may cause species declines. For example, habitat loss has been considered for a long time as the key reason for extinctions (Fahrig 1997, 2003, Baillie et al. 2004, BirdLife International 2004, Hanski 2005). Also, invasive species have been shown to cause a large number of extinctions especially on oceanic islands (Simberloff 1986, Caughley & Gunn 1996, Baillie et al. 2004, BirdLife International 2004). A combination of climate change, species invasions, habitat loss and fragmentation poses a particularly severe threat (Root et al. 2003, Pounds & Puschendorf 2004, Thomas et al. 2004). Thus, there is an urgent need to make conservation decisions quickly.

In order to direct conservation measures to the most critical and important cases, we need to recognize which species or groups of species are likely to be most vulnerable to climate

change. As global warming has recently become a popular topic, there is an increasing risk that population declines may be prejudged to be caused by climate change without any evidence, despite the fact that human activities such as overharvesting or resource competition may be the real reason for the decline (Munilla et al. 2007). This highlights the need of unbiased studies of the real consequences of a changing climate.

### *1.4. Outline of the thesis*

The aim of this thesis is to investigate the importance of climatic conditions for life history events, particularly breeding performance, of large-sized non-passerine birds. Despite the growing knowledge of the effects of climate change, most of the avian studies have dealt with small-sized passerines or seabirds (Dunn 2004), but large-sized species may have a poorer ability to respond to changing environmental circumstances than small-sized species (Stevenson & Bryant 2000, Perry et al. 2005). The reason why large species are generally more vulnerable to environmental changes is their longevity which is associated with low annual reproductive rates (commonly classified as K-strategists), which is why their recovery from decline is slow (Newton 1998, Begon et al. 2006). They also have long generation times, which make them slower in adapting to changing living conditions and to face higher magnitudes of environmental stochasticity (Sæther et al. 2005). The range margins of larger species also shift more slowly than those of smaller species (Brommer 2008).

Therefore, large-sized species may be especially well suited for studying climate change forcing on avian life histories.

I compared the relative importance of climatic conditions and food abundance for regulating the breeding parameters of several species of birds of prey. The effects of food abundance and weather conditions have rarely been assessed simultaneously, even though it is well known that both factors can affect population numbers (Newton 1998). Especially in Finland, with a strong research tradition in investigating vole and grouse cyclicity, the breeding of several birds of prey has conventionally been considered to be affected mainly by prey abundance (e.g. Sulkava 1964, Lindén & Wikman 1983, Korpimäki & Hakkarainen 1991, Pietiäinen & Kolunen 1993), and therefore weather conditions and their interactions with food availability have seldom been considered in the earlier studies.

To improve the reliability of the results, I analyzed all study species in a larger spatial setting based on long-term data. This necessitated the use of large nation-wide data sets, such as the Finnish ringing database of broods of birds of prey and Danish hunting statistics on waterfowl. This study is based on existing data, which covers a large geographic area. Therefore, it can be easier to generalize the observed effects of large-scale phenomena compared to a single-locality study, the results of which may be more strongly affected by local conditions.

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### 2. Material and Methods

#### 2.1. Study systems

I used the eider *Somateria mollissima*, the most abundant seabird breeding in the Baltic, as an example species of waterfowl. Data on the breeding biology of eiders stem from a population in the

Tvärminne archipelago, Hanko, southwestern Finland (59° 50' N, 23° 15' E), studied during 1991–2004 (study site described in detail by Öst & Kilpi 2000 and Kilpi et al. 2001; Fig. 2). Based on Danish hunting statistics, I also studied the breeding success of eiders of the entire Baltic Sea (I).

Furthermore, I studied how climate affects the life history events of seven species of birds of prey, namely, the common buzzard *Buteo buteo* (n = 8522 broods; 1973–2004), the northern goshawk *Accipiter gentilis* (n = 4203; 1989–2004), the sparrowhawk *A. nisus* (n = 5722; 1973–2004), the pygmy owl *Glaucidium passerinum* (n = 3738; 1973–2004), the Tengmalm's owl *Aegolius funereus* (n = 13267; 1973–2004), the tawny owl *Strix aluco* (n = 9125; 1973–2004) and the Ural owl *S. uralensis* (n = 12396; 1973–2004; Fig. 2), using nationwide ringing data (II, III, IV, V). The breeding numbers of these birds of prey are often reflecting the dynamics, abundance, availability and quality of their prey and hence the "health" of their ecosystem (e.g. Mikkola 1983, Newton 1986, Reif et al. 2004, Tornberg et al. 2005, Honkala & Saurola 2008). I selected brood records south of 67° N, since the main distribution of all of these species in Finland is situated in the southern and central parts of the country, and broods are only occasionally ringed further north.

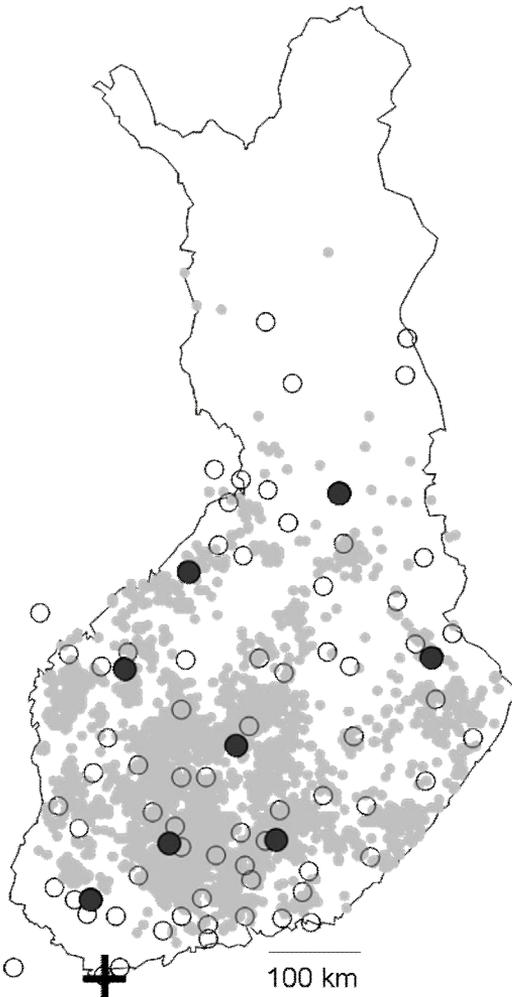


Fig. 2. Map of Finland showing vole trapping sites (black dots), weather stations (open dots) and as an illustrative example the brood ringing sites of Ural owls (grey dots) (III). The Hanko peninsula, where the Hanko Bird Observatory and the Tvärminne archipelago are situated, is indicated as a black cross (I).

#### 2.2. Data on phenology and breeding parameters

The eider, the common buzzard and the sparrowhawk are mainly migratory species in Finland, whereas the goshawk

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and the owls are mainly resident (pygmy owls and Tengmalm's owl females show tendencies for nomadic behaviour; Mikkola 1983, Korpimäki et al. 1987). Migration data of eiders and sparrowhawks were collected at the Hanko Bird Observatory, southwestern Finland (59° 49' N, 22° 54' E) from 1979 to 2007 (Lehikoinen & Vähätalo 2000, Vähätalo et al. 2004, Lehikoinen et al. 2008). Based on daily totals of migrating individuals, the beginning, median and end of the migration season were defined as the Julian dates when the season's cumulative bird sum reached 5%, 50% and 95%, respectively (Lehikoinen & Vähätalo 2000, Vähätalo et al. 2004; I,V). Both spring and autumn seasons were included in the analysis for sparrowhawks (V), whereas for eiders, only spring data were used since the autumn migration of this species is much more difficult to determine (Lehikoinen & Vähätalo 2000; I).

I studied the breeding phenology and breeding success of all eight study species. In eiders, the timing of breeding was expressed as the laying date (Kilpi & Lindström 1997; I), whereas in birds of prey, the hatching date was used as a phenology variable (for a goshawk example, see Byholm 2003). If offspring wing length was measured (32–72% of cases depending on the species), hatching date was estimated by backdating age from wing length (Jokinen 1975, Bijlsma 1993, Pihlaja 1999, [www.nic.fi/~mattisj/](http://www.nic.fi/~mattisj/)); otherwise I used the mean ringing age to estimate the hatching dates (III, IV).

In eiders, reproductive success was measured as fledging success (Öst 1999; I), and in birds of prey, brood size at

ringing was used as a measure of breeding success (Byholm 2003). This latter measure is a good indicator of fledging success in birds of prey, since mortality of older nestlings is generally low, with most of the mortality occurring fairly soon after hatching (e.g., Kostrzewa & Kostrzewa 1990, Byholm 2005; II, III, IV, V).

In eiders, I also analyzed annual variation in mean clutch size and body condition of females at the hatching of the clutch based on data from Tvärminne (Kilpi & Lindström 1997, Öst 1999). To assess whether climate affects the breeding success of eiders on a larger scale, I used data on the Danish hunting bag statistics in the wintering areas during the winters 1986–2005. The annual proportion of juvenile birds was measured based on wings of shot eiders collected by hunters. The annual proportion of young of all bagged eiders in the wintering area reflects the breeding success in the previous summer over the entire Baltic area (Noer et al. 1995). Wing data were obtained from Noer et al. (1995) and yearly reports published by Danmarks Miljøundersøgelser ([www.dmu.dk](http://www.dmu.dk); I).

### 2.3. Data on prey abundance

Since prey abundance commonly affects the breeding density and success of birds of prey (Pietiäinen 1989, Korpimäki & Hakkarainen 1991, Korpimäki & Norrdahl 1991, Pietiäinen & Kolunen 1993, Byholm et al. 2007), it was essential to include data on prey density in the studies dealing with birds of prey. The sparrowhawk is a generalized predator feeding mainly on passerines and other

## Summary

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small-sized bird species (Newton 1986), whereas grouse species are considered as the main food of goshawks (Sulkava 1964, Lindén & Wikman 1983). Common buzzards and owls are specialized on small rodents (Mikkola 1983, Reif et al. 2001), the abundance of which fluctuates in a 3–4 year cycle in the study area (Hanski et al. 1991, Sundell et al. 2004). For the common buzzard and the owls, I used indices of vole abundances as a prey variable (Mikkola 1983, Reif et al. 2001; II, III). I used long-term data on fluctuations of autumn and spring vole (*Microtus* and *Myodes* spp.) numbers in eight study sites (Fig. 2); the vole trapping methods are described elsewhere (Brommer et al. 2002, Korpimäki et al. 2005). The vole trapping indices (voles/100 trapping days) were log-transformed prior to analysis. Common buzzard and owl broods situated within a 50 kilometre radius from the vole-trapping sites were used in the analyses, and the data from each site were annually pooled. I used only those vole-trapping sites where at least five broods had been ringed annually within the 50 km radius from the trapping site. The spatial scale of the synchrony of vole dynamics exceeds the spatial scale we used (Sundell et al. 2004; Huitu et al. 2008). In case of resident owls, both autumn and spring abundances of voles were included in modelling (III), but in models of migratory common buzzards only spring vole abundance (II) was included. Common buzzards seldom winter in Finland (Cramp & Simmons 1980) and thus their breeding is unlikely affected by autumn vole abundance.

