BOREAL ENVIRONMENT RESEARCH 13: 303–318 © 2008
ISSN 1239-6095 (print) ISSN 1797-2469 (online) Helsinki 28 August 2008

# Long-term trends in spring phenology in a boreal forest in central Finland

Hanna K. Lappalainen[1)3)], Tapio Linkosalo[2)] and Ari Venäläinen[3)]

[1)] *Department of Physical Sciences, P.O. Box 64, FI-00014 University of Helsinki, Finland*
[2)] *Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland*
[3)] *Finnish Meteorological Institute, P.O. Box 503, FI-00101 Helsinki, Finland*

*Received 5 Feb. 2007, accepted 21 Aug. 2007* (*Editor in charge of this article: Jaana Bäck*)

Lappalainen, H. K., Linkosalo, T. & Venäläinen, A. 2008: Long-term trends in spring phenology in a boreal forest in central Finland. *Boreal Env. Res.* 13: 303–318.

We studied the onset of spring phenology and the long-term trends of 31 species at the Oulainen-Ohineva site (64°13´N, 24°53´E) in central Finland. The species studied represented a wide range including deciduous trees, shrubs, grasses, 18 species of migratory birds and six insect species. The duration of the species-specific time series varied from 4 years up to 54 years during the 1952–2005 observation period. An advancing trend ($p < 0.05$) in the timing of spring phenology was only found for five species (with over 15 years of observations), namely, *Formica rufa* group, *Rana temporaria*, *Grus grus*, *Ficedula hypoleuca* and *Hirundinidae*. In local species with more than 38 years of observations, the temperature trend turned out to be the best variable to describe the advancement of the phenological event. For birds in six cases out of ten the best factor for explaining the advancement, as well as the temperature, was the NAO index.

## Introduction

During recent decades, the value of phenological datasets in reflecting trends of life history events or growth rhythm has been recognized, and phenological recordings have become an essential part of environmental monitoring, especially with regard to climate change (Sparks 1999, Sparks *et al*. 2000, Menzel 2002). The European climate at the end of the 20th century, as well as during the first years of the 21st, has been warmer than that of any period during the past 500 years, and the year 2003 was by far the hottest summer since the 16th century (Luterbacher *et al*. 2004). The observations indicate the advancing long-term trends in phenology, also a northward shift in species distribution ranges and a climate-linked invasion of new species as a response to this warming (Hughes 2000, Kullman 2001, Menzel 2002, Fitter and Fitter 2002, Walther *et al*. 2002, Menzel 2003). Furthermore, on a global scale the advancement of spring phenological events in general has been estimated to be of the order of 2.3 days per decade (Parmesan and Yohe 2003). Menzel *et al*. (2006) reported results that showed a similar order of change for Europe, with an average advance of phenological events in spring or summer of 2.5 days per decade. In plants, the highest advances and variation have been reported for phenological events that take place in early spring. It seems that early-flowering annuals and insect-pollinated species are more sensitive as compared with wind-pollinated species, and show an even stronger advancing trend (Fitter and Fitter 2002, Walther *et al.* 2002). According to 30 years of observations in Europe, the average annual growing season has been estimated to have lengthened by 10.8 days since the early 1960s (Menzel and Fabian 1999).

The phenological recordings of fauna demonstrate a similar response toward an earlier occurrence of phenological events in spring. The spring migration of birds has been connected either to the North Atlantic Oscillation (NAO) index or to rising spring temperatures (Stenseth *et al.* 2002, Lehikoinen *et al.* 2004). A positive NAO, associated with mild, moist winters, increases temperatures and precipitation over northern Europe, while roughly the opposite conditions take place during a negative index (Hurrell 1995). For example, observations from Finland and Sweden have demonstrated that many species, including long-distance migrants from Africa, arrive earlier in the spring when the NAO index is positive (Rainio *et al.* 2005, Stervander *et al.* 2005, Jonzen *et al.* 2006). Thus, most Finnish migratory birds seem to be able to adjust their spring arrival in response to climatic change without any time delay (Vähätalo *et al.* 2004). Sparks (1999) reported that a tendency for earlier arrival in bird migration is related to warmer springs, but he pointed out the importance of choosing the most appropriate temperature data along the migration route.

The observed spatial and temporal changes in phenological events are evidently part of an ongoing wider ecological response to climate change that is also interfering with predator–prey relationships and reproduction biology (Stenseth *et al.* 2002). Furthermore, a decoupling of species interactions, e.g., between plants and pollinators or offspring and food, owing to mismatches in phenology, is becoming evident. Consequently, a mismatch between food abundance and offspring needs might increase, if one species is cued, for example, to day length while the other species is cued to temperature (Visser *et al.* 1998, Hughes 2000). Further research has been called for, particularly studies dealing with several species or linked species; making use of existing long-term datasets, there is a need to identify vulnerable species communities close to the latitudinal limits of their distribution area (Hughes 2000, Sparks *et al.* 2000). Many of the phenological datasets are relatively short, e.g., less than 20 years of data from scattered locations. Also the limited number of consistent time series, that have been recorded by carefully-defined observation methods, has in many cases hindered the detection of long-term trends (Lappalainen and Heikinheimo 1992). The most extensive long-term phenological datasets are available from central Europe, Britain and Russia. For example, the most well-known datasets are the Marsham family records (years 1736–1958), and the networks of the Royal Meteorological Society (1875–1947) from Britain, and the phenological databank of the Deutscher Wetterdienst in Germany (Chmielewski 1996). Except for Russia, large-scale datasets representing European northern taiga forests and their biota are few (Kozlov and Berlina 2002). In Finland, a tradition of volunteer phenological recordings has been mainly maintained by the Finnish Society of Sciences and Letters, most of the recordings being concentrated in southern and central Finland (Lappalainen and Heikinheimo 1992). In general, data from a single location can be valuable if they exist as part of a long run of years, usually more than 20 (Sparks *et al.* 2000).

The aim of this study is to discover evidence of the phenological responses of biota to climate warming, especially for species living near the northern limits of their distribution areas in the boreal vegetation zone. Based on earlier studies, it was expected that the timing of phenological events would have advanced during recent decades as a consequence of changed temperature conditions (Tuomenvirta 2004, Menzel *et al.* 2006). Furthermore, there should be certain species or groups of species responding more sensitively to changed climate conditions (Fitter and Fitter 2002). Here we analyse 54-year-long phenological datasets of different phenological events for 31 species or taxa representing both plant and animal species at a single locality in central Finland. We also study the relationships between the onset of phenological events and climate variables such as temperature, precipitation and the NAO index.

# Material and methods

## Phenological data collection

### Observation site

The Juhonsalo phenological observation site is at Oulainen-Ohineva (64°13´N, 24°53´E, 78 m above sea level) in the middle-boreal vegetation zone of central Finland. The site is situated on a 20 ha drained marsh-type field area bounded by a mixed forest whose dominating tree species are Scots pine and birch. The forest structure and composition have remained unchanged during the observation period, with trees of varying ages being present. The mean annual precipitation at the site is 577 mm and the mean annual temperature 2.1 °C, having a mean daily maximum of 15.3 °C in July and mean daily minimum temperatures of –9.4 °C in January.

### Observation program of the Juhonsalo dataset

In the year 1952, at the instigation of Aarne Juhonsalo, the Juhonsalo family started a private phenological observation program on the first sightings of migratory birds and spring phenological events of local biota in his farm fields and in the surrounding spruce mire and forest area. In 1970 the Finnish Meteorological Institute's Oulainen-Ohineva weather station was established at the Juhonsalo farm. Since then the Juhonsalo family has continued to perform phenological recordings along with meteorological observations.

