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Life history events of the Eurasian sparrowhawk *Accipiter nisus* in a changing climate

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Current climate change has been found to advance spring arrival and breeding dates of birds, but the effects on autumn migration and possible responses in the distribution of wintering individuals are poorly known. To thoroughly understand the consequences of climate change for animal life histories and populations, exploration of whole annual cycles are needed. We studied timing of migration (years 1979–2007), breeding phenology (1979–2007) and breeding success (1973–2007) of Eurasian sparrowhawks *Accipiter nisus* in Finland. We also investigated whether the migration distance of Finnish sparrowhawks has changed since the 1960s, using ringing recovery records. Since the late 1970s Finnish sparrowhawks have advanced their spring arrival, breeding and autumn departure considerably, but the migration distance has not changed. Early migrants, who are the ones with the highest reproductive success, show the strongest advance in the timing of spring migration. In autumn, advanced departure concerns young sparrowhawks. Late autumn migrants, who are mainly adults, have not advanced their migration significantly. The sparrowhawk is the most common bird of prey and the main predator of most passerines in Finland. Therefore, changes in sparrowhawk migration phenology may affect the migration behaviour of many prey species. The breeding success of sparrowhawks has increased significantly over the study period. This is however more likely caused by other factors than climate change, such as reduced exposure to organochlorine pollutants.

Recent climate change has been shown to affect the spring phenology of different organisms (Roy and Sparks, 2000, Abu-Asab et al. 2001, Philippart et al. 2003, Stefanescu et al. 2003, Lehikoinen et al. 2004, Menzel et al. 2006). In birds, several studies have shown advanced spring migration and laying dates to be associated with increased ambient temperatures. Our knowledge about the potential effects of climate change on avian reproductive performance, timing of autumn migration and location of wintering areas are still limited, partly due to the fact that studies on responses to climatic change among birds are highly biased towards small sized passerines, and breeding data mainly concern species breeding in nest boxes or colonial seabirds (Böhning-Gaese and Lemoine 2004, Dunn 2004, Lehikoinen et al. 2004, Newton 2008). The reason for this bias may be the proposition that responses to climate change are weaker in large-sized species compared to small-sized ones (Stevenson and Bryant 2000, Perry et al. 2005). Considering the narrow taxonomic span of studies regarding avian responses to climate change, it is clear that more information is needed before this view can be rigorously anchored.

Some recent studies have put forward evidence that both breeding and wintering ranges of several northern Hemisphere bird species are moving north or northeast (breeding areas: Böhning-Gaese and Lemoine 2004, Brommer 2004, Hitch and Leberg 2007; wintering areas e.g. Nilsson 2005, La Sorte and Thompson 2007, Rivalan et al. 2007, Newton 2008). However, the majority of such studies have concentrated only on one seasonal life history event at a time (arrival, breeding, departure or wintering).

Our aim was to find out how weather conditions affect the phenology of different life history events in a small-sized raptor species, the Eurasian sparrowhawk *Accipiter nisus* (hereafter sparrowhawk). Newton (1986) has shown that dry and warm conditions during April advance the timing of breeding and increase breeding success in British sparrowhawks probably by affecting the hunting conditions and thus resources used for egg laying (Newton 1986). Weather conditions during the post hatch period are also important because of their effect on the survival of small raptor nestlings (Kostrzewa and Kostrzewa 1990, Lehikoinen et al. 2009).

Breeding of sparrowhawks has been studied earlier in relation to climate change and Nielsen and Møller (2006) and Both et al. (2008) have reported that sparrowhawks in Central Europe have not advanced their breeding, despite a rapid advance in the timing of breeding of many important prey species. The novelty of the present study is that our over 29 years long dataset covers all main annual events from migration to breeding and wintering. To the best of our knowledge, this is the first study that investigates the effect of climate change on phenology and spatial distribution during the entire annual cycle of any bird species.

Methods

Study species

The breeding distribution of the sparrowhawk covers large areas of Eurasia, from Ireland (10° W) to Kamchatka (160° E) (Cramp and Simmons 1980). Birds breeding in Northern Europe are mostly short distant migrants and typically winter in western Europe (e.g. Cramp and Simmons 1980, Saurola 1981). The sparrowhawk is the most abundant raptor species in Europe (BirdLife International 2004), and in Finland thousands of individuals have been ringed and later recovered during autumn, winter and spring (Saurola 1981, Valkama and Haapala 2008). According to the Finnish bird-of-prey monitoring program, the sparrowhawk has shown a weak declining population since the early 1990s (Honkala and Saurola 2008, Saurola 2008). However, the migration numbers of Hanko Bird Observatory show an increasing trend during 1979–2007 (Lehikoinen et al. 2008).

Sparrowhawks mainly arrive in Finland during April (Lehikoinen and Vähätalo 2000; see also Fig. 1), and show a tendency to arrive earlier after milder winters (as measured by the NAO-index; Vähätalo et al. 2004). Egg-laying usually takes place in early May and chicks hatch in June (Solonen 1985; see also Fig. 2). The young fledge at an age of one month and they leave their breeding areas soon after the parents have ceased feeding them about four weeks after fledging (Cramp and Simmons 1980, Solonen 1985, Newton 1986). During the autumn young birds migrate south before the adults (Cramp and Simmons 1980, Saurola 1981, Kjellén 1992).