In the case of goshawks, I used the density of forest grouse as an index of

prey abundance pooled in 50 x 50 km squares. The grouse data originate from a nationwide monitoring program, which is organized by the Finnish Game and Fisheries Research Institute and run by volunteer hunters. Grouse were counted along permanent, randomly located triangle transect lines in August during 1989–2004, covering a length of 12 kilometres (Lindén et al. 1996). 12711 triangle counts were included in the study. I used the combined log-transformed densities (individuals/km<sup>2</sup>) of black (*Tetrao tetrix*), hazel (*Bonasa bonasia*) and willow grouse (*Lagopus lagopus*) as an index of grouse density, since these three species are the most abundant grouse species in the study area and thus constitute the main prey of goshawks (Lindén & Wikman 1983, Tornberg 1997, Sulkava et al. 2006; IV).

### 2.4. Weather and climate data

All data on birds of prey were supplemented with data on localized weather variables collected on a monthly basis (Table 1). Data from the weather station (n = 70) closest to each focal brood were used to score which of the available localized weather variables were most important for describing the hatching date and size of the focal brood. The weather variables were mean monthly temperature, cumulative monthly precipitation and in owls, snow depth on 15 March. Weather variables were chosen species-specifically to cover the most relevant periods (prelaying, laying, brood rearing), and relevant variables were selected based on species' ecology (e.g. Solonen 1985, Newton 1986). To explain variation in hatching

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dates, we used two to three monthly weather variables before or at the peak laying date (February to April), since this period covers arrival (in migratory species), laying and early incubation. For the corresponding analysis of brood size, we used two to three species-specific weather variables from March to June covering the periods around laying (determining the clutch size) and brood rearing (survival of offspring) (see Table 2; II, III, IV, V).

Monthly weather data from Hanko (Tvärminne Zoological Station, 59° 50' N, 23° 15' E) were used to investigate whether local weather conditions affected the migration of sparrowhawks at Hanko Bird Observatory (V). The weather data were provided by the Finnish Meteorological Institute (Venäläinen et al. 2005; II, III, IV, V). The winter North Atlantic Oscillation, NAO index, which describes the general winter and early spring weather conditions from the Atlantic to Western

Siberia (Hurrell 1995), was uploaded at [www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html) (I, V). In addition, the Julian date of ice break-up at Jussarö, western Gulf of Finland, and maximum ice-cover of the Baltic Sea, were used as local indices of ice conditions in the breeding area of eiders; these variables may be directly linked to the onset of breeding in waterfowl (Kalliosaari 1982, Kalliosaari & Seinä 1987, Seinä & Kalliosaari 1991, Seinä et al. 1996, 2001, 2006; I). The summary statistics for all climatic data are shown in Table 1.

### 2.5. Modelling of phenology and breeding parameters

In the eider, I examined whether migration and breeding parameters were more affected by ice conditions or the general severity of the winter as indicated by the NAO index (I). For analysis I used partial correlation because both climatic variables are

Table 1. Climate statistics used in the analyses, including mean values, standard deviations, minimum and maximum values and potential temporal trends. Weather statistics are based on data from 70 weather stations in 1973–2007 (snow cover 1973–2004). Ice data and the North Atlantic Oscillation (NAO) index in 1979–2004 are from the publications of Finnish Institute of Marine Research and [www.cgd.ucar.edu/cas/jhurrell/indices.html](http://www.cgd.ucar.edu/cas/jhurrell/indices.html), respectively. The shown variables were used to model responses on phenology and breeding success of the study species.

Weather variable	Mean ± sd	Min	Max	Annual trend, $r_s$	P
Temperature, February	-7.9 ± 4.7 °C	-24.9	2.6	None, 0.16	0.38
Temperature, March	-3.5 ± 2.6 °C	-8.7	1.2	None, 0.04	0.84
Temperature, April	2.0 ± 1.5 °C	-0.4	4.5	Positive, 0.39	0.02
Temperature, May	8.7 ± 1.5 °C	6.2	12.1	None, -0.04	0.80
Temperature, June	13.8 ± 1.6 °C	10.3	17.1	None, 0.10	0.56
Precipitation, April	30 ± 15 mm	8	70	None, -0.09	0.61
Precipitation, June	58 ± 20 mm	0	243	None, 0.15	0.37
Snow cover, March	41 ± 24 cm	0	118	None, -0.03	0.89
Ice-break at Jussarö	16 March ± 41	No ice	30 April	Negative, -0.44	0.02
Maximum ice cover of Baltic	177 000 ± 75 000 km <sup>2</sup>	52 000	405 000	Negative, -0.36	0.08
NAO index	1.12 ± 2.08	-3.78	+5.08	None, -0.07	0.75

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correlated. In birds of prey, two to three species-specific localized weather variables were selected to model the timing of breeding and brood size by using multiple linear regressions. I built 15 candidate models using nest coordinates, year, vole density and two to three monthly weather variables as initially considered variables. Candidate models were ranked according to the Akaike Information Criterion, AIC (Burnham & Anderson 2002, Johnson & Omland 2004). I did the analysis by using normalized (mean 0, standard deviation 1) values of the variables in order to be able to directly compare the relative importance of different variables, such as food abundance and weather conditions, on the timing of breeding and brood size (II, III, IV, V).

### 3. Main results and Discussion

#### 3.1. Spring phenology

In the eider, earlier ice-break at the breeding grounds significantly advanced the timing of spring migration (I; Fig. 3). Both the eider and the sparrowhawk have advanced their spring migration since the 1970s (I, V; Fig. 4A).

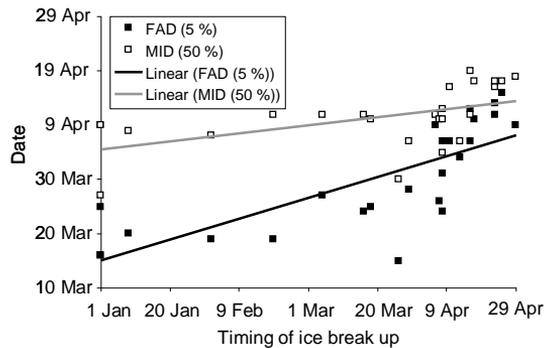


Fig. 3. Annual arrival dates (FAD = first 5 % of the annual sum of migrants, MID = median migration date) of eiders at the Hanko Bird Observatory in relation to ice break-up at Jussarö, Gulf of Finland. Linear trend lines illustrate significant correlations between the timing of migration and ice break-up

Furthermore, in both species, the earliest migrants have advanced their migration schedule relatively more than later migrants (I, V; Fig. 4A).

The results add to the growing number of studies showing that the spring phenology of numerous species representing a wide array of taxa is forced by climate and that phenology has advanced (Walther et al. 2002, Lehikoinen et al. 2004, Parmesan 2006, Cleland et al. 2007, Berlin 2008). Results also show that the phenology of the earliest migrants has, in relative terms, advanced more than that of later

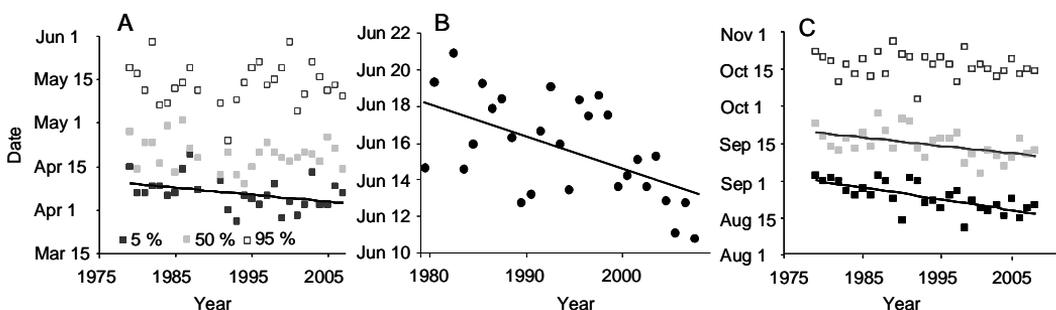


Fig. 4. The timing of spring (A) and autumn (C) migration of sparrowhawks at the Hanko Bird Observatory in 1979–2007 and mean annual hatching dates (B) based on Finnish brood ringing data in 1979–2007. The migration is divided into early (first 5 % of the annual sum of migrants), median and late (95 %) migrants. Solid regression lines indicate significant advancement (V).

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migrants (Lehikoinen et al. 2004, Rainio 2008; I, V; Fig. 4A).

Early spring migrants, which mainly belong to the breeding cohort, more closely track the changes in climate than late migrants (Vähätalo et al. 2004, Rainio et al. 2006). This hierarchy in arrival dates is supported by the fact that breeding dates of sparrowhawks have clearly advanced since the 1970s concurrent with the advancing trend in arrival dates of early migrants (V; Figs. 4A–B). Late migrants are typically young, inexperienced, non-breeding or of poor quality (Vähätalo et al. 2004, Rainio et al. 2006), and since earlier breeding birds have higher breeding success (Klomp 1970, Daan & Tinbergen 1997), the contribution of late migrants to the reproductive output of the population is likely lower than that of early migrants. Thus their representation in the currently used breeding data is also likely to be small, particularly so as the data originate from successful breeding attempts (Newton 1986; V). One must also note, that local temperatures at the

arrival site are not necessary the proxy explaining the arrival dates. However, temperatures can be strongly autocorrelated over large areas and thus changes in weather at the arrival site can reflect the conditions at the departure areas (see Ahola et al. 2004).