The daily observation routines were performed by Aarne Juhonsalo (in 1952–1962), Aarne Juhonsalo Jr. (since 1952), Matti Juhonsalo (in 1952–1962), Tuomo Juhonsalo (in 1952–1959), Eeva Juhonsalo (in 1952–1975), Erkki Juhonsalo (in 1952–1998) and Anna-Liisa Juhonsalo (since 1975). The main responsibility for the observation routines has been borne by Aarne Juhonsalo Jr. The Juhonsalo data have been recorded by a single family, altogether seven persons, dedicated to the phenological observation routines. In the case of an uncertain first observation, it has been omitted and has only been recorded when confirmed as definite. Different observers also compared notes in order to assure the data quality.

The observation program was started with eight species: the first croak of the common frog (*Rana temporaria*), the leaf unfolding of birch (*Betula* spp.), the flowering of rowan (*Sorbus aucuparia*) and the first appearance of the following migratory birds: yellow wagtail (*Motacilla flava*), common crane (*Grus grus*), cuckoo (*Cuculus canorus*), swallows (*Hirundinidae*) and white wagtail (*Motacilla alba*). These species were followed intensively throughout the eintire 54-year period. New species were added to the observation routines during later years. In 2005 the Juhonsalo dataset covered altogether 31 species (analyzed in this study), of which 6 were plant species and 25 animal species. As a whole the dataset includes several groups of species such as deciduous trees, shrubs, grasses, terrestrial and flying insects, amphibians and migratory birds wintering in different areas. The time series presented here contain several gaps in the individual "first observation" time series. These gaps are due to the fact that (1) the species concerned were not found at the site in that year or (2) they were not included in the annual observation program due to the relatively limited amount of observational resources (Table 1). However, when an observation has been recorded it can be considered reliable. Although time series with gaps due to reason (1) — "not found" — are relatively short, for example for *Turdus merula, Oenanthe oenanthe* and *Jynx torquilla*, they are reported in this paper. These observations might contain valuable information that would be relevant at a later time to further studies.

### Observed phenological events

#### *Trees*

The average timing of birch (*Betula* spp.) budburst was defined as the day when the buds were open to a leaf length of about 8 mm, commonly known in Finland as the "mouse-ear" phase. The species common silver birch (*Betula pendula*)

**Table 1.** List of observed species of the Juhonsalo dataset grouped by their ecology. The following symbols have been used for missing data in a given year: (#) = not included in the annual observation program due to limited observer resources, (?) = not found at observation site. Symbols for pollination type: W = wind or I = insect and P = pollinator; For birds O = omnivorous, G = granivorous, I = insectivorous.

| | Observed phase | Remarks on missing data |
|---|---|---|
| **Deciduous trees** | | |
| Birch *Betula* spp. (W) | budburst “mouse ear” | (#) 1994 |
| Rowan *Sorbus aucuparia* (I) | full flowering | recorded in 1952–2005, no missing observations |
| Bird cherry *Prunus padus* (I) | full flowering | (#) 1952–1954, 1956–1960, 1962 |
| **Shrubs** | | |
| lingonberry *Vaccininum vitis-idaea* (I) | full flowering | (#) 1952–1960, 1962–1963, 1965, 1967, 1969, 1971, 1973, 1975–1979, 1982, 1985–2005 |
| **Grass** | | |
| Chickweed wintergreen *Trientalis europaea* (I) | full flowering | (#) 1952–1960, 1962–1964, 1969–1971, 1974–1975, 1977–1980, 1982, 1985–2005 |
| Timothy grass *Phleum pratense* (W) | budburst (50% opened) | recorded since 1970, no missing observations |
| | full flowering | recorded since 1970, no missing observations |
| **Insects** | | |
| **Terrestrial insects** | | |
| Red wood ant *Formica rufa* group | first observation | recorded since 1964, no missing observations |
| Dor beetle *Geotrupes stercorarius* | first observation | (#) 1952–1961, 1963, 1966, 1968–1971, 1974–2005 |
| **Flying insects** | | |
| Mosquito Culicidae | first main swarm | (#) 1952–1972, 1975–1980, 1982–1983, 1985, 1987–1996, 1999–2000, 2002–2003 |
| Horseflies *Tabanidae* | first observation | (#) 1952, 1954, 1956, 1958, 1960, 1963 |
| Bumblebee *Bombus* spp. (P) | first observation | (#) 1952–1956, 1959–1961, 1963, 1975–1977, 1979, 1982, 1985, 1999 |
| Small tortoiseshell *Aglais urticae* (P) | first observation | (#) 1952–1959, 1961, 1963-1964, 1969–1971, 1975–1976, 1978–2004 |
| **Amphibians** | | |
| Common frog *Rana temporaria* | onset of spawning season | recorded since 1952, no missing observations |
| **Birds** | | |
| **Short-distance migrators overwintering in Europe** | | |
| Northern lapwing *Vanellus vanellus* (O) | first observation | first observation 1965, (?) 1976, 1979, 1983–2005 |
| Curlew *Numenius arquata* (O) | first observation | (#) 1968–1969, 1974–1977, 1979–1982, 1985–1987, 1989–1992<br>(?) 1994, 1997, 1998 |
| Skylark *Alauda arvensis* (O) | first observation | (#) 1970, 1973, 1976, 1979, 1981, 1985, 1988–1990, 1992–1994, 1996–2000, 2002–2005 |
| Fieldfare *Turdus pilaris* (O) | first observation | (#) 1965, 1967–1970, 1975–1976, 1982–1984, 1986–1991, 1996 |
| Blackbird *Turdus merula* (O) | first observation | observations in 1969, 1970, 1973, 1974 |
| Common starling *Sturnus vulgaris* (O) | first observation | (#) 1956, 1959–1960, 1963–1965, 1967–1969<br>(?) 1975–1976, 1978–1981, 1984–1993, 1995; the observation site infrequently visited |
| Woodpigeon *Columba palumbus* (G) | first observation | (#) 1963, 1967–1968, 1970, 1975–1977, 1981–1982, 1985, 1987, 1989–1990, 1992–1993 |
| Chaffinch *Fringilla coelebs* (O) | first observation | recorded since 1954, no missing observations |

| | | |
|---|---|---|
| **Medium-distance migrators overwintering in the Mediterranean** | | |
| Common snipe *Gallinago gallinago* (O) | first observation | (#) 1963, 1970–1971 |
| Common crane *Grus grus* (O) | first observation | recorded since 1952, no missing observations |
| White wagtail *Motacilla alba* (I) | first observation | recorded since 1952, no missing observations |
| Song thrush *Turdus philomelos* (O) | first observation | (#) 1957, 1962–1964, 1966–1971, 1974–1976, 1978–2005<br>the observation site infrequently visited |
| **Long-distance migrators overwintering in Africa** | | |
| Pied flycatcher *Ficedula hypoleuca* (I) | first observation | (#) 1952–1973, 1975–1979, 1984–1986, 1988–1991, 1998–1999 |
| Yellow wagtail *Motacilla flava* (I) | first observation | recorded since 1952, (?) 1998 |
| Swallow *Hirundinidae* (I) | first observation | recorded since 1952, no missing observations |
| Northern wheatear *Oenanthe oenanthe* (I, O) | first observation | (#) 1952–1956, 1958–1959, 1963–1972, 1975–1993, (?) 1995 |
| Wryneck *Jynx torquilla* (I) | first observation | (?) 1964–1970, 1972–1980, 1984–1985, 1989, 1991–1993, 1997–1998, 2000–2005 |
| Cuckoo *Cuculus canorus* (I) | first observation | recorded since 1952, no missing observations |

and downy birch (*Betula pubescens*) were not differentiated. The observer recorded the event as seen across an open field to the birch trees at the edge of the forest 200 m away. The event was recorded as the date when the forest zone had a generally greenish appearance; thus the date represents an average date for the budburst in the area. Supporting evidence for the average observation was gathered from trees growing in the Juhonsalo farmyard. Single trees ahead of the average progress were ignored. The observation of budburst was thus made on a forest scale and included trees of different ages.