Measuring migration phenology

To assess the timing of spring and autumn migration, we used daily count data on migrating sparrowhawks collected at the Hanko Bird Observatory (59° 49'N, 22° 54'E) during 1979–2007 (Lehikoinen and Vähätalo 2000, Vähätalo et al. 2004). The spring migration period was considered to span the period from 20 February to 30 June, and the autumn migration 15 July to 30 November. The springs 1989, 1990 and 1993 were excluded from the analysis due to poor observation activity (<20 days of observation), or too little data (<20 observed individuals). The spring migration data included a total of 2 318 individuals (average: 89 individuals/year, range 21–188) and the autumn migration data 117 107 individuals (average: 4 038 individuals/year, range 795–7 862). The large difference between spring and autumn numbers cannot be attributed entirely to reproduction, but is further pronounced by small-scale differences in seasonal migration routes. The autumn migration is funnelled to the south-western tip of the Hanko peninsula, where the observatory is situated, whereas the spring migration moves in a broad front over southwest Finland.

The timing of both spring and autumn migration was modelled using seasonal distribution curves (Knudsen et al. 2007), describing the expected daily numbers of observed birds. When focusing on large-scale seasonal patterns, this approach is robust for bias caused by missing days of observation and noise introduced by day-to-day variation in migration intensity (Knudsen et al. 2007). Expected daily numbers of observed birds for the spring migration were modelled using a skew normal distribution (Azzalini 1985), multiplied by a constant to adjust the height of the distribution to the total number of migrating birds. Expected daily numbers of observed birds for the autumn migration were modelled using the sum of two normal distributions with potentially different heights (Knudsen et al. 2007). This approach was chosen because juveniles and adults migrate at different times (Kjellén 1992). The models were fitted by maximum likelihood estimation, assuming that the count for a specific day (N_i) was scattered around its expectation (λ_i) according to a negative binomial distribution (see Equation 1). The parameter w denotes overdispersion in comparison to a pure Poisson process, such that low values gives higher variance.

$$N_i \sim \text{NegBin}\left(w, \frac{w}{(w + \lambda_i)}\right) \qquad (1)$$

The 5_{th}, 50_{th} and 95_{th} percentiles were calculated from the fitted curves for each season, to describe migration start,

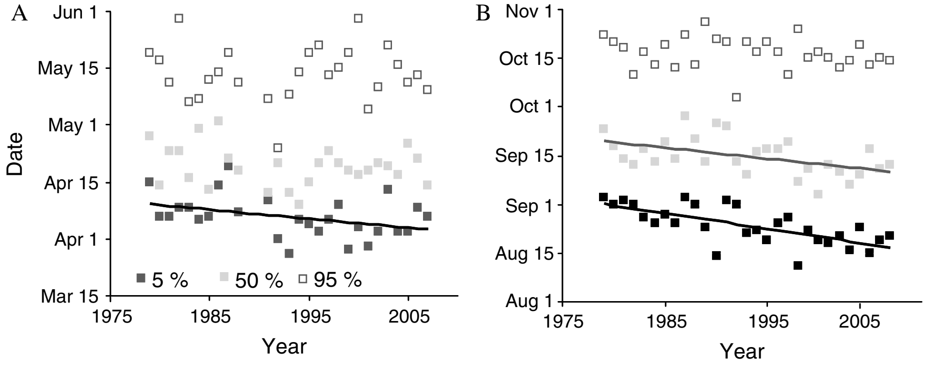

Figure 1. The timing of spring (A), and autumn (B), migration of sparrowhawks at Hanko in 1979 – 2007. The migration is divided into early (5th percentile), median and late (95th percentile) migrants. Solid regression lines indicate significant advancement (model Yr, linear trend, in Table 2). Phenology trends in spring were -0.40 ± 0.13, -0.15 ± 0.08 and 0.04 ± 0.11 for 5th, 50th and 95th percentile, respectively, and in autumn -0.38 ± 0.10, -0.31 ± 0.11 and -0.15 ± 0.10 for 5th, 50th and 95th percentile, respectively.

median and end, respectively. Separate curves with independent parameters were fitted for each season. Numerical minimization of the deviance ($-2 \times$log-likelihood) was done iteratively using the Nelder–Mead simplex algorithm in MATLAB® (version 7.6.0, R2008a, Natick, Massachusetts: The MathWorks Inc.). Each season specific search had a different starting value and was repeated a maximum of 1000 times, or until 100 consecutive converged results were produced, without improving the previous best fit. All solutions were visually judged to provide at least reasonably good descriptions of the seasonal variation in migration numbers. For spring seasons, five parameters were fitted: location (ξ), scale (θ), shape/skewness (α), total expected number of migrating birds (n) and overdispersion of residuals (w). As starting values we used log-normally distributed random values with a coefficient of variation (CV) of 0.20 and expectations as following: $E(\xi)$ = sample mean, $E(\theta)$ = sample standard deviation, $E(\alpha) = 0$, $E(n)$ = the total number of observed birds and $E(w) = 1$. For autumn the two summed normal distributions were described with seven parameters: the means for distribution 1 and 2 ($\mu1$; $\mu2$), corresponding standard deviations ($\sigma1$; $\sigma2$), expected number of birds (n1; n2) and the overdispersion of residuals (w). The starting values for these parameters were also randomly log-normally distributed with CV = 0.20 and expectations: $E(\mu1) = E(\mu2)$ = sample mean, $E(\sigma1) = E(\sigma2)$ = sample standard deviation, $E(n1) = E(n2)$ = the total number of observed birds/2 and $E(w) = 1$. The correlation ($\pm$ SE) between percentiles calculated from raw data and from fitted curves were in spring $r_p = 0.68 \pm 0.15$, $r_p = 0.63 \pm 0.16$ and $r_p = 0.54 \pm 0.17$, and in autumn $r_p = 0.89 \pm 0.09$, $r_p = 0.90 \pm 0.09$ and $r_p = 0.83 \pm 0.11$ for 5%, 50% and 95% percentiles, respectively. This indicates that the used approach corresponds quite well to using raw percentiles for the autumn data. In spring the lower correlation is probably due to much lower numbers, introducing more noise in the estimates of percentiles. The used approach, accounting for missing days and daily variation, is likely to effectively improve these estimates.