In eiders, earlier break-up of the ice-cover at the breeding grounds allowed earlier migration and ice-conditions had a stronger impact on migration dates than the general severity of the preceding winter (I; indicated as the NAO index). Previously the timing of eider migration has been shown to be strongly correlated with the winter NAO index (Rainio et al. 2006). However, the earlier study by Rainio et al. (2006) did not directly compare the relative contribution of ice conditions and NAO on the timing of spring migration, and my results (I) therefore provide the first concrete evidence for the hypothesis that in waterfowl the migration patterns in northern Europe may be controlled by ice conditions (Rainio et al. 2006). The timing of ice-break has advanced

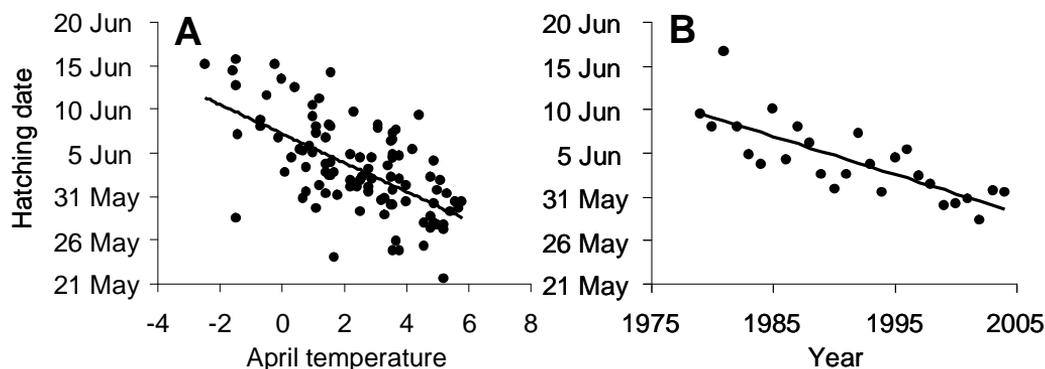


Fig. 5. Hatching dates of Finnish common buzzards in relation to (A) mean April temperature and (B) year. Panel A is based on pooled data near vole trapping sites (see Material and Methods), while panel B is based on the data from the whole country. The inclusion of a solid regression line indicates a significant relationship between variables. The timing of breeding has advanced approximately 0.44 days per year and the total advancement during 1979–2004 is 11 days (II).

## Summary

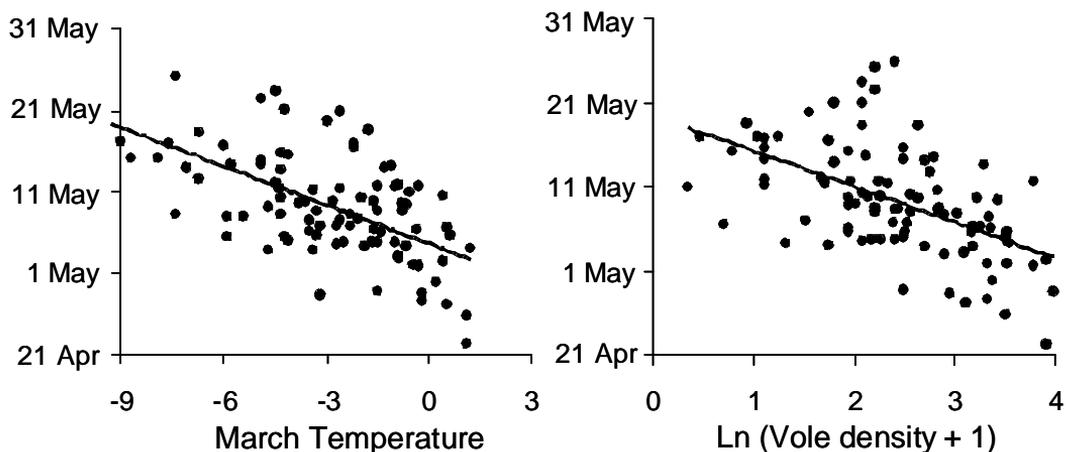


Fig. 6. Hatching dates of Ural owls in relation to (A) March temperature and (B) vole abundance in Finland in 1973–2004 (III). The inclusion of a solid regression line indicates a significant relationship between variables.

significantly since the 1970s; in response, the timing of spring migration in eiders as well as in other waterfowl has become earlier (Kilpi 1992, Rainio et al. 2006; I; Table 1, Fig. 3).

The breeding dates of all species except for the eider, pygmy and Tengmalm's owl, were affected by climatic conditions: increasing temperatures before or around laying advanced the timing of breeding (I, II, III, IV, V; Table 2, Figs. 5A, 6A). However, only the sparrowhawk and the common buzzard, in which the timing of breeding was affected by April temperatures, have shown advancing laying dates since the 1970s (II, V; Table 2, Figs. 4B, 5A–B). There are two likely reasons for the lack of temporal response in the other species. Firstly, climatic factors do not necessarily have significant impact on timing of breeding, but other factors, such as resource availability, determine when to breed (eider, pygmy owl, Tengmalm's owl; see Korpimäki & Hakkarainen 1991). Secondly, due to asymmetric warming April is the only

spring month when temperatures have increased significantly since the 1970s (Ahola et al. 2004; II; Table 1). Thus, study species in which breeding commences already in February or March (tawny owl, Ural owl, northern goshawk) did not show advancing laying dates.

Laying in eiders typically occurs in late April (I), but there was no correlation between the laying date and the timing of ice-break or the NAO index. It may be possible that our study period was too short to detect this interaction or, alternatively, other factors may control the onset of breeding, such as long-term carry-over effects which are determined at the wintering areas, local feeding conditions which have gradually deteriorated in the past decades (e.g. Westerborn 2006), predation pressure on the breeding grounds or moistness of nesting sites. In line with these suggestions, the time interval between the mean laying date at Tvärminne and peak spring arrival at the Hanko Bird Observatory, i.e. the time during which

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Table 2. Normalized coefficients (mean 0 and standard deviation 1, also including 95 % confidence intervals) of (a) hatching date and (b) brood size models in pygmy owl (PO), Tengmalm's owl (TeO), tawny owl (TaO), Ural owl (UO), common buzzard (CB), sparrowhawk (SH) and goshawk (GH) based on model averaging. Coefficients that significantly differ from zero are bolded.

(a) Species	PO	TeO	TaO	UO	CB	SH	GH
Voles, autumn	-0.06±0.30	<b>-0.46±0.22</b>	<b>-0.30±0.22</b>	<b>-0.40±0.16</b>	.	.	.
Voles, spring	-0.24±0.43	-0.13±0.28	-0.23±0.37	-0.02±0.30	-0.01±0.07	.	.
Grouse	.	.	.	.	.	.	<b>-0.10±0.07</b>
Feb. temp.	.	0.02±0.15	-0.09±0.30	<b>-0.25±0.22</b>	.	.	<b>-0.17±0.09</b>
Mar. temp.	-0.06±0.28	-0.12±0.28	<b>-0.46±0.32</b>	-0.13±0.25	-0.05±0.13	<b>-0.01±0.03</b>	-0.02±0.08
Apr. temp.	0.01±0.16	.	.	.	<b>-0.37±0.14</b>	<b>-0.30±0.04</b>	<b>-0.29±0.08</b>
Apr. precip.	.	.	.	.	.	<b>0.13±0.04</b>	.
Mar. snow	-0.03±0.20	0.20±0.27	0.11±0.26	<b>0.27±0.18</b>	.	.	.

(b) Species	PO	TeO	TaO	UO	CB	SH	GH
Voles, autumn	-0.13±0.30	0.04±0.21	0.15±0.27	<b>0.30±0.20</b>	.	.	.
Voles, spring	<b>0.49±0.43</b>	<b>0.33±0.29</b>	<b>0.46±0.30</b>	<b>0.36±0.23</b>	<b>0.28±0.15</b>	.	.
Grouse	.	.	.	.	.	.	0.07±0.08
Mar. temp.	.	0.15±0.26	0.02±0.17	0.13±0.25	.	.	.
Apr. temp.	0.01±0.15	.	.	.	.	0.00±0.03	<b>0.25±0.08</b>
May temp.	.	0.00±0.10	0.00±0.14	-0.02±0.13	.	.	.
Jun. temp.	-0.21±0.38	.	.	.	<b>0.34±0.16</b>	0.01±0.02	<b>0.16±0.07</b>
Apr. precip.	.	.	.	.	.	<b>-0.05±0.03</b>	.
Jun. precip.	.	.	.	.	-0.17±0.19	.	<b>-0.15±0.06</b>
Mar. snow	0.10±0.31	<b>0.39±0.22</b>	0.04±0.21	-0.05±0.18	.	.	.

female eiders replenish body reserves, increased with earlier spring arrival dates (A. Lehtikoinen, unpubl. data). These results support the findings of Ahola et al. (2004), suggesting that earlier arrival does not necessarily lead to earlier breeding, but may actually increase the time lag between arrival and laying.

In all birds of prey except for the common buzzard and pygmy owl (sparrowhawk not analyzed), increasing prey abundance prior to laying advanced breeding dates (II, III, IV; Table 2, Fig. 6B). This was an expected finding in the light of previous research (Pietiäinen 1989, Korpimäki & Hakkarainen 1991, Pietiäinen & Kolunen 1993). However, this study shows that temperature can strongly affect laying dates even in highly

specialized predators. The common buzzard, sparrowhawk, goshawk, tawny owl and Ural owl all advanced their breeding by about 0.5 to 2 days for every one degree increase in temperature around laying or in the month before laying (II, III, IV, V; Figs 5A, 6A). When comparing the magnitude of coefficients of temperature and prey abundance, temperature showed at least as high an importance as food abundance in explaining the timing of breeding in common buzzards, goshawks, tawny owls and Ural owls (II, III, IV; Table 2, Fig. 6). In general, breeding dates were delayed towards the north and the east (II, IV, V). This result reflects the climatic gradient between the milder southern and western Finland and the northern and

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eastern Finland, characterized by lower winter and early spring temperatures (Maanmittaushallitus & Suomen maantieteellinen seura 1987).