The full flowering of rowan (*Sorbus aucuparia*) and bird cherry (*Prunus padus*) were recorded as occurring when the flower buds were clearly open and the trees had turned white in their general appearance. The average date of the flowering was determined on the same basis as for the *Betula* spp. budburst.

### *Shrubs and grasses*

The observation of the full flowering of lingonberry (*Vaccinium vitis-idaea*) and of chickweed wintergreen (*Trientalis europaea*) represented the mean value of the event. The observations of these species were not made on a regular basis, so the time series are lacking in observations in some years.

The flowering of cultivated timothy grass (*Phleum pratense*) was recorded as two point events. The budburst was defined as occurring when 50% of the flower buds were opened, and full flowering as occurring when 100% of the flower buds had opened.

### *Insects*

The first observation of the red wood ants (*Formica rufa* group) was recorded based on the first anthill noted as active out of the ten observed. These anthills were situated in the Juhonsalo farmyard and in the nearby forest.

Other insect species observed were the dor beetle (*Geotrupes stercorarius*), horseflies (*Tabanidae*), bumblebees (*Bombus* spp.) and the small tortoiseshell (*Aglais urticae*); also noted was the first main swarm of mosquitoes (Culicidae). Observations of *Aglais urticae* were not included in the program every year.

## *Amphibians*

The spawning season of the common frog (*Rana temporaria*) was detected as the first croak heard.

## *Migratory birds*

The arrival date of migratory birds was observed for 18 species, with uncertain observations omitted. The first observation for species *Columba palumbus, Gallinago gallinago, Turdus philomelos* and *Cuculus canorus* was based on the first hearing of birdsong (and/or visual observation) and for species *Alauda arvensis* and *Fringilla coelebs* on both. The recording was based on the

**Table 2.** Statistics of observed phenological events (*see* Table 1) at Oulainen-Ohineva (64°13´N, 24°53´E) in 1952–2005. Species are listed according to ecological groups. Years = the earliest and the latest observed years, *N* = number of years with observations, CL = 95% confidence limits of the mean date, Earliest = date of the earliest observation, Latest = date of the latest observation, Range = difference (days) between the latest and the earliest observations, Trend: + = delayed occurence, – = advanced occurrence. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

| | Years | *N* | Mean date | CL (95%) (days) | Earliest | Latest | Range | Trend |
|---|---|---|---|---|---|---|---|---|
| Plants | | | | | | | | |
| 1. *Betula* spp. | 1952–2005 | 53 | 18 May | 2.1 | 1 May 1988 | 1 June 1996 | 31 | –1.07 |
| 2. *Sorbus aucuparia* | 1952–2005 | 54 | 15 June | 1.8 | 2 June 2002 | 3 July 1955 | 31 | –2.54 |
| 3. *Prunus padus* | 1955–2005 | 45 | 2 June | 2.2 | 17 May 1993 | 19 June 1955 | 33 | –7.03 |
| 4. *Vaccinium vitis-idaea* | 1961–1984 | 11 | 12 June | 4.5 | 1 June 1974 | 25 June 1964 | 24 | –8.61 |
| 5. *Trientalis europaea* | 1961–1984 | 11 | 2 June | 4.5 | 23 May 1981 | 11 June 1965 | 19 | **–16.42**$^{**}$ |
| 6a. *Phleum pratense* b. | 1970–2005 | 36 | 23 June | 1.6 | 14 June 1984 | 1 July 1982 | 17 | 2.05 |
| 6b. *Phleum pratense* f. | 1970–2005 | 36 | 19 July | 2.0 | 9 July 1989 | 31 July 1987 | 22 | –0.36 |
| Insects | | | | | | | | |
| 7. *Formica rufa* group | 1964–2005 | 42 | 6 April | 3.0 | 11 March 1997 | 24 April 1970 | 44 | **–12.21**$^{*}$ |
| 8. *Geotrupes stercorarius* | 1962–1993 | 6 | 17 May | 10.0 | 9 May 1973 | 5 June 1965 | 27 | –10.56 |
| 9. Culicidae | 1973–2004 | 9 | 4 June | 4.6 | 26 May 1984 | 11 June 1997 | 16 | 7.44 |
| 10. *Tabanidae* | 1953–2005 | 48 | 15 June | 2.7 | 22 May 1993 | 1 July 1982 | 40 | –1.52 |
| 11. *Bombus* spp. | 1957–2005 | 38 | 1 May | 2.4 | 13 April 1967 | 14 May 1958 | 30 | –6.13 |
| 12. *Aglais urticae* | 1960–2005 | 11 | 15 April | 4.8 | 2 April 1974 | 28 April 1966 | 26 | –9.09 |
| Amphibians | | | | | | | | |
| 13. *Rana temporaria* | 1952–2005 | 54 | 6 May | 1.8 | 22 April 1990 | 28 May 1955 | 36 | **–7.62**$^{*}$ |
| Birds | | | | | | | | |
| 14. *Vanellus vanellus* | 1965–1982 | 16 | 17 April | 4.2 | 30 March 1968 | 4 May 1971 | 35 | –4.63 |
| 15. *Numenius arquata* | 1954–2005 | 33 | 22 April | 1.9 | 7 April 1967 | 1 May 1988 | 24 | –2.03 |
| 16. *Alauda arvensis* | 1953–2001 | 32 | 15 April | 2.3 | 3 April 1959 | 27 April 1966 | 24 | 4.97 |
| 17. *Turdus pilaris* | 1957–2005 | 30 | 24 April | 3.2 | 5 April 1958 | 20 May 1970 | 45 | 3.89 |
| 18. *Turdus merula* | 1969–1974 | 4 | 10 April | 18.0 | 26 March 1973 | 22 April 1974 | 27 | – |
| 19. *Sturnus vulgaris* | 1954–1994 | 18 | 16 April | 3.7 | 1 April 1973 | 30 April 1970 | 29 | 6.44 |
| 20. *Grus grus* | 1952–2005 | 54 | 19 April | 2.0 | 4 April 1991 | 9 May 1973 | 35 | **–13.98**$^{***}$ |
| 21. *Columba palumbus* | 1958–2005 | 33 | 21 April | 2.2 | 8 April 1994 | 3 May 1986 | 25 | –4.49 |
| 22. *Fringilla coelebs* | 1954–2005 | 52 | 13 April | 2.1 | 26 March 1990 | 3 May 1966 | 38 | –6.04 |
| 23. *Gallinago gallinago* | 1955–2005 | 48 | 29 April | 2.3 | 4 April 1995 | 15 May 1981 | 41 | –6.84 |
| 24. *Motacilla alba* | 1952–2005 | 54 | 21 April | 1.4 | 8 April 1983 | 2 May 1977 | 24 | –2.11 |
| 25. *Turdus philomelos* | 1956–1977 | 9 | 25 April | 4.6 | 15 April 1959 | 3 May 1956 | 18 | 4.17 |
| 26. *Ficedula hypoleuca* | 1974–2005 | 18 | 3 May | 5.0 | 9 April 2005 | 15 May 1980 | 36 | **–22.15**$^{**}$ |
| 27. *Motacilla flava* | 1952–2005 | 53 | 11 May | 1.3 | 28 April 1995 | 22 May 2005 | 24 | 0.96 |
| 28. *Hirundinidae* | 1952–2005 | 54 | 12 May | 1.6 | 2 May 1992 | 24 May 1965 | 22 | **–5.39**$^{*}$ |
| 29. *Oenanthe oenanthe* | 1957–1994 | 7 | 6 May | 7.5 | 23 April 1960 | 13 May 1973<br>13 May 1974 | 20 | 9.65 |
| 30. *Jynx torquilla* | 1961–1999 | 15 | 9 May | 4.8 | 23 April 1963 | 23 May 1999 | 31 | 10.85 |
| 31. *Cuculus canorus* | 1952–2005 | 54 | 19 May | 1.0 | 13 May 1961 | 29 May 1987 | 17 | 0.95 |

first individual observed at the observation site, i.e. the Juhonsalo farmyard. The observations of *Hirundo rustica* and *Delichon urbica* were not differentiated. *Delichon urbica* was recorded for the first time in 1957. In the 1960s altogether 60 couples nested at the site, of which 30 couples were *Delichon urbica* and 30 *Hirundo rustica*. Nowadays there are around 15 pairs, of which *Hirundo rustica* is dominant.