Breeding data

Breeding data included 5 717 brood records (between 59–66°N and 21–31°E), collected by bird ringers during 1973–2007. Ringing data enable us to estimate the timing of breeding (as measured by hatch date) and the brood size. Hatch dates were estimated by subtracting the age of the oldest chick from the date of ringing. The age of the chicks, as measured in numbers of days since hatching were estimated by comparing the length of the chicks' wings to a known growth curve of sparrowhawk young (Patrik Byholm, unpublished). To make sure that the mean ringing age of nestlings has not changed during the study period, we regressed nestling age against year. If wing length was not measured (56% of cases), these broods were omitted from the hatch data analysis. The age during ringing showed only a trendsetting decreasing trend during the study period (-0.057 ± 0.030 SE); $F_{1,27} = 3.61$, $p = 0.07$). We tested whether the ringing dates differed between included and excluded brood data to make sure that the results are not biased because of excluded data. We found that in both groups the annual mean ringing date had advanced significantly during 1979–2007, but ringing dates of birds with measured wing length was advancing 2.9 days more than ringing dates of birds without wing measure details (wing measured: advance 0.24 ± 0.04 days/year; $F_{1,27} = 29.35$, $p < 0.001$; wing length not measured: advance 0.14 ± 0.04 days/year; $F_{1,27} = 15.36$, $p < 0.001$). We obtained exact hatch dates for 19 broods during 1993–2007 by observing growth of chicks since hatching event (Patrik Byholm, unpublished). The exact hatch dates were strongly associated with the hatch dates estimated from wing length ($F_{1,17} = 968.5$, $p < 0.001$, $r^2 = 0.98$), thus validating our method for hatch date estimation. Also these data did not provide any support for the possibility that the reliability of the age-estimates linearly changed during 1993 and 2007 ($F_{1,17} = 0.33$, $p = 0.57$, $r^2 = 0.02$). We also measured the annual proportion of nests where breeding failed before nestlings were old enough to be ringed, during the period 1986–2007. This was done in order to control for possible bias from a potential change in the proportion of failed nests.

Ringing recovery data

We investigated the migration distances of Finnish sparrowhawks since the 1960s by using ringing recoveries of birds ringed as nestlings and recovered during November–February. The criteria for defining recoveries follow those of Visser et al. (2009), where the recovery was excluded: (1) if the bird was recaptured alive, (2) if the recovery condition of the bird was unknown or if the bird had been dead for a long time (EURING codes 0 and 3), (3) if the inaccuracy of the

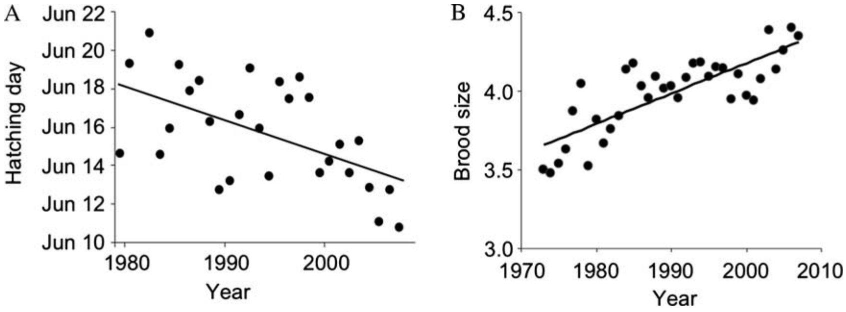

Figure 2. The annual mean hatch date (A), and brood size (B) of Finnish sparrowhawks based on ringing records and fitted least-squares lines.

finding date was more than ± 2 weeks, (4) if the inaccuracy of finding place was more than ± 10 min, and (5) if the bird was killed by humans. Birds recovered in Finland were also included in the analysis.

To test for a temporal trend in the migration distances of adult and juvenile birds we regressed log-transformed migration distances against time (see Visser et al. 2009). The analysis was done separately for young birds (1st winter; $n = 313$) and adults (2nd winter or older; $n = 147$).