In the Ural owl, increasing snow depths in March were found to delay the timing of breeding (III; Table 2). This supports the hypothesis that thick snow cover reduces success of finding prey, which may negatively affect the condition of breeding birds, and thus delay breeding (Pietiäinen & Kolunen 1993). Mild late winters and early springs result in earlier snow melt, enhancing the hunting success of owls (Korpimäki 1986).

Somewhat surprisingly and in contrast to the larger tawny and Ural owls, the laying dates of pygmy and Tengmalm's owls were not affected by winter or spring temperature (III; Table 2). This contradicts earlier findings which suggest that as a response to increasing temperature, small species should advance their breeding schedule more than larger species (Stevenson & Bryant 2000). This discrepancy may be caused by general differences in breeding strategies. Based on the existing literature (Hirons et al. 1984, Hörnfeldt & Eklund 1990, Korpimäki & Hakkarainen 1991, Pietiäinen & Kolunen 1993), large owl species are to a higher extent capital breeders (sensu Drent & Daan 1980), where the resources needed for egg laying and incubation are acquired from stored reserves. Smaller species, which are to a higher degree income breeders, continuously acquire resources for laying and incubation during the course of the breeding season (Drent & Daan 1980, Jönsson 1997, Meijer & Drent 1999, Klaassen 2003). The breeding conditions

of capital breeders may be enhanced if the winter has been mild, thus allowing earlier breeding.

The capital breeding tactic is beneficial compared to income breeding in unpredictable and resource-limited circumstances (Jönsson 1997). Large-sized species are unable to increase their body condition as swiftly as smaller species in preparation for breeding, whereas small species can not carry as high body reserves as large species, which may explain why large species are generally more often capital breeders than small ones (Meijer & Drent 1999, Klaassen 2003). My results confirm the hypothesis that replenishing and sustaining energy reserves are easier in mild than in harsh winters (I; see also Nilsson 1979, Birkhead et al. 1983, Fox et al. 1992, Kenward 2006). This conclusion is also supported by the fact that in tawny owls, ovarian growth starts about three months prior to the breeding season and it is positively associated with body mass (Hirons et al. 1984). This strongly suggests that the physiological preparation for breeding begins well in advance of egg laying, and hence it can be extensively affected both by weather conditions and food abundance over a longer time period.

### 3.2. Reproductive success

The breeding success of eiders, common buzzards, sparrowhawks, goshawks and Tengmalm's owls was affected by climatic variables (I, II, III, IV, V; Figs. 7, 8A–B). On the other hand, also higher prey abundance improved reproductive output (II, III; Fig. 8C). In common buzzards and goshawks, the influence of

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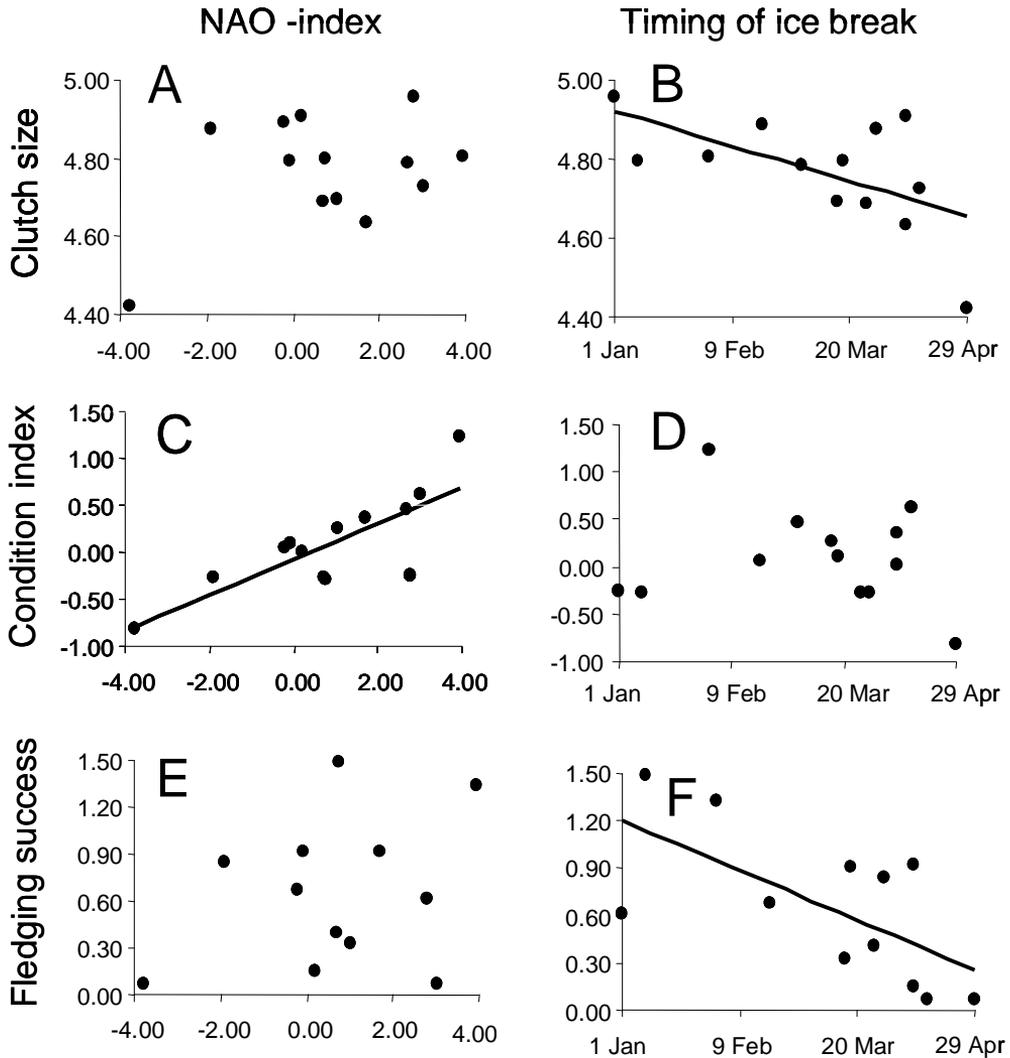


Fig. 7. Average clutch size (A-B), length-weight standardized body condition of females at hatching of their clutch (C-D) and fledging success (E-F) of eiders breeding at Tvärminne in relation to the NAO index and the timing of ice break-up at Jussarö. Linear trend lines illustrate significant correlations between variables (I).

weather conditions was at least as high impact on breeding success as did the abundance of the main prey, whereas in owls vole abundance was the main forcing factor (II, III, IV; Table 2). Taken together, these results support the consensus view that climate and food availability are the key factors affecting breeding success (e.g. Newton 1998).

After mild winters, eider females

laid larger clutches, they were in better body condition at the time their clutches hatched and they reared larger broods (I; Fig. 7). Similar results have earlier been documented in whooper swans *Cygnus cygnus* and mute swans *C. olor* (Nilsson 1979, Birkhead et al. 1983), species having a similar overwintering strategy and life-history characteristics. Eiders may pool their broods and form female

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brood-rearing coalitions, where different strategies are state-dependent and linked to the female's ability to protect the brood against predation (Öst et al. 2003a, b, Öst et al. 2007a, b). During brooding disease epidemics and the choice of parental care strategy are key factors affecting fledging success (Öst et al. 2008; I). The eider is regarded as an extreme example of a capital breeding species, in which resources for laying, incubation and post-hatching parental care largely come from energy stored during the pre-breeding phase (Meijer & Drent 1999, Hario & Öst 2002, Waldeck et al. 2004). My findings suggest that

energy resources allocated for reproduction may be less during cold winters, e.g. due to increased energetic demands of temperature regulation or hampered feeding conditions due to more severe ice conditions. In eiders, energy resources available to breeding females are not only affecting laying and incubation, but also determining how much the female can invest in post-hatching parental care (Öst et al. 2003a, b, 2007b). Good-quality females with high body condition may be better able to protect their young against predation (Öst et al. 2003a), and these females also produce larger clutches (Öst et al. 2008).

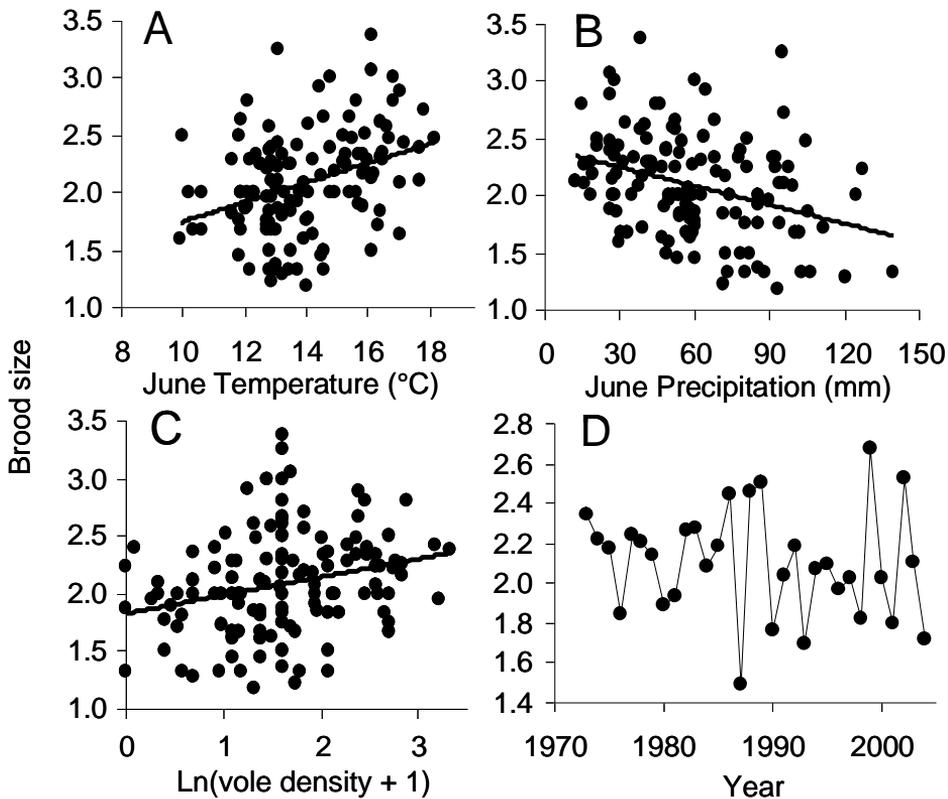


Fig. 8. Brood size of Finnish common buzzards in relation to (A) June temperature, (B) June precipitation, (C) vole density and (D) year in Finland in 1973–2004. Panels A–C are based on pooled data near vole trapping sites (see Material and Methods), while panel D is based on the data from the whole country. The inclusion of a solid regression line in the panels indicates a significant relationship between variables. Note the 3 to 4-year cycle in brood size related to vole abundance (II).