The migratory birds were grouped into three groups based on their wintering areas, i.e., short-distance (Europe), medium-distance (Mediterranean) and long-distance (Africa) migrants (*see* Table 1). The groupings were adopted from Rainio *et al*. (2006)

### Climatological data

Daily temperature (6 am, 12 noon, 6 pm local time) and precipitation data from the Finnish Meteorological Institute weather station Ruukki-Revonlahti (64°41´N, 25°05´E), situated 51 km from the observation site, were used to represent the daily mean temperatures for the Oulainen-Ohineva (64°13´N, 24°53´E) site, as the Oulainen-Ohineva weather station started to operate there in 1970. In the overlapping years, the daily mean temperatures correlated ($r = 0.99$) strongly between the two sites, which justified the use of temperature data from Ruukki-Revonlahti for the years 1952–1969. The mean anomaly of the mean spring temperature was based on the daily mean temperatures for March, April and May in the years 1952–2005. The monthly values of the NAO indices (January, February, March) were obtained from http://www.cru.uea.ac.uk/Cru/data/nao.htm.

### Statistical analysies

Statistics, including mean date, earliest and latest date, range between minimum and maximum date and 95% confidence limits, were calculated for each species (Table 2). The temporal trends were calculated as linear regressions (SAS ver. 9.1 PROC REG) between the year (independent variable) and the phenological dates. Dates were converted to day number starting from 1 January. The regression equations obtained were used to calculate the possible advance or delay in each observed phenological event between the earliest and the latest recorded date. A positive trend indicated that the onset date was delayed over the years, while a negative trend indicated advancement of the event concerned.

The relationships between phenological dates and climate variables (mean monthly temperatures and precipitation for March, April and May) were studied with linear regression analysis (SAS 9.1 PROC REG). For analysis of the relationship between the arrival dates of migratory birds and climate variables, we used monthly NAO-index values for January, February and March and the local mean monthly temperatures for March, April and May. The best model was selected stepwise with forward selection ($p = 0.05$) and backward elimination ($p = 0.10$).

### Phenological index

The local spring phenology index ($N = 418$) was constructed by calculating the mean of the anomalies of the local species: *Betula* spp., *Sorbus aucuparia*, *Prunus padus*, *Vaccinium vitis-idaea*, *Trientalis europaea*, *Rana temporaria, Formica rufa* group, *Geotrupes stercorarius*, *Tabanidae*, *Bombus* spp., *Aglais urticae* and *Culicidae*.

## Results

### Overview of phenological statistics and trends

The sequence of spring phenological events observed at Oulainen-Ohineva starts in early April with the first observations of ants, and ends in mid-July with the flowering of *Phleum pratense* (Fig. 1 and Table 2). The range between the earliest and the latest observations for the trees observed is around one month during the observation periods. The species-specific ranges of phenological events were greatest in May and diminished towards the summer. In plants, the greatest advancement was observed for *Prunus padus* with 7 days per 45 years, whereas for *Betula* spp. the corresponding value was only

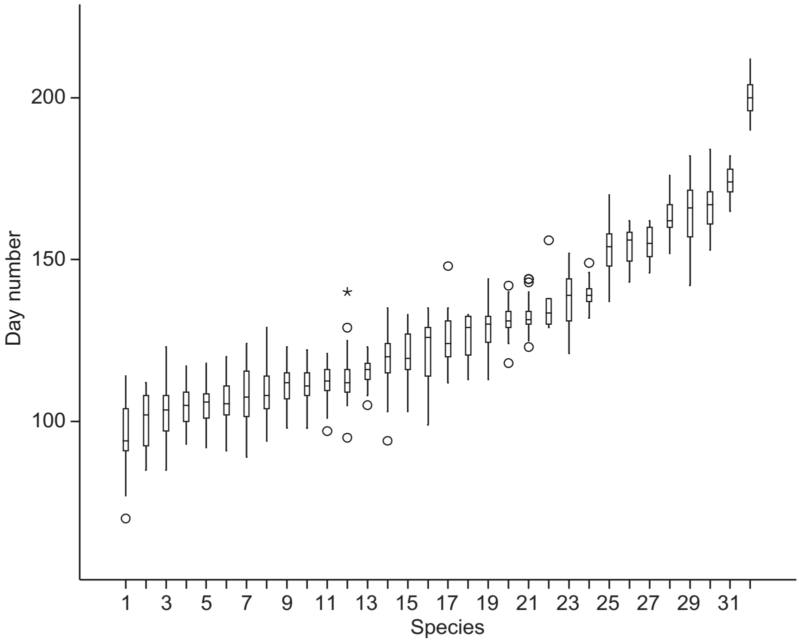

**Fig. 1.** The average timing of observed phenological events at the Oulainen-Ohineva site, as the number of days from 1 January during the period 1952–2005. The boxes show the median quartiles, extreme values of each species are shown as open circles and outlier observations are marked with asterisks: 1 = *Formica rufa* group, 2 = *Turdus merula*, 3 = *Fringilla coelebs*, 4 = *Alauda arvensis*, 5 = *Aglais urticae*, 6 = *Sturnus vulgaris*, 7 = *Vanellus vanellus*, 8 = *Grus grus*, 9 = *Columba palumbus*, 10 = *Motacilla alba*, 11 = *Numenius arquata*, 12 = *Turdus pilaris*, 13 = *Turdus philomelos*, 14 = *Gallinago gallinago*, 15 = *Bombus spp.*, 16 = *Ficedula hypoleuca*, 17 = *Rana temporaria*, 18 = *Oenanthe oenanthe*, 19 = *Jynx torquilla*, 20 = *Motacilla flava* , 21 = *Hirundinidae*, 22 = *Geotrupes*, 23 = *Betula spp.*, 24 = *Cuculus canorus*, 25 = *Prunus padus*, 26 = *Trientalis europaea*, 27 = *Culicidae*, 28 = *Vaccinium vitis-idaea*, 29 = *Tabanidae*, 30 = *Sorbus aucuparia*, 31 = *Phleum pratense* budburst and 32 = *Phleum pratense* flowering.

1 day per 53 years of observations. For fauna, the range in all the observed events was equal to or greater than 30 days. The highest variations, clearly over one month, were observed for *Formica rufa* group and *Tabanidae*. The greatest advancements were detected for the earliest events in spring for *Formica rufa* group: 12 days per 42 years, and for *Rana temporaria*: 8 days per 54 years of observations (Fig. 2).

The pattern of bird migration is such that species wintering in Europe will be the first to arrive, in April, followed by birds from the Mediterranean and Africa. On average the migratory birds from Europe arrive at Oulainen-Ohineva on 17 April followed, about one week later, by migratory birds from the Mediterranean area. The birds wintering in Africa arrive last, around 10 May. Furthermore, the omnivorous and granivorous bird species (*Alauda arvensis*, *Turdus pilaris*, *Turdus merula*, *Sturnus vulgaris*, *Grus grus*, *Columba palumbus*, *Gallinago gallinago* and *Turdus philomelos*), being short-distance migration species, arrive first, followed by the insectivore species, mainly the long-distance migratory species (*Fringilla coelebs*, *Ficedula hypoleuca*, *Motacilla flava*, *Oenanthe oenanthe* and *Cuculus canorus*) (Table 2).

There was no clear tendency regarding the magnitude of the inter-annual variation of the first observations between groups based on their wintering areas. It seems more likely that the differences are species-specific. The highest inter-annual variation, ranging over 40 days during the observation period from the early 1950s to 2005, was observed for *Motacilla alba*, *Gallinago gallinago* and *Turdus pilaris*. The smallest variation, 17 days, was observed for *Cuculus canorus*. *Turdus merula* was omitted due to the low number of observations ($N = 4$).