Weather and climate data

We used local weather data collected by the Finnish Meteorological Institute (Venäläinen et al. 2005) from 70 weather stations (see Lehikoinen et al. 2009). To study the effect of weather on hatch date and brood size, we used brood-specific weather data from the closest weather station (the distance between nests and weather stations were 23 ± 16 km (mean ± SD)). Weather data from Hanko (Tvärminne biological station, 59° 50'N, 23° 15'E) were used to investigate potential effects of local weather on the migration of sparrowhawks at Hanko Bird Observatory. The weather variables and descriptive statistics are shown in Table 1. The winter North Atlantic Oscillation, NAOdjfm-index data (Hurrell 1995) was downloaded from http://www.cgd.ucar.edu/cas/jhurrell/indices.html.

Statistics

Factors affecting spring migration dates, as measured by the start, median and end of migration, were investigated using multiple regression models where the year of observation, the NAO-index and average monthly temperatures at Hanko, were used as explanatory variables. Whenever year of observation was included in a model, it was regarded as a fixed effect that accounted for a linear temporal trend in the response variable, which is the case throughout the paper. Temperatures were used for the month when the specific phase of migration typically occurs, as well as the previous month: for example, regarding median migration in April, March and April temperatures were considered. Based on year, two monthly mean temperature variables and NAO we constructed eight different models. The models were evaluated and ranked using the Akaike Information Criterion corrected for small sample size, AICc (Burnham and Anderson 2002), and they are presented in Table 2. Advancement of phenological events was measured using the models with year as the only explanatory variable (Yr; Tables 2–3), and considered to be statistically significant if the evidence ratio (ER) of the Yr models compared to the respective null-models were greater than 5.

Regarding timing of autumn migration, we investigated whether departure dates were related to year of observation (accounting for temporal trend), mean monthly autumn air temperatures (from July to October), and if the timing of breeding (mean annual hatch date based on ringing records) affected the departure dates (e.g. see Lehikoinen et al. 2004). As in the spring analysis, two monthly temperatures were used, the month coinciding best with the considered phase of autumn migration and the month prior to that one. Model combinations were evaluated and ranked in the same way as for the spring data (see Table 2).

The analyses regarding the timing of breeding and brood size were conducted with S-Plus ver. 6.1 (Insightful Corporation, Seattle, Washington, USA) using linear mixed models. Since the models compared have different fixed effects structure, maximum likelihood (ML) estimation was used (Crawley 2002). In the model selection procedures we used the Akaike Information Criterion, AIC (Burnham and Anderson 2002). To account for potential spatial trends in the breeding data, we used the polynomial approach presented by Legendre and Legendre (1998), such that all models included the normalized (zero mean and unit variance) geographical coordinates X (longitude) and Y (latitude), their second and third powers (χ^2, Y^2, X^3, Y^3) and some cross- products (XY, X^2Y, XY^2) as explanatory variables. Year of observation (accounting for the temporal trend) and weather data from the nearest weather station for each brood record were used to model the timing of breeding and brood size as fixed effects (Tables 3–4). In addition, year was included as a categorical random effect to account for inter-annual variation in the timing of breeding and brood size. The weather variables which were used to explain the climatic conditions of the arrival, mating and nest building phases were the monthly mean temperatures (° C) of March and April and summed April precipitation (100 mm). Temperature variables correspond to previous findings of advanced breeding resulting from high spring temperatures (Dunn 2004), and April precipitation has

Table 1. Descriptive statistics of weather and climate variables in 1973–2007 used to explain responses on migration phenology, hatch date and breeding success. In temperature the unit is ° C, in precipitation millimeters (sum of month) and in the NAO standard deviations (1979–2007). The strength of a linear temporal trend is given as the regression slope and 95% CI.

Weather variable	Mean ± SD	Min	Max	Annual change	CI
Temperature (° C), March	−3.5 ± 2.6	−8.7	1.20	0.011	[−0.079; 0.101]
Temperature (° C), April	2.0 ± 1.5	−0.4	4.50	0.064	[0.015; 0.113]
Temperature (° C), May	8.7 ± 1.5	6.20	12.10	−0.005	[−0.056; 0.046]
Temperature (° C), June	13.8 ± 1.6	10.30	17.10	0.019	[−0.039; 0.077]
Temperature (° C), July	16.4 ± 1.5	14.10	19.70	0.049	[0.000; 0.097]
Temperature (° C), August	14.4 ± 1.4	11.30	17.40	0.067	[0.025; 0.109]
Temperature (° C), September	9.3 ± 1.7	5.40	11.90	0.059	[0.005; 0.113]
Temperature (° C), October	3.9 ± 2.0	−1.7	7.50	0.055	[−0.013; 0.123]
Precipitation (100 mm), April	0.30 ± 0.15	0.08	0.70	−0.002	[−0.007; 0.003]
Precipitation (100 mm), June	0.58 ± 0.20	0.00	2.43	0.004	[−0.008; 0.016]
NAO	1.07 ± 2.04	−3.78	5.08	−0.020	[−0.114; 0.074]

Table 2. Ranked hypothesized models used to explain different phases of migration in sparrowhawk (5th, 50th and 95th percentiles, see Methods). Model specific no. of parameters (Par), AIC_c differences (ΔAIC_c), Akaike weights (ω), evidence ratios (E-ratio), coefficient of determinations (R^2) and temporal autocorrelation values (a.c.) are shown. T3–T10 are mean temperatures (° C) of months from March to October, NAO is winter NAO of months from December to March and HD is mean annual hatch date of broods based on ringing data.