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The survival of offspring in several precocial waterfowl species is enhanced in larger broods (Lepage et al. 1998, Loonen et al. 1999, Smith et al. 2005, Öst et al. 2008). Another non-exclusive explanation is that the survival of young of good-condition parents may be enhanced through maternally induced immune defence, since good-condition females may have a better capacity to produce antioxidants in eggs, thus reducing the risk of disease once the offspring have hatched (Blount et al. 2003; I).

The brood size of goshawks was larger in years characterized by high temperatures around the time of laying (IV). Sparrowhawks showed a higher breeding success when the period around laying was dry (V; Table 2). In accordance with these results, Newton (1986) found that increasing temperature and decreasing precipitation during spring improved the breeding success of sparrowhawks. He explained this pattern by the earlier arrival of migrating passerines in warm and dry years, improving the hunting conditions of breeding resident birds, thus leading to earlier breeding and larger clutches. This could be the case in the Finnish resident goshawks and migratory sparrowhawks too, even though the pattern is not as clear as in the resident sparrowhawks in Britain. Many migratory bird species have been shown to arrive in Finland earlier after mild winters (Vähätalo et al. 2004, Rainio et al. 2006), and arrival dates have become earlier with time (Sparks et al. 2005, Jonzén et al. 2006). In addition, since higher temperatures already as early as in February advanced the

breeding of goshawks, higher pre-laying temperatures may positively affect the body condition of females, since temperature regulation is energetically less demanding than during colder years (see I). Following this chain of logic, higher temperatures can lead to improved body condition, which allows females to lay larger clutches, resulting in larger broods later in spring (IV).

In common buzzards and goshawks, increased temperature during brood rearing positively affected brood size, whereas increased precipitation had a negative impact (II, IV; Figs. 8A–B). These results are in line with several studies showing that in birds in general (e.g. Walsberg 1985, Huey 1991), and in birds of prey in particular (Mearns & Newton 1988, Kostrezewa & Kostrezewa 1990, Selås 2001, Rodriguez & Bustamante 2003, Krüger 2004), nestling mortality is higher in cold or wet circumstances. Under such conditions, offspring may face increasing heat loss (e.g. Walsberg 1985, Huey 1991) that may expose them to hypothermia and starvation. Rainy weather may also have indirect effects by decreasing the hunting efficiency of parents, thus leading to brood reduction.

In Tengmalm's owl, breeding success improved with the thickness of the snow cover in March (III; Table 2). Thinner snow cover and earlier snow melt may increase predation on voles (Hansson & Henttonen 1985, Korpimäki 1986, Halonen et al. 2007) and alternating thaw and freezing cycles (frost seesaw) can be harmful for wintering voles (Aars & Ims 2002, Solonen 2006). Reduction of the snow layer could lead to a paradoxical pattern

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where hunting conditions before and around laying are improved due to thinner snow cover (III; see Ural owl in Table 2) and breeding could be started earlier due to better body condition. However, increased predation during late winter and early spring may cause decreased vole densities at the time when owl parents should start to feed their offspring. Compared to the other studied owl species, Tengmalm's owl is more of a vole specialist, whereas the other species to some extent also use birds in their diet during breeding (e.g. Mikkola 1983, Kullberg 1995). This may be a reason why only the breeding success of Tengmalm's owls showed a relationship with snow cover.

### 3.3. Autumn migration

Sparrowhawks have also advanced their autumn migration (V; Fig. 4C) as a response to an earlier breeding schedule (V). Young sparrowhawks start their autumn migration soon after parents have given up food provisioning (Newton 1986). Therefore it is hardly surprising that the species' departure times have also advanced in parallel with the advancing arrival times, so that the timing of the entire life cycle of sparrowhawks has shifted towards earlier migration and breeding (V; Fig. 4). However, in contrast to the early-migrating young that have advanced their autumn migration, late-phase migrants, mainly representing adults, have not advanced their autumn migration. Adults migrate later than juveniles, since they need to moult their flight feathers before departure (Cramp & Simmons 1980, Saurola 1981, Kjellén

1992).

Two hypotheses have been proposed regarding the effects of climate change on the autumn phenology of migratory birds. Jenni and Kery (2003) suggested that single-brooded short-distance migrants, such as sparrowhawks (Cramp & Simmons 1980), should show delayed rather than advanced autumn phenology despite advancing spring arrival. In a warming climate, they would not need to migrate so far any more, and wintering as close to breeding areas as possible would be beneficial with respect to earlier arrival and territory establishment (Jenni & Kery 2003, Newton 2008). On the other hand, Tøttrup et al. (2006) have documented advancing autumn migration times in many North European short- and long-distance migrating passerines. These authors have hypothesized that the time interval that the species are spending in their breeding areas (BART: breeding area residence time) is constant, and thus earlier spring arrival and breeding would lead to a correspondingly earlier autumn migration of both adult and young birds (Thorup et al. 2007). Earlier arrival to wintering areas may enable the acquisition of better wintering territories and thus result in better body condition in preparation for spring migration (Alerstam 1990, Newton 2008).

The migration data of sparrowhawks (V) provide support for both hypotheses. The migration patterns of juvenile sparrowhawks agree with the constant BART hypothesis. However, because both spring and breeding dates have advanced, whereas autumn migration dates of late-phase migrating adults have not, the BART of adults has

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increased, which better agrees with the hypothesis proposed by Jenni and Kery (2003). This highlights that different age groups of the same species following the same flyway may respond differently to climate change. The main autumn migration period of different passerine species in Finland covers the entire migration period of sparrowhawks from late July (long-distant tropical migrants, warblers) to late October (short-distance migrants, finches) (Lehikoinen & Vähätalo 2000), which enables sparrowhawks to migrate at the same time as their prey.

### *3.4. Implications and future prospects*

The results of this study suggest that climate directly affects many aspects of the breeding cycle of large-sized bird species in Northern Europe, the general trend being that increasing temperatures tend to improve breeding conditions and advance breeding dates. The findings suggest that short-distance migrants or resident species (eider, goshawk and large owls), which all show characters of a capital breeding strategy, are the ones that might be expected to benefit from the ongoing warming, everything else being equal (but see Guillemain et al. 2008). However, before further generalizations are possible, the effect of increasing temperatures on capital and income breeders should be evaluated in other study systems, also including other taxa than birds.

Regardless of food availability, asymmetric warming may cause mismatches between the timing of breeding and the optimal weather conditions during brood rearing.

Increasing early spring temperatures have advanced the breeding of black grouse and common buzzards, but temperature during brooding has not risen and nestlings are facing colder post-hatching conditions (Ludwig et al. 2006; II; see also Fig. 1). Similar mismatches could be also found in other systems than birds. For example, advanced plant blooming (Abu-Asab et al. 2001) may expose flowers to higher risk of frost damage and lack of critical pollinators, which can cause crop failure (Inouye 2008). It would be important to investigate how general these types of mismatches are in Northern Europe, and how much they potentially explain current population trends of species. The population decline of a particular species may have indirect effects affecting various levels of the food web. For example, the decline of the black grouse, which at least partly can be ascribed to asymmetric climate change (Ludwig et al. 2006), may directly suppress the breeding success of birds of prey using grouse as their prey, but indirectly it may also affect the population dynamics of important alternative prey species (Lindén & Wikman 1983, Reif et al. 2001, 2004).

Indirect effects are often difficult to predict, since the mechanisms by which climate affects prey abundance are seldom known in sufficient detail. The relationship between snow cover and vole abundance provides an illustrative example. It is well known that the cyclic population dynamics of voles in Fennoscandia occurs only in areas where the ground is snow-covered during normal winters (Hansson & Henttonen 1985, Hanski et al. 1991). Even though

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there are growing numbers of publications suggesting that snow conditions may affect over-winter survival of small rodents so that a thinner, harder and more humid snow cover may reduce survival rate of small mammals (Lindström & Hörnfeldt 1994, Aars & Ims 2002, Boonstra & Krebs 2006, Korslund & Steen 2006, Kausrud et al. 2008), it is not comprehensively understood how warming temperatures will affect vole numbers and thus the staple food of many birds of prey (see also Solonen 2006). The consequences of warming for the abundance of voles may appear indirectly through the community structure of prey and predators, where increase in the amount of generalist predators could stabilize vole dynamics (see Hanski et al. 1991).

It is also important to notice that the effects forced by climate change may not necessarily act in the same direction. For example, my results have shown that decreasing ice cover due to warming temperature will likely increase the breeding success of eiders (I). However, climatic models suggest that especially due to increasing winter precipitation

(Jylhä et al. 2004), the salinity of the Baltic Sea will likely continue to decrease (Meier et al. 2006; Mackenzie et al. 2007), which will negatively affect the distribution of the salinity-demanding blue mussel *Mytilus edulis*, the main food of eiders (Westerbom 2006). Increasing sea temperature has also shown to decrease the growth of mussels (Honkoop & Beukema 1997). The net outcome of these opposite climatic effects, where climate change may increase the body condition of breeding eiders but simultaneously reduce the quality and range of suitable breeding areas of eiders in the Baltic, is extremely difficult to predict. Judged by the current declining population trend of Baltic eiders (Hario & Rintala 2008, see also Westerbom 2006), it seems that the negative effects of climate change may actually outweigh the positive effects in this particular case. Correspondingly, the population sizes of the main prey of goshawks, forest grouse, have suffered from asymmetric climate change (Ludwig et al. 2006), although the warming by itself should improve the breeding success of goshawks (IV).

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### 4. Conclusions

The general conclusion of this thesis is that climatic variables have considerable impact on the life history traits of large-sized birds in northern Europe. Previously, the common opinion has been that density dependence and prey abundance mainly influence life history, and hence weather conditions have seldom been taken into account in previous studies. My findings show that climate is controlling not only the phenology of the species but also their reproductive output, thus affecting the entire population dynamics. Furthermore, interactions between climate and food resources can be complex and potentially need to be tackled at the population level.