To summarize, 5 species (23%) out of 23

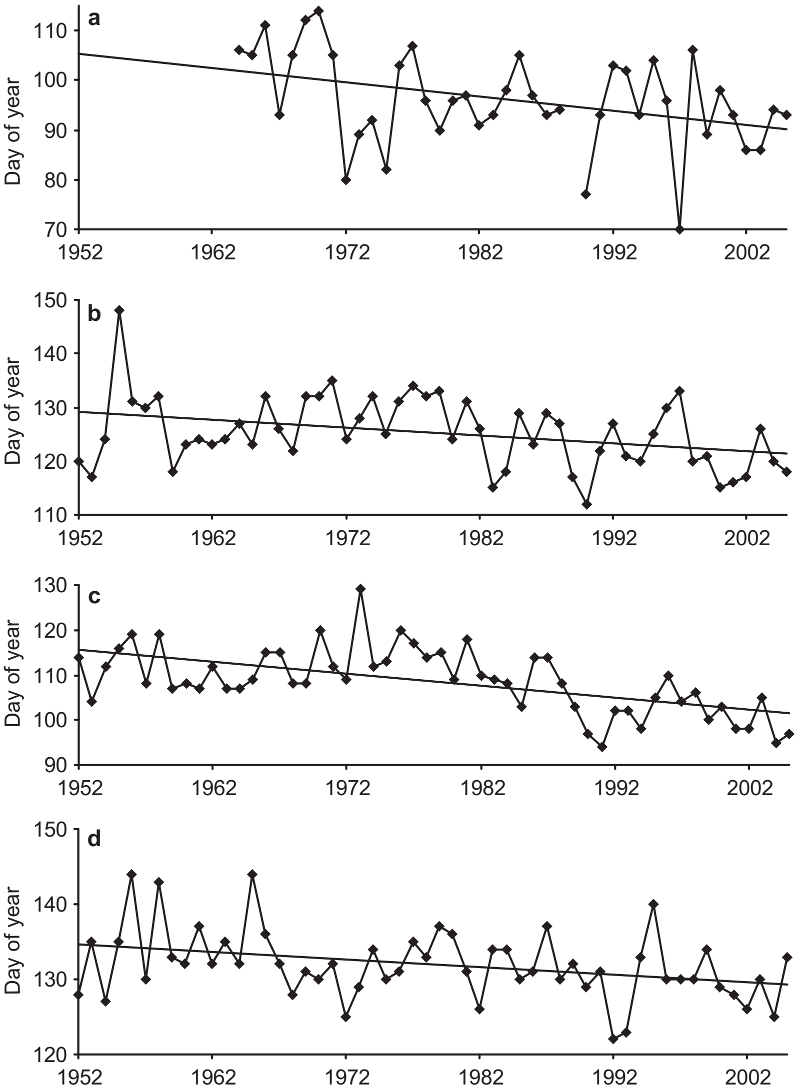

**Fig. 2.** Trends in the timing of phenological events with fitted linear regression models for the observed period (**a**) *Formica rufa* group ($y = -0.2977x + 686.47$, $R^2 = 0.14$), (**b**) *Rana temporaria* ($y = -0.1438x + 409.72$, $R^2 = 0.12$), (**c**) *Grus grus* ($y = -0.2638x + 630.5$, $R^2 = 0.33$), and (**d**) *Hirundinidae* ($y = -0.1017x + 333.13$, $R^2 = 0.1203$).

having more than 15 years of observations showed trends ($p < 0.05$) towards an earlier appearance. This advancing trend was observed for *Rana temporaria* and *Formica rufa* group representing local biota, and for the migratory birds *Ficedula hypoleuca*, *Grus grus* and *Hirundinidae* (Fig. 2). *Trientalis europaea* is omitted here due to the low number of observations ($N = 11$). No positive trends, indicating delays in arrival, were found for any of the studied species. However, although not statistically significant, we did also find some indications of delayed arrival. Among short-distance migrant birds ($N > 14$) the arrival of *Alauda arvensis* occured 5 days later in the 2000s than in the 1950s, *Turdus pilaris* arrived 4 days later in the 2000s than in the late 1950s and *Sturnus vulgaris* 6 days later in 1990s than in the 1950s; correspondingly, for long-distance migrants, *Motacilla flava* arrived 1 day later in the 2000s than in the 1950s, and *Jynx torquilla* 11 days later in the 2000s than in the mid-1960s

## The relation between phenology and climate variables

The Oulainen-Ohineva site is situated in the middle of the boreal vegetation zone typically

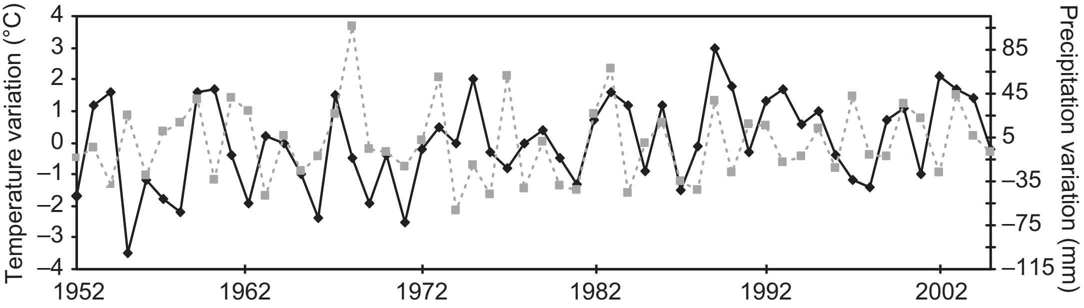

**Fig. 3**. Variations of the mean spring temperature (mean of 2.2 °C in March, April, and May) (continuous line) and the mean spring precipitation (mean of 89.76 mm in March, April and May) (grey dotted line) based on Ruukki-Revonlahti data (years 1952–2005).

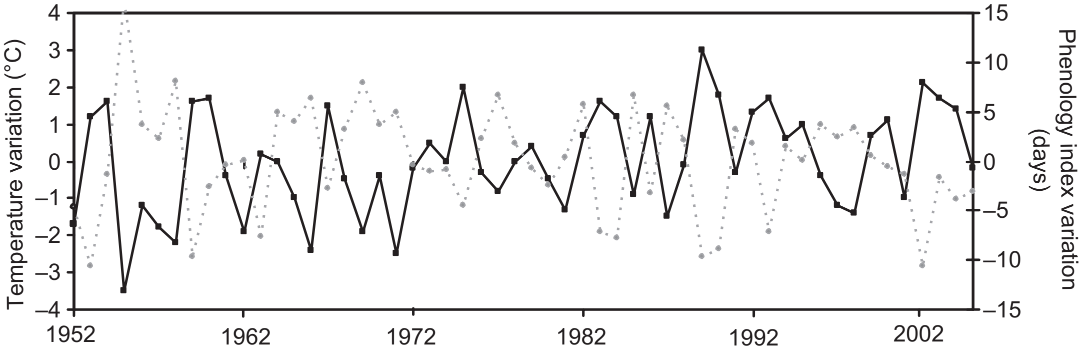

**Fig. 4.** Variations of the local spring phenology index (grey dotted line) and the mean spring temperature (mean of 2.2 °C March, April and May) (continuous line).

characterized by spruce–mire ecosystems and relatively large diurnal temperature changes and occasional night-time frosts in the summer. The individual yearly 3-month average values of temperature and precipitation sums (for March, April and May) differed from the corresponding long-term (1952–2005) average values by –3.5 to 3 °C and –20.23 to 35.01 mm, respectively. The trend in the temperature indicated warming of 1.6 °C for the period 1952–2005 (Fig. 3).