Spring 5%							Autumn 5%						
Variables	Par	ΔAICc	ω	E-ratio	R^2	a. c.	Variables	Par	ΔAICc	ω	E-ratio	R^2	a.c.
Yr	3	0.00	0.54	1.0	0.29	−0.06 [−0.44; 0.35]	Yr	3	0.00	0.65	1.0	0.34	−0.00 [−0.38; 0.38]
Yr+NAO	4	2.47	0.16	3.4	0.30	−0.10 [−0.48; 0.31]	Yr+HD	4	2.27	0.21	3.1	0.35	−0.17 [−0.39; 0.37]
Yr+T3+T4	5	3.37	0.10	5.4	0.35	−0.19 [−0.54; 0.23]	Yr+T7+T8	5	4.21	0.08	8.2	0.37	−0.04 [−0.41; 0.35]
T3+T4	4	3.63	0.09	6.1	0.26	−0.14 [−0.51; 0.27]	HD	3	6.68	0.02	28.2	0.16	0.13 [−0.26; 0.49]
NAO+T3+T4	5	4.60	0.05	10.0	0.32	−0.16 [−0.52; 0.25]	Yr+HD+T7+T8	6	6.86	0.02	30.8	0.39	−0.06 [−0.43; 0.32]
–	2	6.21	0.02	22.3	0.00	0.21 [−0.20; 0.56]	–	2	9.05	0.01	92.3	0.00	0.32 [−0.07; 0.62]
Yr+NAO+T3+T4	6	6.32	0.02	23.6	0.36	−0.17 [−0.53; 0.24]	HD+T7+T8	5	10.12	0.00	157.9	0.23	−0.05 [−0.42; 0.34]
NAO	3	8.62	0.01	74.5	0.01	0.19 [−0.22; 0.55]	T7+T8	4	10.73	0.00	214.3	0.12	0.05 [−0.34; 0.42]
Spring 50%							Autumn 50%						
Variables	Par	ΔAICc	ω	E-ratio	R^2	a. c.	Variables	Par	ΔAICc	ω	E-ratio	R^2	a.c.
T3+T4	4	0.00	0.28	1.0	0.25	−0.39 [−0.68; 0.01]	Yr	3	0.00	0.63	1.0	0.22	0.17 [−0.22; 0.52]
Yr+NAO	4	0.56	0.21	1.3	0.23	−0.36 [−0.66; 0.04]	Yr+HD	4	2.65	0.17	3.8	0.22	0.17 [−0.22; 0.52]
Yr	3	1.53	0.13	2.1	0.11	−0.23 [−0.57; 0.19]	–	2	4.38	0.07	9.0	0.00	0.36 [−0.02; 0.65]
NAO	3	1.57	0.13	2.2	0.11	−0.20 [−0.55; 0.21]	Yr+T8+T9	5	4.84	0.06	11.2	0.24	0.15 [−0.24; 0.50]
–	2	2.10	0.10	2.9	0.00	−0.13 [−0.50; 0.28]	HD	3	5.66	0.04	16.9	0.04	0.30 [−0.09; 0.61]
NAO+T3+T4	5	2.83	0.07	4.1	0.26	−0.39 [−0.68; 0.00]	T8+T9	4	6.53	0.02	26.2	0.11	0.18 [−0.22; 0.52]
Yr+T3+T4	5	2.94	0.06	4.3	0.25	−0.38 [−0.68; 0.02]	Yr+HD+T8+T9	6	7.97	0.01	53.8	0.25	0.14 [−0.25; 0.49]
Yr+NAO+T3+T4	6	5.68	0.02	17.1	0.27	−0.40 [−0.68, 0.00]	HD+T8+T9	5	9.16	0.01	97.5	0.12	0.18 [−0.21; 0.53]
Spring 95%							Autumn 95%						
Variables	Par	ΔAICc	ω	E-ratio	R^2	a. c.	Variables	Par	ΔAICc	ω	E-ratio	R^2	a.c.
NAO	3	0.00	0.46	1.0	0.13	0.09 [−0.32; 0.47]	–	2	0.00	0.20	1.0	0.00	−0.03 [−0.41; 0.35]
–	2	1.10	0.26	1.7	0.00	0.09 [−0.31; 0.47]	T9+T10	4	0.03	0.20	1.0	0.17	0.01 [−0.37; 0.39]
Yr+NAO	4	2.72	0.12	3.9	0.14	0.08 [−0.33; 0.46]	Yr	3	0.36	0.17	1.2	0.07	−0.08 [−0.45; 0.31]
Yr	3	3.55	0.08	5.9	0.00	0.08 [−0.33; 0.46]	Yr+HD	4	0.71	0.14	1.4	0.15	−0.10 [−0.46; 0.30]
NAO+T4+T5	5	4.42	0.05	9.1	0.18	0.09 [−0.32; 0.47]	HD+T9+T10	5	0.95	0.12	1.6	0.23	0.01 [−0.37; 0.39]
T4+T5	4	6.32	0.02	23.6	0.01	0.10 [−0.30; 0.48]	HD	3	2.31	0.06	3.2	0.01	−0.01 [−0.39; 0.37]
Yr+NAO+T4+T5	6	7.59	0.01	44.5	0.19	0.10 [−0.31; 0.47]	Yr+HD+T9+T10	6	2.49	0.06	3.5	0.28	−0.03 [−0.40; 0.36]
Yr+T4+T5	5	8.99	0.01	89.5	0.02	0.07 [−0.33; 0.46]	Yr+T9+T10	5	2.76	0.05	4.0	0.18	0.00 [−0.38; 0.38]

Table 3. Ranked hypothesized models used to explain hatch date and brood size. Number of parameters (*K*), AIC differences (ΔAIC), Akaike weights (ω), evidence ratios (E-ratio) and coefficients of determination (R^2) of each model are shown. GEO is coordinates of broods (see methods), Yr is year, T3, T4 and T6 are effects of mean temperatures (°C) of March, April and June, whereas P4 and P6 are effects of precipitation (100 mm) during April and June, respectively.