According to global climate scenarios, the mean temperature in Finland is expected to increase by 2–5°C within the next 40 years, higher temperature increases during the winter months during the summer months. Correspondingly, the overall precipitation is predicted to increase whereas days with snow and ice cover are likely to decrease in the future (Jylhä et al. 2004, 2008). Based on my thesis and the current climate scenarios, the following not mutually exclusive responses are possible in the near future. Firstly, asymmetric climate change may result in a mistiming of breeding because mild winters and early spring may lead to earlier breeding, whereas offspring are hatching into colder conditions which elevated mortality (Ludwig et al. 2006; II;

Fig. 1). Secondly, climate induced responses can differ between species with different breeding tactics (income vs. capital breeder), so that especially capital breeders can gain advantage on global warming as they can sustain higher energy resources. Thirdly, increasing precipitation has the potential to reduce the breeding success of many species by exposing nestlings to more severe post-hatching conditions and hampering the hunting conditions of parents (II, III, IV, V). Fourthly, decreasing ice cover and earlier ice-break in the Baltic Sea (Meier 2002; I) will allow earlier migration in waterfowl. In eiders, this can potentially lead to more productive breeding (I). Fifthly, warming temperatures can favour parents preparing for breeding and increase nestling survival (II, IV). Lastly, the climate-induced phenological changes in life history events will likely continue (I, II, III, IV, V). However, it is vitally important to emphasize that to be able to definitely address the question how climate change will affect the breeding success of species, indirect effects mediated by the food chain should be taken into account, e.g., how climate affects food abundance (Martin 2007). As exemplified by the eiders caught in the crossfire between more benign ice conditions and lower salinity negatively affecting their prime food resource, climatic effects on avian life history and population dynamics are often complex and interact with other factors in often unforeseen ways.

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## Summary

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### 5. References:

- Aars, J & Ims, R.A. 2002: Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. – *Ecology* 83: 3449–3456.
- Abu-Asab, M. S., Peterson, P. M., Shetler, S. G. & Orli, S. S. 2001: Earlier plant flowering in spring as a response to global warming in the Washington, CD, area. – *Biodiversity and Conservation* 10: 597–612.
- Acquarone, C., Cocco, M. & Malacarne, G. 2003: Reproduction of the Crag Martin (*Ptyonoprogne rupestris*) in relation to weather and colony size. – *Ornis Fennica* 80: 79–85.
- Ahola, M., Laaksonen, T., Sippola, K., Eeva, T., Rainio, K. & Lehtikoinen, E. 2004: Variation in climate warming along the migration route uncouples arrival and breeding dates. – *Global Change Biology* 10: 1610–1617.
- Alerstam, T. 1990: *Bird Migration*. – Cambridge University Press. New York.
- Alerstam, T. & Högstedt, G. 1982: Bird migration and reproduction in relation to habitats for survival and breeding. – *Ornis Scandinavica* 13: 25–37.
- Baele, C. M., Burfield I. J., Sim, I. M. W., Rebecca, G. W., Pearce-Higgins, J. W. & Grant, M. C. 2006: Climate change may account for the decline in British ring ouzels *Turdus torquatus*. – *Journal of Animal Ecology* 75: 826–835.
- Baillie, J.E.M., Hilton-Taylor, C., Stuart, S.N. (eds.) 2004: *IUCN Red List of Threatened Species. A Global Species Assessment*.
- Begon, M., Townsend, C. R., Harper, J. L. 2006: *Ecology. Individuals, Populations and Communities*. Blackwell Science. 4<sup>rd</sup> edition. 738 pp.
- Berlin, R. I. 2008: Plant phenology and distribution in relation to recent climate change. – *Journal of the Torrey Botanical Society* 135: 126–146.
- Bijlsma, R. G. 1993: *Ecologische Atlas van der Nederlandse Roofvogels*. – Schuyt & Co, Haarlem.
- BirdLife International 2004: *State of the world's birds 2004: indicators for our changing world*. – Cambridge, UK: BirdLife International.
- Birkhead, M., Bacon, P. & Walter, P. 1983: Factors affecting the breeding success of the mute swan *Cygnus olor*. – *Journal of Animal Ecology* 52: 727–741.
- Blount, J. D., Houston, D. C., Surai, P. F. & Møller, A. P. 2003: Egg-laying capacity is limited by carotenoid pigment availability in wild gulls *Larus fuscus*. – *Proceedings of the Royal Society B* 271 (Suppl. 3): S79–S81.
- Böhning-Gaese, K. & Lemoine, N. 2004: Importance of Climate Change for Ranges, Communities and Conservation of Birds. – In: Møller, A. P., Berthold, P. & Fiedler, W. (eds): *Advances in Ecological Research: Birds and Climate Change* 35: 211–236.
- Boonstra, R. & Krebs, C. J. 2006: Population limitation of the northern red-backed vole in the boreal forests of northern Canada. – *Journal of Animal Ecology* 75: 1269–1284.
- Both, C., van Asch, M., Bijlsma, R.G, van den Burg, A.B. & Visser, M.E. 2009: Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? – *Journal of Animal Ecology* 78: 73–83.
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006: Climate change and population declines in a long-distance migratory bird. – *Nature* 441: 81–83.
- Brommer, J. E. 2004: The range margins of northern bird species shift polewards. – *Annales Zoologici Fennici* 41: 391–397.
- Brommer, J. E. 2008: Extent of recent polewards range margin shifts in Finnish birds depends on their body mass and feeding ecology. – *Ornis Fennica* 85: 109–117.
- Brommer, J., Pietiäinen, H. & Kolunen 2002: Reproduction and survival in a variable environment: Ural Owls (*Strix uralensis*)

## Summary

---

- and the three-year vole cycle. – *Auk* 119: 544–550.
- Burnham, K. & Anderson, D. 2002: Model selection and multimodel inference: a practical information-theoretic approach. – 2<sup>nd</sup> Edition. Springer-Verlag, New York, New York, USA.
- Byholm, P. 2003: Reproduction and dispersal of goshawk in a variable environment. – PhD-thesis. University of Helsinki.
- Byholm, P. 2005: Site-specific variation in partial brood loss in northern goshawks. – *Annales Zoologici Fennici* 42: 81–90.
- Byholm, P., Nikula, A., Kenttä, J. & Taivalmäki, J.-P. 2007: Interactions between habitat heterogeneity and food affect reproductive output in a top predator. – *Journal of Animal Ecology* 76:392-401.
- Caughley, G. & Gunn, A. 1996: Conservation Biology in Theory and Practice. – Blackwell Science, Cambridge.
- Chase, M. K., Nur, N. & Geupel, G. R. 2005: Effects of weather and population density on reproductive success and population dynamics in a Song Sparrow (*Melospiza melodia*) population: A long-term study. – *Auk* 122: 571–592.
- Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & Schwartz, M. D. 2007: Shifting plant phenology in response to global change. – *Trends in Ecology & Evolution* 22: 357–365.
- The CNA Corporation (CNAC) 2007: The National Security and Threat of Climate Change. Available at: <http://securityandclimate.cna.org/>. 35 pp.
- Cramp, S. and Simmons, K.E.L. (eds) 1980: Handbook of the birds in Europe, the Middle East and North Africa. The Birds of Western Palearctic. Vol II. – Oxford University Press, New York.
- Daan, S. & Tinbergen, J. M. 1997: Adaptation of Life History. – In: Krebs, J.R. & Davies, N.B. (eds): Behavioural Ecology. 4th Edition. Blackwell Science Ltd. Oxford. pp. 311–333.
- 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. – In: Møller, A. P., Berthold, P. & Fiedler, W. (eds): Advances in Ecological Research: Birds and Climate Change 35: 69–87.
- Fahrig, L. 1997: Relative effects of habitat loss and fragmentation on population extinction. – *Journal of Wildlife Management* 61: 603–610.
- Fahrig, L. 2003: Effects of habitat fragmentation on biodiversity. – *Annual Review of Ecology Evolution and Systematics* 34: 487–515.
- Fox, A.D., King, R. & Watkin, J. 1992: Seasonal variation in weight, body measurements and condition of free-living Teal. – *Bird Study* 39: 53–62.
- Gaston, A. J. Gilchrist, H.G., Hipfner, J.M. 2005: Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). – *Journal of Animal Ecology* 74: 832–841.
- Guillemain, M., Elmberg, J., Arzel, C., Johnson, A.R. & Simon, G. 2008: The income-capital breeding dichotomy revisited: late winter body condition is related to breeding success in an income breeder. – *Ibis* 150: 172–176.
- Halonen, M., Mappes, T., Meri, T. & Suhonen, J. 2007: Influence of snow cover on food hoarding in Pygmy Owls *Glaucidium passerinum*. – *Ornis Fennica* 84: 105–111.
- Halupka, L., Dyrz, A. & Borowiec, M. 2008: Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. – *Journal of Avian Biology* 39: 95–100.
- Hanski, I. 2005: The Shrinking World: Ecological Consequences of Habitat Loss. – International Ecology Institute, Oldendorf/Luhe.
- Hanski, I., Hansson, L. & Henttonen, H. 1991: Specialist predators, generalist predators, and the microtine rodent cycle. – *Journal of Animal Ecology* 60: 353–367.