In order to obtain a holistic indication of the effects of temperature on local phenology, we formed a spring phenology index as the average date of the annual anomalies of local biota (Fig. 4). We first studied the relationships between spring temperature and phenological index with years (1952–2005) and then between phenological index and spring temperature. The relationship between temperature and year ($R^2 = 0.12$, $p = 0.0115$, $F = 6.86$) was positive, but relationship between phenological index and year was not significant ($R^2 = 0.03$, $p = 0.2361$, $F = 1.44$). The relation between the phenological index and spring temperature was statistically highly significant ($R^2 = 0.57$, $p < 0.0001$, $F = 67.46$). These results indicated that the timing of the spring phenology of local biota has advanced with warming of the climate by 3 days in 54 years parallel with the 1.6 °C rise in the spring temperature during the years 1952–2005.

In the regression model analysis of all local species having more than 38 years of observation, temperature turned out to be the best explanatory variable (Table 3). Only for *Bombus* spp. was March precipitation the best explanatory variable together with April temperature. In all these models, temperature had a negative effect, i.e., increasing temperature seems to advance the phenological event concerned (Table 3).

For birds, the NAO index was the strongest explanatory variable for six species out of the ten studied (Table 4). In four species out of ten, the mean temperature in April was selected as the best model. In all models where NAO was selected, it affected phenology in a similar manner to temperature, with positive values advancing the arrival of the birds. A minor exception was the best model for *Cuculus canorus*, where a positive NAO index in February delayed the timing of migration.

## Discussion

The Juhonsalo dataset provides a valuable resource with which to examine the long-term trends of spring phenological events in a middle-boreal forest. Albeit being from a single site, the material covers a wide range of species over a relatively long time-scale. The species selection covers local biota and a selection of migratory birds, with twenty species having over 30 years of observations. The Juhonsalo daily observation routines were performed in a systematic, detailed manner, so the data should avoid most of the subjective inaccuracy often related to these kind of observations (Menzel 2002).

We used a linear regression model to detect possible advancing or delayed long term-trends for each observed phenological event. The use of linear regression can be considered as a simple approach that may not reveal more complicated patterns of change. However, the observed periods, with a maximum time series of 54 years, are relatively short when the inter-annual variation of climate factors is considered: the use of more complicated trends would thus be highly questionable. Another aspect often related to spring phenological events is data autocorrelation reflecting, for example, a delayed impact of previous seasons. This feature can be seen e.g. in the intensity of the flowering of wind-pollinated boreal trees (Masaka and Makushi 2001, Ranta *et al*. 2005). The timing of the spring phenological events of boreal forest trees, however, seems to depend mostly on the temperature conditions in spring (Sarvas 1972, Cannell and Smith 1983,

**Table 3**. Stepwise regression analysis for local species and monthly mean temperatures (*T* in March, April, May) and precipitation (*P* in March-April-May) during period 1952–2000. The dependent variable (*y*) was the phenological event concerned.

| Species | Best model | *F* | $R^2$ | Pr > *F* | *N* |
|---|---|---|---|---|---|
| *Betula* spp. | $y = 157.02 - 2.49T_{APR} - 1.62T_{MAY}$ | 32.71 | 0.57 | < 0.0001 | 53 |
| *Prunus padus* | $y = 183.57 - 0.57T_{MAR} - 2.21T_{MAY}$ | 82.26 | 0.80 | < 0.0001 | 45 |
| *Sorbus aucuparia* | $y = 183.57 - 0.57T_{MAR} - 2.21T_{MAY}$ | 23.33 | 0.48 | < 0.0001 | 54 |
| *Formica rufa* group | $y = 94.26 - 1.26T_{MAR} - 1.89T_{APR}$ | 6.89 | 0.26 | 0.0119 | 42 |
| *Rana temporaria* | $y = 131.14 - 3.07T_{APR}$ | 113.68 | 0.69 | < 0.0001 | 54 |
| *Bombus* spp. | $y = 128.46 - 3.17T_{APR} - 2.66P_{MAR}$ | 26.62 | 0.60 | < 0.0001 | 38 |
| *Tabanidae* | $y = 168.89 - 1.67T_{APR}$ | 5.29 | 0.10 | 0.0261 | 48 |

**Table 4.** Stepwise regression analysis for migratory birds, NAO index (January, February, March) and monthly mean temperatures (*T*), period 1952–2000. The dependent variable (*y*) was the first observation.

| Overwintering area | Species | Best model | *F* | $R^2$ | Pr > *F* | *N* |
|---|---|---|---|---|---|---|
| Europe | *Fringilla clebs* | $y = 107.39 - 1.86T_{APR} - 1.56NAO_{JAN}$ | 23.52 | 0.52 | < 0.0001 | 47 |
| | *Alaunda arvensis* | $y = 108.83 - 2.54NAO_{JAN}$ | 20.46 | 0.41 | < 0.0001 | 31 |
| | *Sturnus vulgaris* | $y = 106.57 - 1.90NAO_{JAN}$ | 5.11 | 0.24 | 0.0380 | 18 |
| | *Numenius arquata* | $y = 112.14 - 1.61NAO_{MAR}$ | 10.81 | 0.29 | 0.0029 | 28 |
| Mediterranean | *Gallinago galinago* | $y = 124.47 - 2.5T_{APR}$ | 17.73 | 0.30 | 0.0001 | 43 |
| | *Motacilla alba* | $y = 114.05 - 1.65T_{APR}$ | 20.44 | 0.30 | < 0.0001 | 49 |
| | *Grus grus* | $y = 112.98 - 1.93T_{APR}$ | 15.45 | 0.25 | 0.0003 | 49 |
| Africa | *Motacilla flava* | $y = 132.76 - 0.87T_{APR}$ | 6.06 | 0.12 | 0.0176 | 48 |
| | *Hirundinidae* | $y = 132.64 - 0.63NAO_{FEB}$ | 4.13 | 0.08 | 0.0479 | 49 |
| | *Cuculus canorus* | $y = 139.52 - 0.69NAO_{JAN} + 0.482NAO_{FEB}$ | 5.75 | 0.20 | 0.0059 | 49 |

Häkkinen and Hari 1988, Linkosalo *et al*. 2006), and the studies on these events do not indicate delays. From an evolutionary point of view, it would make little sense, as the weather itself does not show such an autocorrelation between successive years.

The onset of bird migration is generally known to be triggered by changes in day length, but insectivore birds would benefit if they could optimize the timing of their arrival in relation to the availability of local nutriment (Sparks 1999). At Oulainen-Ohineva the local insect first occurrences, an essential part of migratory birds' nutrition, were not delayed.

The rising trend of mean spring temperatures at the Oulainen-Ohineva site got us interested in studying the changes in spring phenology in the context of climate change. As demonstrated by phenological modelling studies, temperature is known to be the key factor controlling the timing of the spring phenological events of plants (Sarvas 1972, Cannell and Smith 1983, Hänninen and Kramer 2007). Furthermore, day length has been included in these types of models (Suni *et al*. 2003). For birds the role of the NAO index is demonstrated by several recent studies (Sparks *et al*. 2005, Stervander *et al*. 2005, Jonzen *et al*. 2006, Rainio et al. 2006).

## Local flora

The unexpected result was that none of the local plant species (*Trientalis europaea* omitted, however, due to the low number of years observed) had a statistically significant advancing trend in the timing of occurrence of their phenological events. Similar results, with no change in long-term phenological trends, have been presented for some plant species growing in the most northern part of Europe, i.e., in the Kola Peninsula (Kozlov and Berlina 2002, Shutova *et al*. 2006). Kozlov and Berlina (2002) did not find any changes in the spring phenology of mountain birch leaf unfolding, or in the onset of flowering of lingonberry and cloudberry in the observations from taiga forest during the observation period of 1930 to 1998. Furthermore, Shutova *et al*. (2006) detected no significant changes in the timing of bud burst of Nordic mountain birch (*Betula pubescens* ssp. *tortuosa*) during 1964–2003.