	Hatch date					
Model	K	Dev	ΔAIC	ω	E-ratio	R^2
GEO+Yr+P4+T4	15	15448.2	0.0	0.531	1.0	0.213
GEO+Yr+T3+P4+T4	16	15446.5	0.4	0.445	1.2	0.210
GEO+P4+T4	14	15457.3	7.2	0.015	35.9	0.179
GEO+T3+P4+T4	15	15456.3	8.1	0.009	58.5	0.176
GEO+Yr+T3	14	15472.9	22.7	0.000	>1000	0.163
GEO+Yr	13	15476.7	24.6	0.000	>1000	0.163
GEO+T3	13	15482.7	30.5	0.000	>1000	0.126
GEO	12	15486.3	32.2	0.000	>1000	0.120

	Brood size					
Model	K	Dev	ΔAIC	ω	E-ratio	R^2
GEO+Yr	13	18877.4	0.0	0.533	1.0	0.014
GEO+Yr+P6+T6	15	18875.1	1.7	0.230	2.3	0.014
GEO+Yr+P4+T4	15	18876.2	2.9	0.127	4.2	0.014
GEO+Yr+P4+T4+P6+T6	17	18872.6	3.2	0.109	4.9	0.015
GEO	12	18907.1	27.8	0.000	>1000	0.003
GEO+P4+T4	14	18904.2	28.9	0.000	>1000	0.004
GEO+P6+T6	14	18906.5	31.1	0.000	>1000	0.003
GEO+P4+T4+P6+T6	16	18903.4	32.0	0.000	>1000	0.004

been found to delay breeding of British sparrowhawks (Newton 1986). Correspondingly, for brood size, the weather variables we used were the annual mean temperatures of April and June and the amount of precipitation in April and June. April weather conditions could affect laying conditions and thus clutch size, whereas weather condition in June could affect mortality of nestlings (Newton 1986, Kostrzewa and Kostrzewa 1990).

Model uncertainty was accounted for by model averaging (Burnham and Anderson 2002, Johnson and Omland 2004). The residuals of the best ranked model in terms of AIC (or AIC_c), and the averaged model were tested for temporal autocorrelation. In the breeding analyses the random effects of year were tested for temporal autocorrelation and residuals were tested for spatial autocorrelation using Moran's I, with contiguity defined by distance classes 0–50 km, 50–100 km, 100–150 km and 150–200 km. The statistical significances of Moran's I were calculated using permutation tests based on 500 permutations (Schabenberger and Gotway 2005).

Table 4. Estimated parameters and their standard errors for models on hatch date and brood size. Model average and best model parameters are presented (see Tables 3 and 5; Burnham and Andersson 2002). X is the longitude coordinate and Y is the latitude coordinate. Coefficients that significantly differ from zero are shown in bold.

Variables	Hatch date				Variables	Brood size			
	Average model		Best model			Averaged model		Best model	
	Estim.	SE	Estim.	SE		Estim.	SE	Estim.	SE
Intercept	**18.484**	0.883	**18.687**	0.794	Intercept	**3.776**	0.133	**3.732**	0.057
X	0.551	0.307	0.566	0.306	X	−0.005	0.048	−0.005	0.048
Y	0.479	0.290	0.508	0.287	Y	0.027	0.047	0.030	0.046
X^2	−0.318	0.195	−0.320	0.194	X^2	0.007	0.024	0.008	0.024
Y^2	**−1.884**	0.434	**−1.910**	0.433	Y^2	−0.033	0.064	−0.027	0.064
X^3	0.085	0.376	0.085	0.376	X^3	0.010	0.048	0.009	0.048
Y^3	**2.601**	0.555	**2.617**	0.554	Y^3	−0.035	0.087	−0.039	0.087
XY	**−0.440**	0.183	**−0.437**	0.183	XY	**0.057**	0.026	**0.055**	0.026
X^2Y	0.510	0.302	0.510	0.302	X^2Y	−0.067	0.035	−0.067	0.035
XY^2	−0.134	0.338	−0.128	0.338	XY^2	0.011	0.048	0.011	0.047
Year	**−0.115**	0.040	**−0.116**	0.037	Year	**0.016**	0.003	**0.016**	0.003
T3	−0.049	0.079	0	0	P4	−0.026	0.074	0	0
P4	**2.755**	0.961	**2.689**	0.953	T4	−0.003	0.008	0	0
T4	**−0.688**	0.127	**−0.700**	0.126	P6	−0.041	0.071	0	0
–	–	–	–	–	T6	0.000	0.007	0	0
σ (year)	1.108	–	1.108	–	σ (year)	0.079	–	0.085	–
σ (res)	5.169	–	5.169	–	σ (res)	1.259	–	1.259	–

Results

Migration dates and distance

During the study period the early spring migrants (5th percentile) advanced their arrival with 0.40 ± 0.13 days/year (Evidence ratio, ER = 22.3). The timing of spring migration did not show significant changes among the later phases (Fig. 1, Table 2), meaning that the spring migration period, i.e. the time between the 5th and the 95_{th} percentiles, has increased in length by 0.44 ± 0.17 days/year ($F_{1,24} = 6.66$, $p = 0.016$).