## Summary

---

- Hansson, L. & Henttonen, H. 1985: Gradients in density variations of small rodents: the importance of latitude and snow cover. – *Oecologia* 67: 394–402.
- Hario, M. & Öst, M. 2002: Does heavy investment in foraging implicate low food acquisition for female Common Eiders *Somateria mollissima*? – *Ornis Fennica* 79: 111–120.
- Hario, M. & Rintala, J. 2008: Population trends of the Common Eider and four gull species in Finnish coastal areas in 1986–2007. – *Linnut-vuosikirja 2007*: 52–59. In Finnish with English summary.
- Hickling, R., Roy, D. B., Hill, J. K., Fox, R. & Thomas, C. D. 2006: The distributions of a wide range of taxonomic groups are expanding polewards. – *Global Change Biology* 12: 450–455.
- Hirons, G. J. M., Hardy, A. R. & Stanley, P. I. 1984: Body weight, gonad development and moult in the Tawny Owl (*Strix aluco*). – *Journal of Zoology* 202: 145–164.
- Honkala, J. & Saurola, P. 2008: Breeding and population trends of common raptors and owls in Finland in 2007. – *Linnut-vuosikirja 2007*: 36–51. In Finnish with English summary.
- Honkoop, P.J.C. & Beukema, J.J. 1997: Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. – *Journal of Experimental Marine Biology & Ecology* 212: 277–297.
- Hörnfeldt, B. & Eklund, U. 1990: The effect of food on laying date and clutch-size in Tengmalm's Owl *Aegolius funereus*. – *Ibis* 132: 395–406.
- Hörnfeldt, B., Hipkiss, T. & Eklund, U. 2005: Fading out of vole and predator cycles? – *Proceedings of the Royal Society B* 272: 2045–2049.
- Huey, R.B. 1991: Physiological consequences of habitat selection. – *American Naturalist* 137: S91–S115.
- Huitu, O., Laaksonen, J., Klemola, T. & Korpimäki, E. 2008: Spatial dynamics of *Microtus* vole populations in continuous and fragmented agricultural landscapes. – *Oecologia* 155: 53–61.
- Hurrell, J. W. 1995: Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. – *Science* 269: 676–679.
- Intergovernmental Panel on Climate Change (IPCC) 2007: Climate Change 2007: Synthesis Report. Fourth Assessment Report. Available at: <http://www.ipcc.ch/>. 52 pp.
- Inouye, D.W. 2008: Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. – *Ecology* 89: 353–362.
- Jenni, L. & Kery, M. 2003: Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. – *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 1467–1471.
- Johnson, J. B. & Omland, K. S. 2004: Model selection in ecology and evolution. – *Trends in Ecology and Evolution* 19: 101–108.
- Jokinen, M. 1975: Lehtopöllöpoikasten kasvu ja energiankäyttö ja niiden vaikutus pesimätuloksen määrittämiseen. – M.Sc. thesis, University of Turku.
- Jönsson, K. I. 1997: Capital and income breeding as alternative tactics of resource use in reproduction. – *Oikos* 78: 57–66.
- 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., Edvardsen, E., Solvang, R. & Stenseth, N. C. 2006: Rapid advance of spring arrival dates in long-distance migratory birds. – *Science* 312: 1959–1961.
- Jylhä, K., Fronzek, S., Tuomenvirta, H., Carter,

## Summary

---

- T. R. & Ruosteenoja, K. 2008: Changes in frost, snow and Baltic sea ice by the end of the twenty-first century based on climate model projections for Europe. – *Climatic Change* 86: 441–462.
- Jylhä, K., Tuomenvirta, H. & Ruosteenoja, K. 2004: Climate change projections for Finland during the 21st century. – *Boreal Environment Research* 9: 127–152.
- Kalliosaari, S. 1982: Ice winters 1976–1980 along the Finnish coast. – *Finnish Marine Research* 249: 3–61.
- Kalliosaari, S. & Seinä, A. 1987: Ice winters 1981–1985 along the Finnish coast. – *Finnish Marine Research* 254: 5–63.
- Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Ostbye, E., Cazelles, B., Framstad, E., Eikeset, A. M., Mysterud, I., Solhoy, T. & Stenseth, N.C. 2008: Linking climate change to lemming cycles. – *Nature* 456: 93–97.
- Kenward, R. 2006: *The Goshawk*. – T & AD Poyser Ltd (A & C Black).
- Kilpi, M. 1992: Responses of Herring Gull and Common Gulls to warm years: early migration and early breeding. – *Ornis Fennica* 69: 82–87.
- Kilpi, M. & Lindström, K. 1997: Habitat-specific clutch size and cost of incubation in common eiders, *Somateria mollissima*. – *Oecologia* 111: 297–301.
- Kilpi, M. & Öst, M., Lindström, K. & Rita, H. 2001: Female characteristics and parental care mode in the crèche system of eiders, *Somateria mollissima*. – *Animal Behaviour* 62: 527–534.
- Kjellén, N. 1992: Differential timing of autumn migration between sex and age-groups in raptors at Falsterbo, Sweden. – *Ornis Scandinavica* 23: 420–434.
- Klaassen, M. 2003: Relationship Between Migration and Breeding Strategies in Arctic Breeding Birds. – In: Berthold, P., Gwinner, E. & Sonnenschein, E.: *Avian migration*. Springer-Verlag, Berlin, Heidelberg. pp. 237–249.
- Klomp, H. 1970: The determination of clutch-size in birds. A review. – *Ardea* 58:2–123.
- Korpimäki, E. 1986: Seasonal changes in the food of Tengmalm's owl *Aegolius funereus* in western Finland. – *Annales Zoologici Fennici* 23: 339–344.
- Korpimäki, E. & Hakkarainen, H. 1991: Fluctuating food supply affects the clutch size of Tengmalm's owl independent of laying date. – *Oecologia* 85: 543–552.
- Korpimäki, E., Lagerström, M. & Saurola, P. 1987: Field evidence for nomadism in Tengmalm's owl *Aegolius funereus*. – *Ornis Scandinavica* 18: 1–4.
- Korpimäki, E. & Norrdahl, K. 1991: Numerical and functional responses of Kestrels, Short eared Owls, and Long eared Owls to vole densities. – *Ecology* 72: 814–826.
- Korpimäki, E., Norrdahl, K., Huitu, O. & Klemola, T. 2005: Predator-induced synchrony in population oscillations of co-existing small mammal species. – *Proceedings of the Royal Society B* 272: 193–202.
- Korslund, L. & Steen, H. 2006: Small rodent winter survival: snow conditions limit access to food resources. – *Journal of Animal Ecology* 75: 156–166.
- Kostrzewa, A. & Kostrzewa, R. 1990: The relationship of spring and summer weather with density and breeding performance of the Buzzard *Buteo buteo*, Goshawks *Accipiter gentilis* and Kestrel *Falco tinnunculus*. – *Ibis* 132: 550–559.
- Krüger, O. 2004: The importance of competition, food, habitat, weather and phenotype for the reproduction of Buzzard *Buteo buteo*. – *Bird Study* 51: 125–132.
- Kullberg, C. 1995: Strategy of the Pygmy Owl while hunting avian and mammalian prey. – *Ornis Fennica* 72: 72–78.
- Lehikoinen, A., Christensen, T. K., Öst, M., Kilpi, M., Saurola, P. & Vattulainen, A. 2008: Large-scale change in the sex ratio of a

## Summary

---

- declining eider population. – *Wildlife Biology* 14: 288-301.
- Lehikoinen, A. & Vähätalo, A. 2000: Phenology of bird migration at the Hanko Bird Observatory, Finland, in 1979–1999 (In Finnish with English summary). – *Tringa* 27: 150–227.
- Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. 2004. Arrival and departure dates. – In: Møller, A.P., Berthold, P. and Fiedler, W. (eds) *Advances in Ecological Research: Birds and Climate Change*. Elsevier, Amsterdam, pp. 1–31.
- Lepage, D., Gauthier, G. & Desrochers, A. 1998: Larger clutch size increases fledging success and offspring quality in a precocial species. – *Journal of Animal Ecology* 67:210-216.
- Lindén, H., Helle, E., Helle, P. & Wikman, M. 1996: Wildlife triangle scheme in Finland: methods and aims for monitoring wildlife populations. – *Finnish Game Research* 49: 4–11.
- Lindén, H. & Wikman, M. 1983: Goshawk predation on tetraonids – available of prey and diet of the predator in the breeding season. – *Journal of Animal Ecology* 52: 953–968.
- Lindström, E. R. & Hörnfeldt, B. 1994: Vole cycles, snow depth and fox predation. – *Oikos* 70: 156–160.
- Loonen, M. J. J. E., Bruinzeel, L. W., Black, J. M. & Drent, R. H. 1999: The benefit of large broods in barnacle geese: a study using natural and experimental manipulations. – *Journal of Animal Ecology* 68:753-768.
- 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. – *Proceedings of the Royal Society of London Series B-Biological Sciences* 273: 2009–2016.
- Maanmittaushallitus & Suomen maatieteellinen seura 1987: *Atlas of Finland*. – Folio 131. Climate.
- Mackenzie, B. R., Gislason, H., Mollman, C. & Koster, F. W. 2007: Impact of 21<sup>st</sup> century climate change on the Baltic Sea fish community and fisheries. – *Global Change Biology* 13: 1348–1367.
- Martin, T. E. 2007: Climate correlates of 20 years of trophic changes in high-elevation riparian system. – *Ecology* 88: 367–380.
- Mearns, R. & Newton, I. 1988: Factors affecting breeding success of Peregrines in southern Scotland. – *Journal of Animal Ecology* 57: 903–916.
- Meier, H. E. M. 2002: Regional ocean climate simulations with a 3D ice-ocean model for the Baltic Sea. Part 2: results for sea ice. – *Climate Dynamics* 19: 255–266.
- Meier, H. E. M., Kjellström, E. & Graham, L.P. 2006: Estimating uncertainties of projected Baltic Sea salinity in the late 21st century. – *Geophysical Research Letters* 33: L15705.
- Meijer, T. & Drent, R. 1999: Re-examination of the capital and income dichotomy in breeding birds. – *Ibis* 141: 99–114.
- Mikkola, H. 1983: *Owls of Europe*. – T & A D Poyser, Calton.
- Moline, M. A., Karnovsky, N. J., Brown, Z., Divoky, G. J., Frazer, T. K., Jacoby, C. A., Torrese, J. J. & Fraser, W. R. 2008: High latitude changes in ice dynamics and their impact on polar marine ecosystems. – *Year in Ecology and Conservation Biology 2008*. *Annals of the New York Academy of Sciences* 1134: 267–319.
- Munilla, I., Diez, C. & Velando, A. 2007: Are edge bird populations doomed to extinction? A retrospective analysis of the common guillemot collapse in Iberia. – *Biological Conservation* 137: 359–371.
- Murphy, E. J., Trathan, P. N., Watkins, J. L., Reid, K., Meredith, M. P., Forcada, J., Thorpe, S. E., Johnston, N. M. & Rothery, P. 2007: Climatically driven fluctuations in Southern Ocean ecosystems. – *Proceedings of the Royal*