The local temperature trend at the Oulainen-Ohineva site, indicating warming of 1.6 °C degrees over a 53-year period (in spring: March, April, May), led us to expect to find an advancing trend in the timing of spring phenology. The outcome, that only two local specific species showed such an advancement, made us think that a possible trend might be obscured by the inter-annual variation in the weather and thus also in the events themselves. In these kinds of situations the use of a phenological index or a "statistical plant" estimate have been used in order to overcome the problems of short or sparse datasets (Studer *et al*. 2005). The phenological index calculated for the Oulainen-Ohineva site, supporting the robust expectation that the timing of the spring phenology of biota has advanced with warming of the climate by 3 days in 54 years, was not however statistically significant. Menzel (2000) reported an advancement of, on average, 6.3 days in Europe during a period of 30 years (1959–1996). Shutova *et al*. (2006) speculated that the reason for a possible different response in the north could be related to the positive North Atlantic Oscillation resulting in higher precipitation. In spring at higher elevations and in cold regions the increased snow cover may melt later and thus delay the local phenology. In fact, the current phenological datasets from northern Scandinavia are spatially sparse and allow us only to speculate on the long-term response of spring phenology to climate change, whether it is different in central Europe as compared with that in northern Europe or not. Supporting satellite observations, providing the normalized difference vegetation index NDVI data, will prove to be useful for detecting this kind of larger-scale and ecosystem level changes in phenology (Chen *et al*. 2000, Cook *et al*. 2005).

The changes in the timing of species-specific annual events also raises the question as to whether they alter population level interactions. Fitter and Fitter (2002) studied an extensive dataset, a comparison of over three hundred species, and reported that, in Britain, insect-pollinated species showed a greater advancement than wind-pollinated ones. In plants, for example, we had both wind- (*Betula* spp.) and insect- (*Prunus* *padus*, *Sorbus acuparia*) pollinated species. In our case no difference was found for these species in their flowering confidence limit values. Furthermore they demonstrated that flowering is especially sensitive to temperature in the previous month, which was also the case in our study. Sparks (2000) suggested that insect-pollinated plants should have a tendency to remain in approximate synchrony with the pollinating species upon which they rely. In the Oulunsalo-Oulainen dataset, in the case of *Bombus* spp., pollinator species, the start of the first flight occurred 6 days earlier in the 2000s as compared with that in the late 1950s. The discrepancy with the timing of the insect-pollinated plant species included in this dataset may be due to *Bombus* spp. having their first flight relatively early in the spring, on average on 1 May.

## Local fauna

The phenological recordings of local fauna at Oulainen-Ohineva covered three prominent time series for insect species and for the Eurasian frog. The trend for local fauna was 2 days advancement in 42 years, with 1 day of advancement for *Formica rufa* group and 8 days of advancement for *Rana temporaria* over 54 years, both species being poikilothermic and consequently strongly affected by changes in temperature (Walther *et al*. 2002, Risch *et al*. 2005). In the case of *Formica rufa* group the impact of micro-climatological conditions is also prominent. At Oulainen-Ohineva the first observation was based on the monitoring of ten anthills. As a consequence of different insolation conditions, the variation between the anthills was on average two weeks, some hills still having snow cover while others in sunny places had thawed out. The reproductive physiology of *Rana temporaria* is also heavily influenced by temperature, but depends also on humidity (Walther *et al*. 2002). However, in our study, temperature alone turned out to be the best explanatory variable for both species.

One of the most representative time series in the Oulunsalo-Oulainen data set was the first flight of *Tabanidae*. *Tabanidae* are known to lay their eggs in swampy soil or aquatic environment areas, where they hatch into larvae. Development is generally considered to take place somewhat underground, and it is very difficult to estimate how long it takes for a larva to develop into a mature fly. Meteorological factors, especially spring temperature, are very important for the beginning of the flight activity of tabanids (Krcmar 2005). In our case we did not detect any advancing trend during the observation period. The mean date for the first swarm was 15 June; however, the mean temperature of April, i.e., two months earlier, turned out to be the best explanatory variable for the first observation of a *Tabanidae* main swarm.

## Migratory birds

Along with local biota, the first observation of migratory birds formed a separate group of observations in the Juhonsalo dataset. This dataset also included some signs of potential population declines in birds that might have been seen at the Oulainen-Ohineva site. *Sturnus vulgaris*, for example, was abundant during the first decades of the observation period, but is nowadays missing. *Oenanthe oenanthe* has vanished from the observation site since 1995 and *Alauda arvensis* since 2000. These observations are interesting, since recent climate changes have also been linked to both increases and rapid declines in population sizes (McCarthy 2001). The reason behind these potential declines may also be related to local environmental and structural changes in forestry or agriculture in their typical distribution areas in Finland.

At the Oulainen-Ohineva site, omnivorous and granivorous bird species arrived first, followed by the insectivorous species that are long-distance migrants. Even if the onset of migration is triggered by the changing day length, climatic conditions at the destination should also be considered. Invertebrate production is closely related to climate, and insectivore birds will benefit if their arrival time is optimized and fine-tuned to local climatic conditions (Sparks 1999). According to Walter *et al*. (2002), it generally seems that short-distance migrating species, which tend to migrate early in the season, often exhibit a trend towards earlier arrival, whereas the later arrivals, the long-distance migrants, show a more complex response, with many species not changing their arrival times at all or even delaying them.

An advancing trend was detected for three species, namely *Grus grus,* a medium-distance migrant, and *Ficedula hypoleuca* and *Hirundinidae*, both being long-distance migrants. Similar kinds of results have been reported in other studies. Sparks (1999) detected an advancing trend for swallows in Britain. Jonzen *et al.* (2006) reported a rapid advancement of spring arrival in Scandinavia for long-distance migratory birds compared to short-distance migrants. The observations in Finland were obtained from the southern coast, thus representing the percentiles of arrival observations in Finland. Even though the Oulainen-Ohineva site is situated about 650 km north of this point, the results for *Ficedula hypoleuca* and *Hirundinidae* were in line with those results. Also Sparks *et al.* (2005) reported a trend towards earlier arrival of *Ficedula hypoleuca*, with data obtained from Finland's southern coast. Although these results are parallel, it should be kept in mind that inter-comparison is difficult, due to the different observation methods utilized in data collection. In particular, the first arrival date may not be comparable to the mean arrival date (Sparks *et al.* 2001, Stervander *et al.* 2005).

In general, the changes of arrival times during the observed periods at the Oulainen-Ohineva site showed a considerable variation from one species to another, and for some species even indicated delays. These opposite changes indicate the complexity of the event, especially with birds. Consequently, some long-distance migrants may be expected to suffer from the climate change, either because their migration strategy is unaffected by climate changes, or because the climate in their breeding and wintering areas may be changing at different rates, preventing adequate adaptation (Both and Visser 2001).

It would be a challenging task to analyze the dataset of migratory species taking into account the appropriate temperatures along the migration route and at the destination, as well as the prevailing wind conditions (Sparks 1999). Several studies have also demonstrated the effect of large-scale climate features like the Northern Atlantic Oscillation (NAO) on the timing of bird migration (Vähätalo *et al.* 2004, Stervander *et al.* 2005). In our case, the NAO index was the best explanatory variable for four species out of ten, with April mean temperature the best in five cases out of ten. In all models for which NAO was selected, it behaved in the same direction as temperature, advancing the arrival of birds. Rainio *et al.* (2006) studied the migration of boreal and arctic bird species from different wintering areas, utilizing a more extensive dataset, and found that most species arrive earlier after a winter with a high NAO-index. Furthermore, the degree of NAO response diminished with the phase of migration. The wintering area affected the strength of the NAO response in a complicated way. In general, medium-distance migrants responded most strongly, followed by the short-distance and partial migrants. The importance of examining the whole distribution of migration warrants the use of datasets from several sampling stations when studying climatic effects on the timing of avian life history events (Rainio *et al.* 2006). Our data allowed us to study only a single-point event as a measure of phenology; in spite of data limitations, the first observation of eighteen migratory bird species did provide parallel results to earlier studies on their migratory behaviour, indicating that some long-distance migrants have advanced their spring arrival in Scandinavia

## Conclusions

Many recent research results covering wide geographical ranges have indicated a definite advancement in spring phenology. The Juhonsalo 54-year-long dataset, from a single site situated in the middle boreal forest zone in Finland, and covering a relatively large selection of species, showed only partly parallel results. The advancing trend in spring phenology as a whole was not as strong as one might expect. The local phenological index did not show statistically significant advancement, and studying species-specific time series, only five species showed a statistically significant advancing trend during the observation period. Furthermore, three of these five advanced trends were for migratory birds known to be subject to environmental factors over the whole migration route. Our approach was based on the assumption of linear changes.