Early and median autumn migrants advanced their migration by 0.38 ± 0.10 days/year (ER = 92.3) and 0.31 ± 0.11 days/year (ER = 9.0), respectively, early autumn migrants being exclusively juveniles. However, the late phase of departure did not change during the study period (Table 2), and the overall autumn migration period length has also not increased significantly (0.23 ± 0.16 days/year, $F_{1,27} = 2.03$, $p = 0.165$). Autumn temperatures did not affect departure dates (Table 2). The total time during which at least a part of the adult population is present on the breeding grounds (counting from 5% date of spring arrival to 95% date of autumn departure of the whole migration curve) has not changed significantly (0.25 ± 0.14 days/year, $F_{1,24} = 3.17$, $p = 0.09$).

After having corrected for the temporal trend, there is no clear evidence for ambient temperatures, NAO-index or timing of breeding affecting the timing of migration (Table 2). No statistically significant autocorrelations were found in the residuals of the models regarding timing of migration (Table 2), suggesting that the model assumption of independent residuals holds.

Based on ringing recoveries, the log-transformed migration distance has not changed since the 1960s, neither for juveniles (1960–2007: $F_{1,312} = 0.13$, $p = 0.72$), nor for adults ($F_{1,146} = 0.31$, $p = 0.58$).

Breeding variables

The timing of breeding has significantly advanced by −0.18 ± 0.05 days/year (ER = 44.3 between model with temporal trend and null model; Fig. 2A). Increasing average April temperature advanced breeding with 0.69 ± 0.13 days/° C, while increasing precipitation in April slightly delayed breeding, with 2.75 ± 0.96 days/100 mm (Fig. 2A, Tables 3 – 4). There is a clear geographical trend in hatch date, increasing towards the northeast. The difference in hatch dates between the extreme south-western area, and the corresponding extreme in the northeast, is according to the model averaged prediction approximately 15 days (11 June in the far southwest and 26 June in the far northeast). Comparing the slopes of the temporal trends of the timing of early spring arrival and breeding shows an increasing time period between the two events (0.22 ± 0.14 days/year), but the difference is not statistically significant ($t = 1.60$, $df = 32.11$, $p = 0.12$). The corresponding period between breeding and early departure of juveniles shows a non-significant decrease of 0.21 ± 0.12 days/year ($t = -1.76$, $df = 40.16$, $p = 0.09$).

The mean annual time interval between 5% spring migration and mean hatching date was 73 ± 6.3 (SD) days. Furthermore, the annual time interval between mean assumed time of independence (60 days after hatching) and median of autumn migration in Hanko was 30 ± 5.7 (SD) days.

Brood size increased with 0.016 ± 0.003 young/year (Fig. 2B), but there was no clear evidence of weather effects, although a tendency of weak negative effects of June precipitation were present in the 2nd and 4th best models (Tables 3 – 4). According to model averaged predictions, brood size varied geographically with a range of approximately one young (ca 4.4 in far south-west, and ca 3.4 in far north-east).

The fitted models of importance for inference corresponded rather well to the assumptions of independent residuals and random effects. All migration models showed serially independent residuals and the models of breeding (phenology and success) showed no evidence of spatial autocorrelation on any scale. Only in the models of brood size the random effect of year showed moderate positive temporal autocorrelation (averaged model: $\varrho = 0.38$, $SE = 0.16$, 95% $CI = [0.04, 0.63]$; best model: $\varrho = 0.37$, $SE = 0.16$, 95% $CI = [0.03, 0.63]$). The proportion of failed nests was 10.2% ± 2.3 (SD) and did not show a significant annual trend that could likely affect the results ($F_{1,20} = 2.79$, $p = 0.11$).

Discussion

Early migrant sparrowhawks advanced their spring migration dates with approximately 11 days during the 29-year long study period, whereas late migrating birds still arrive approximately at the same time as three decades ago. The pattern coincides with temporal trends in local April temperatures, which can be used as proxies for weather conditions during migration. After having corrected for the temporal trend in migration dates, April temperatures explained little of the variation in the timing of migration. The timing of arrival is likely to be better explained by weather conditions on a larger scale, including those at the departure areas and weather *en route* (see Ahola et al. 2004).

Our results show that the spring migration period of Finnish sparrowhawks has increased in length. This is likely caused by differing responses of different conspecific groups. The negative correlation between timing of breeding and reproductive success is a well-documented pattern in birds (Daan and Tinbergen 1997) and it is also observed in sparrowhawks (Newton 1986). Thus the earliest migrants, that are typically experienced adult birds, are more likely to breed successfully than later migrants that are typically inexperienced young and/or lower-quality individuals (e.g. Newton 2008). Therefore it is not surprising that the early part of the spring migration shows the strongest response (Vähätalo et al. 2004). Our results support the hypothesis that increasing temperature due to climate change can lengthen migration (Vähätalo et al. 2004), and breeding periods (Møller 2006).