## Summary

---

- Society of London Series B-Biological Sciences 274: 3057–3067.
- Newton, I. 1986: The Sparrowhawk. – T & AD Poyser, Calton.
- Newton, I. 1998: Population limitation in birds. – Academic Press, London.
- Newton, I. 2008: The migration ecology of birds. – Academic Press, London.
- Nilsson, L. 1979: Variation in the production of young of swans wintering in Sweden. – *Wildfowl* 30: 129–134.
- Noer, H., Clausanger, I., Asferg, T. 1995: – *Danish Review of Game Biology* 14: 1–24.
- Öst, M. 1999: Within-season and between-year variation in the structure of common eider broods. – *Condor* 101: 598–606.
- Öst, M. & Kilpi, M. 2000: Eider females and broods from neighboring colonies use segregated local feeding areas. – *Waterbirds* 23: 24–32.
- Öst, M., Ydenberg, R., Kilpi, M. & Lindström, K. 2003a: Condition and coalition formation by brood-rearing common eider females. – *Behavioral Ecology* 14: 311–317.
- Öst, M., Ydenberg, R., Lindström, K. & Kilpi, M. 2003b: Body condition and the grouping behaviour of brood-caring female common eiders (*Somateria mollissima*). – *Behavioral Ecology and Sociobiology* 54: 451–457.
- Öst, M., Clark, C. W., Kilpi, M. & Ydenberg, R. 2007a: Parental effort and reproductive skew in coalitions of brood rearing female common eiders. – *American Naturalist* 169:73–86.
- Öst, M., Jaatinen, K. & Steele, B. 2007b: Aggressive females seize central positions and show increased vigilance in brood-rearing coalitions of eiders. – *Animal Behaviour* 73: 239–247.
- Öst, M., Smith, B. D. & Kilpi, M. 2008. Social and maternal factors affecting duckling survival in eiders *Somateria mollissima*. – *Journal of Animal Ecology* 77:315-325.
- Parmesan, C. 2006: Ecological and evolutionary responses to recent climate change. – *Annual Review of Ecology Evolution and Systematics* 37: 637–669.
- Perry, A. L., Low, P. J., Ellis, J. R. & Reynolds, J. D. 2005. Climate change and distribution shifts in marine fishes. – *Science* 308: 1912–1915.
- Piersma, T., Lindström, A., Drent, R.H., Tulp, I., Jukema, J., Morrison, R.I.G., Reneerkens, J., Schekkerman, H. & Visser, G.H. 2003: High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study. – *Functional Ecology* 17: 356–362.
- Pietiäinen, H. 1989: Seasonal and individual variation in the production of offspring in ural owl. – *Journal of Animal Ecology* 58: 905–920.
- Pietiäinen, H. & Kolunen, H. 1993: Female body condition and breeding of the Ural owl *Strix uralensis*. – *Functional Ecology* 7: 726–735.
- Pihlaja, T. 1999: Growth of nestling Ural owls. – M.Sc. thesis, University of Helsinki.
- Post, E., Pedersen, C., Wilmers, C. C. & Forchhammer, M. C. 2008: Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. – *Proceedings of the Royal Society of London Series B-Biological Sciences* 275: 2005–2013.
- Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sanchez-Azofeifa, G. A., Still, C. J. & Young, B. E. 2006: Widespread amphibian extinctions from epidemic disease driven by global warming. – *Nature* 439: 161–167.
- Pounds, J. A. & Puschendorf, R. 2004: Ecology – clouded futures. – *Nature* 427: 107–109.
- Rainio, K. 2008: Climate change effects on avian migration. – PhD thesis. *Annales Universitatis Turkuensis Ser. All Tom.* 230.

## Summary

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- 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. – *Journal of Avian Biology* 27: 507–515.
- Reif, V., Jungell, S., Korpimäki, E., Tornberg, R. & Mykka, S. 2004: Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions. – *Annales Zoologici Fennici* 41: 599–607.
- Reif, V., Tornberg, R., Jungell, S. & Korpimäki, E. 2001: Diet variation of common buzzards in Finland supports the alternative prey hypothesis. – *Ecography* 24: 267–274.
- Rodríguez, C. R. & Bustamante, J. 2003: The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? – *Journal of Animal Ecology* 72: 793–810.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003: Fingerprints of global warming on wild animals and plants. – *Nature* 421: 57–60.
- Sæther, B.-E., Lande, R., Engen, S., Weimerskirch, H., Lillegård, M., Altwegg, R., Becker, P.H., Bregnballe, T., Brommer, J.E., McCleery, R.H., Merilä, J., Nyholm, E., Rendell, W., Robertson, R.R., Tryjanowski, P. & Visser, M.E. 2005: Generation time and temporal scaling of bird population dynamics – *Nature* 236: 99–102.
- Saurola, P. 1981: Migration of the Sparrowhawk *Accipiter nisus* as revealed by Finnish ringing and recovery data. – *Lintumies* 16: 10–18. In Finnish with English summary.
- Seinä, A., Eriksson, P., Kalliosaari, S. & Vainio, J. 2006: Ice seasons 2001–2005 in Finnish sea areas. – *Meri, Report Series of the Finnish Institute of Marine Research* 57: 1–94.
- Seinä, A., Grönvall, H., Kalliosaari, S. & Vainio, J. 1996: Ice seasons 1991–1995 along the Finnish coast. – *Meri, Report Series of the Finnish Institute of Marine Research* 27: 3–77.
- Seinä, A., Grönvall, H., Kalliosaari, S. & Vainio, J. 2001: Ice seasons 1996–2000 in Finnish sea areas. – *Meri, Report Series of the Finnish Institute of Marine Research* 43, 3–98.
- Seinä, A. & Kalliosaari, S. 1991: Ice winters 1986–1990 along the Finnish coast. – *Finnish Marine Research* 259: 3–61.
- Selås, V. 2001: Breeding density and brood size of Common Buzzard *Buteo buteo* in relation to snow cover in spring. – *Ardea* 89: 471–479.
- Simberloff, D. 1986: The proximate causes of extinction. – In: Raup, D.M. & Jablowski (eds): *Patterns and processes in the history of life*. Springer. Berlin. 259–276 pp.
- Smith, B. D., Boyd, W. S. & Evans, M. R. 2005: A clutch and brood survival model that discriminates random and correlated mortality. – *Ecological Applications* 15:281-293.
- Smyth, K.E. & Boag, D.A. 1984: Production in spruce grouse and its relationship to environmental and population parameters. – *Canadian Journal of Zoology* 62: 2250–2257.
- Solonen, T. 1985: Suomen linnusto. – *Lintutieto, Helsinki*. In Finnish.
- Solonen, T. 2006: Overwinter population change of small mammals in Southern Finland. – *Annales Zoologici Fennici* 43: 295–302.
- Sparks, T.H., Bairlein, F., Bojarinova, J.G., Hüppop, O., Lehikoinen, E.A., Rainio, K., Solokov, L.V. & Walker, D. 2005: Examining the total arrival distribution of migratory birds. – *Global Change Biology* 11: 22–30.
- Stevenson, I. R. & Bryant, D. M. 2000: Climate change and constraints on breeding. – *Nature* 406: 366–367.
- Sulkava, S. 1964: Zur Nahrungsbiologie des Habichts, *Accipiter g. gentilis* (L.). –

## Summary

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- Aquilo Ser. Zoologica 3:1–103.
- Sulkava, S., Linkola, P. & Lokki, H. 2006: The diet of the goshawk *Accipiter gentilis* during nesting season in Häme (Southern Finland). – Suomen Riista 52: 85–96 (in Finnish with English summary).
- Sundell, J., Huitu, O., Henttonen, H., Kaikusalo, A., Korpimäki, E., Pietiäinen, H., Saurola, P. & Hanski, I. 2004: Large-scale spatial dynamics of vole populations in Finland revealed by the breeding success of vole eating avian predators. – Journal of Animal Ecology 73: 167–178.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siquiera, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. & Williams, S. E. 2004: Extinction risk from climate change. – Nature 427: 145–148.
- Thorup, K., Tøttrup, A.P. & Rahbek, C. 2007: Patterns of phenological changes in migratory birds. – Oecologia 151: 697–703.
- Tornberg, R. 1997: Prey selection of the Goshawk *Accipiter gentilis* during the breeding season: The role of prey profitability and vulnerability. – Ornis Fennica 74: 15–28.
- Tornberg, R., Korpimäki, E., Jungell, S & Reif, V. 2005: Delayed numerical response of goshawks to population fluctuations of forest grouse. – Oikos 111: 408–415.
- Tøttrup, A.P., Thorup, K. & Rahbek, C. 2006: Changes in timing of autumn migration in North European songbird populations. – Ardea 94: 527–536.
- Vähätalo, A. V., Rainio, K., Lehtikoinen, A. & Lehtikoinen, E. 2004: Spring arrival of birds depends on the North Atlantic Oscillation. – Journal of Avian Biology 35: 210–216.
- Venäläinen, A., Tuomenvirta, H. & Drebs, S. 2005: A basic Finnish climate data set 1961–2000 – description and illustrations. – Finnish Meteorological Institute, Meteorological Publications.
- Visser, M. E., Both, C. & Lambrechts, M. M. 2004: Global climate change leads to mistimed avian reproduction. – In: Møller, A. P., Berthold, P. & Fiedler, W. (eds): Advances in Ecological Research: Birds and Climate Change 35: 89–110.
- Visser, M. E. & Both, C. 2005: Shifts in phenology due to global climate change: the need for a yardstick. – Proceedings of the Royal Society of London Series B-Biological Sciences 272: 2561–2569.
- Visser, M. E. & Holleman, L. J. M. 2001: Warmer springs disrupt the synchrony of oak and winter moth phenology. – Proceedings of the Royal Society of London Series B-Biological Sciences 268: 289–294.
- Walsberg, G.E. 1985: Physiological consequences of microhabitat selection in birds. – In: M. L. Cody [ed.]: Habitat selection in birds. Academic Press, New York. p. 389–413.
- 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.
- Waldeck, P., Kilpi, M., Öst, M. & Andersson, M. 2004: Brood parasitism in a population of common eider (*Somateria mollissima*). – Behaviour 141: 725–739.
- Westerbom, M. 2006: Population dynamics of blue mussels in a variable environment at the edge of their range. – PhD thesis. University of Helsinki, Faculty of Biosciences, Department of Biological and Environmental Sciences.
- Winder, M. & Schindler, D. E. 2004: Climate change uncouples trophic interactions in an aquatic ecosystem. – Ecology 85: 2100–2106.