However, the changes might also be abrupt and then take another form; to detect such phenomena, a longer dataset would be needed.

*Acknowledgements*: We thank Aarne Juhonsalo for providing the Oulainen-Ohineva dataset for our use. We also thank Jyrki Lappalainen and two anonymous referees for their valuable comments that considerably improved the manuscript.

## References

Both C. & Visser E.M. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411: 296–298.

Cannell M.G.R. & Smith R.I. 1983. Thermal time, chill days and prediction of budburst in *Picea sithensis*. *J. App. Ecol.* 20: 951–963.

Chen X., Tan Z., Scwartz M.D. & Xu C. 2000. Determining the growing season of land vegetation on the basis of plant phenology and satellite data in North China. *Int. J. Biometeorol.* 44: 97–101.

Chmielewski F.-M. 1996. The international phenological gardens across Europe: present state and perspectives. *Phenol. Season.* 1: 19–23.

Cook B.I., Smith T.M. & Mann M.E. 2005. The North Atlantic Oscillation and regional phenology prediction over Europe. *Global Change Biol.* 11: 919–926.

Fitter A.H. & Fitter R.S.R. 2002. Rapid changes in fowering time in British plants. *Science* 296: 1689–1691.

Hughes L. 2000. Biological consequences of global warming: is the signal already. *Trends Ecol. Evol.* 15: 56–61.

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

Häkkinen R. & Hari P. 1988. The efficiency of time and temperature driven regulation principles in plants at the beginning of the active period. *Silva Fennica* 22: 163–170.

Hänninen H. & Kramer K. 2007. A framework for modelling the annual cycle of trees in boreal and temperate regions. *Silva Fennica* 41: 167–205.

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.

Kozlov M.V. & Berlina N.G. 2002. Decline in the length of the summer season on the Kola Peninsula, Russia. *Climate Change* 54: 387–398.

Krcmar S. 2005. Seasonal abundance of horse flies (Diptera: Tabanidae) from two locations in eastern Croatia. *J. Vector Ecol.* 30: 316–321.

Kullman L. 2001. 20th century climate warming and tree-limit rise in the southern Scands of Sweden. *Ambio* 30: 72–80.

Lappalainen H. & Heikinheimo M. 1992. *Relations between climate and plant phenology. Part 1 Survey of plant phenological observations in Finland from 1896 to 1965*. Meteorological publications No. 20, Finnish Meteorological Institute.

Lehikoinen E., Sparks T.H. & Zalakevicius M. 2004. Arrival and departure dates. In: Møller A.P., Fiedler W. & Berthold P. (eds.), *Birds and climate change*, Adv. Ecol. Res. 35, Elsevier Science, London, pp. 1–31.

Linkosalo T., Häkkinen R. & Hänninen H. 2006. Models of the spring phenology of boreal temperate trees; is there something missing? *Tree Physiology* 26: 1165–1172.

Luterbacher J., Dietrich D., Xoplaki E., Grosjean M. & Wanner H. 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. *Science* 303: 1499–1503.

Masaka K. & Maguchi S. 2001. Modelling the masting behaviour of *Betula platyphylla* var. *japonica* using the resource budget model. *Ann. Bot.* 88: 1049–1055.

McCarthy J. 2001. Ecological consequences of recent climate changes. *Conserv. Biol.* 15: 320–331.

Menzel A. 2000. Trends in phenological phases in Europe between 1951 and 1996. *Int. J. Biometeorol.* 44: 76–81.

Menzel A. 2002. Phenology: Its importance to the Global Change community — an editorial Comment. *Climatic Change* 54: 379–385.

Menzel A. 2003. Plant phenological anomalies in Germany and their relation to air temperature and NAO. *Climatic Change* 57: 243–263.

Menzel A. & Fabian P. 1999. Growing season extended in Europe. *Nature* 397: 659.

Menzel A., Sparks T., Estrella N., Koch E., Aasa A., Aha R., Alm-Kuber K., Bissolli P., Braslavska O., Briede A., Chemielewski F.M., Crepinsek Z., Curnel Y., Dhal Å., Defela C., Donnelly A., Filella Y., Jatczak K., Måge F., Mestre A., Nordli O.O.O., Panuelas J., Pirinen P., Remosiva V., Scheifinger H., Striz MMM., Susnik A., Van Vliet A., Wilegolaski F.-M., Zach S. & Zust A. 2006. European phenological response to climate change matches the warming pattern. *Global Change Biol.* 12: 1969–1976.

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

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

Ranta H., Oksanen A., Hokkanen T., Bondestam K. & Heino S. 2005. Masting by *Betula* species; applying the resource budget model to north European data sets. *Int. J. Biometeorol.* 49: 146–151.

Risch A.-C., Schutz M., Jurgensen M.-F., Domisch T., Ohashi M., Finer L. 2005. $CO_2$ emissions from red wood ant (*Formica rufa* group) mounds: seasonal and diurnal patterns related to air temperature. *Ann. Zool. Fennici* 42: 283–290.

Sarvas R. 1972. Investigations on the annual cycle of development of forest trees. Active period. *Communicationes Instituti Forestalis Fenniae* 76: 1–110.

Shutova E., Wielgolaski F.E., Karlsen S.R., Makarova O., Berlina N., Filimonova T., Haraldsson E., Aspholm P.E., Flø L. & Høgda K.A. 2006. Growing seasons of Nordic mountain birch in northernmost Europe as indicated by long-term field studies and analyses of satellite images. *Int. J. Biometeorol* 51: 155–166.

Sparks T.H. 1999. Phenology and the changing pattern of bird migration in Britain. *Int. J. Biometeorol*. 42: 134–138.

Sparks T.H., Jeffree E.P. & Jeffree E.C. 2000. An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from UK. *Int. J. Biometeorol*. 44: 82–87.

Sparks T., Roberts D.R. & Crick H. 2001. What is the value of the first arrival dates of spring migrants in phenology? *Avian Ecol. Behav*. 7: 75–85.

Sparks T.H., F. Bairlein F., Bojarinova J.G., Huppop O., Lehikoinen E.A., Rainio K., Sokolov L.V. & Walker D. 2005. Examining the total arrival distribution of migratory birds. *Global Change Biology* 11: 22–30.

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

Stervander M., Lindström Å., Jonzen N. & Andersson A. 2005. Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *J. Avian Biol*. 36: 210–221.

Studer S., Appenzeller C. & Defila C. 2005. Inter-annual variability and decadal trends in Alpine spring phenology: a multivariate analysis approach. *Climate Change* 73: 395–414.

Suni T., Berninger F., Markkanen T., Keronen P., Rannik U. & Vesala T. 2003. Interannual variability and timing of growing-season CO2 exchange in a boreal forest. *J. Geophysical Research, Atmospheres* 108, D9, 4265, doi:10.1029/2002JD002381

Tuomenvirta H. 2004. Reliable estimation of climatic variations in Finland. *Finnish Meteorological Institute, Contributions* 43: 1–80.

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

Vähätalo A.V, Rainio K., Lehikoinen A. & Lehikoinen E. 2004. Spring arrival of birds depends on the North Atlantic Oscillation. *J. Avian Biol*. 35: 210–216.

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.