The timing of breeding showed a clear advancement, and suggests that earlier arrival leads to earlier breeding. Early breeding was also strongly connected to higher than average temperatures in April, and to some extent, lower precipitation during April. This can be a consequence of improved hunting conditions of adults who are thus able to gain resources for breeding more easily (Newton 1986). The time interval between spring migration and hatching was about 70 days. Since egg laying and incubation takes on average 45 days (Cramp and Simmons 1980, Newton 1986) early arriving adults have during normal years less than a month to settle to breeding grounds, mating and nest building.

Contrary to the results of Nielsen and Møller (2006) and Both et al. (2009), our results show that sparrowhawks have significantly advanced their breeding dates in response to climate change. However, the advance has been less than one week in 30 years, and the rate of advance was about 0.7 days/° C in April, which is clearly less than in many smaller sized passerines (Dunn 2004). Since the mean temperature of April has increased only 2.5 ° C during the study period, it is likely that some other factors, such as earlier spring migration have advanced the timing of breeding.

The start and median dates of autumn migration also showed a clear advancing trend. In sparrowhawks, young birds migrate soon after their parents have ceased feeding them, whereas adults, on the other hand, need to finish the moult of their flight feathers and therefore depart much later than their offspring (Cramp and Simmons 1980, Saurola 1981, Newton 1986, Kjellén 1992). In line with this reasoning, our results imply that earlier breeding produces earlier autumn migration explicitly in young sparrowhawks (unpublished data of Hanko Bird Observatory; see also Saurola 1981). However, late migrating adult birds did not advance their migration dates as much.

Two hypotheses have been proposed regarding the effects of climate change on the autumn phenology of migratory birds. According to Jenni and Kery (2003) single brooded short-distance migrants, such as sparrowhawks (Cramp and 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 anymore, and wintering as close to breeding areas as possible would be beneficial with respect to earlier arrival and territory establishment (Jenni and 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 breeding area residence times (BART) for these species are constant, and thus earlier spring arrival and breeding would lead to a correspondingly early 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. It is also better to migrate as early as possible if resources along the migration route are time limited (e.g. long-distance migrant insectivores; Alerstam 1990, Newton 2008). Autumn migration of juvenile sparrowhawks supports the BART hypothesis; the time period between hatching and migration of juvenile sparrowhawks does not show any significant trend. However, for adult birds there is no clear support for any of the proposed hypotheses. Nevertheless, our results also indicate that the temperature during autumn migration does not play an important role in sparrowhawks and thus reinforces the view that timing of breeding and moulting are the key factors in the timing of autumn migration.

Climate cues for departure dates are still poorly known (e.g. MacMynowski and Root 2007) and further studies are needed to conclude how a warming climate affects timing of autumn migration. So far, studies dealing with autumn migration and climate change have been focused towards passerines (Sokolov et al. 1998, Jenni and Kery 2003, Mills 2005, Tøttrup et al. 2006, Thorup et al. 2007, Mezquida et al. 2007), but investigations should be widened to include non-passerine species in order to get a better understanding within the taxon. One should also keep in mind that sparrowhawks are the main predators of passerines in northern Europe (Newton 1986, Lindström 1989), and thus changes in migration phenology of the sparrowhawk may change the predation pressure along the migration route and possibly lead to behavioural changes in the prey species (Worcester and Ydenberg 2008).

The mean brood size of the sparrowhawks showed a clear increasing trend through the 1970s up to the mid-80s after which the mean brood size has stayed unchanged. This might be the explanation for the observed temporal autocorrelation in the random effect of year, as we fitted a linear trend to the data. Brood size showed no clear relationship to weather variables. Consequently, the observed increase in brood size over the years is probably primarily not caused by concurrent climate change. More likely reasons are the decreasing concentrations of DDT, DDE, HEOD and mercury, which have improved the breeding conditions for birds of prey since the late 1970s (e.g. Newton 1998). However, since early breeders are known to have higher breeding success (Newton 1986), the possibility that the advanced onset of breeding may have increased the breeding success cannot be excluded (also see Nielsen and Møller 2006).

Somewhat surprisingly, the location of the wintering areas of young sparrowhawks has not changed since the 1960s, despite earlier spring and autumn migration. This finding is in contrast to the findings of other studies that have documented a northward shift in the wintering areas of many birds (Nilsson 2005, La Sorte and Thompson 2007, Rivalan et al. 2007, Newton 2008), but is in agreement with the data of Visser et al. (2009) who also failed to find a change in migration distances of Dutch sparrowhawks over recent decades. Sparrowhawks are highly specialized predators of passerines, and therefore depend on the constant supply of passerine prey. In order for sparrowhawks to be able to shift their wintering areas northward, as a response to a warming climate, a shift in the wintering areas of many prey species is required. This interaction between predator and prey may introduce time lag in the northward shift of wintering sparrowhawks.

As we show, the timing of life history events of Finnish sparrowhawks are largely regulated by climatic factors, and in our study population this has lead to earlier onset of life cycle whereas the effect on the production of young and wintering locations appears to be small. However, we have shown that migrants might respond differently to climatic changes during different phases of the migration season and differing migration tactics of age-classes. In conclusion, the best way to understand how climate change will affect any animal species is to study the impacts on the entire life cycle, preferably separately for different age classes.

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