

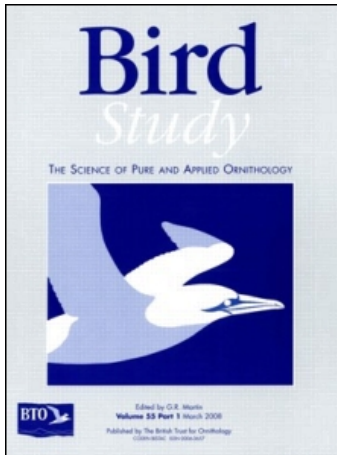
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A method to estimate phenological variation using data from large-scale abundance monitoring programmes

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Capsule Large-scale abundance monitoring programmes can be used to estimate annual phenological shifts.

Aims Phenology refers to the timing of any annually repeated biological event. The method developed here aims at measuring phenological variation in an indirect way by modelling seasonal abundance variations. Thus, it provides the opportunity to use a large number of datasets which have rarely been used in phenological studies. Phenological variations computed using this standardized method are comparable between species.

Methods The data used for the development of this method originates from the French Breeding Bird Survey, a large-scale abundance monitoring programme launched in 2001. For each species, the phenological shift between two seasonal abundance trends is computed using maximum likelihood.

Results Phenological shifts relative to the year 2005 (reference year) were estimated for 46 species over a 5-year period (2001–6). The standard deviations of the shifts do not differ significantly between species with different migratory status. Moreover, at the species level, the computed phenological shifts relate to the shifts of the mean date weighted by abundance. However, mean date, cannot be used in studies incorporating species with different migratory status (e.g. trans-Saharan migrant, sedentary) because of ambiguous changes for the same biological shift in timing.

Conclusions The method described here is of particular value in determining how the phenology of common bird species changes in relation to climate. It offers the opportunity to increase the spatial scale of phenological studies and to include multi-species analyses. This method could be applied to any abundance or constant effort site programme to study the timing of any biological process for which a seasonal distribution is available.

Phenology has become a key research field in the understanding of the effects of climate change on animal or plant populations (Walther *et al.* 2002, Parmesan & Yohe 2003, Crick 2004, Parmesan 2006). However, until now hypotheses concerning the way global change is currently altering the timing of seasonal events of a species mostly originate from sampling protocols dealing with only a few species surveyed intensively at few study sites (Sparks *et al.* 2005, Jonzen *et al.* 2006).

Moreover, most datasets that have until now been analyzed under the phenological framework originate

from designs displaying many temporal but very few spatial replicates. This is a result of the trade-off existing between temporal and spatial replicates as the former are too costly to carry out at a large spatial scale. Among birds, for example, although migration studies are numerous, they are usually carried out at specific migration monitoring stations (Sparks & Braslavská 2001, Moller *et al.* 2004, Sparks *et al.* 2005, Croxton *et al.* 2006, Jonzen *et al.* 2006). These monitoring conditions only allow a maximum of a dozen species to be surveyed accurately due to scarcity of data concerning rare or nocturnal migration (but see Jenni & Kery [2003] concerning autumn migration

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trends). Breeding timing in birds has been followed primarily using nestboxes in localized areas (but see Crick & Sparks 1999).

A major issue about a species phenology is the effective estimation of how early or late it is compared with its average timing over a certain period of time. The aforementioned protocols and their derived methods yield different accuracies for such estimates. On the one hand, it is possible to derive the exact laying dates from nestbox surveys. On the other hand, the first bird seen is a very approximate and unreliable proxy for temporal distribution of migration (van Strien *et al.* 2008). Furthermore, median dates or mean date quantiles might very much depend on the monitoring site and sample sizes (Tryjanowski & Sparks 2001, van Strien *et al.* 2008). However, surveys including many temporal records on few sites allowed estimations concerning gradual advancement of migration arrival dates or laying dates. The accuracy of these approaches has made it possible to compare a species' phenological response to climate change with that of its prey (Visser & Both 2005, Visser *et al.* 2006).

Yet, these approaches raise two different issues. First, they remain spatially limited, and second, they do not tackle the phenological issue for all the species that cannot be surveyed that way. Indeed, staying with the bird example, between 50 and 80 species are fairly common in western Europe depending on the environment. Yet, for most of them, we have hardly any idea of their particular phenology except from data collected by amateurs that may lack standardization and repeatability. Thus, there is a current gap in the knowledge of most common species' temporal responses to climate change.

Here, we propose to take advantage of large-scale abundance monitoring programmes used to survey many different taxa. Most of these sampling protocols are designed to monitor abundance on large spatial scales. Therefore, most of them provide abundance data with many spatial replicates but only few temporal replicates. These data were analyzed using a new method designed to determine for a given species, the temporal phenological shift between two different years, in other words, how a species is late or early in its breeding phenology compared to a reference year. We applied this method to 93 bird species monitored by the French Breeding Bird Survey (BBS) (Jiguet *et al.* 2007). In comparison with costly monitoring methods such as nestbox surveys or permanent migratory counts at a few stations, the dataset analyzed here originates from volunteers' monitoring efforts; counting birds at numerous sites spread

across the whole country using a repeatable and standardized protocol. This method can be applied to data gathered through point counts or transects as long as standardization is ensured throughout the study period.

METHODS

Data collection and data processing

The French BBS programme is based on volunteer ornithologists counting birds in spring on permanent plots. Surveyed sites are 2×2 km squares randomly selected within a 10 km radius around a locality specified by the volunteer. Random selection (one of about 80 possible squares) ensures that surveyed habitats closely match their actual availability (Jiguet *et al.* 2007). In each square, observers carry out ten point counts (separated by at least 300 m) of 5 minutes duration each. Counts are done twice in spring (from 1 April to 8 May, then from 9 May to the end of June) in order to detect both early and late breeders, with 4–6 weeks between both counts. For a given site, counts are repeated yearly by the same observer at the same points, on approximately the same date (± 7 days within April to mid-June), and at the same time in the day (± 15 minutes). Here, counts for the ten points within each square and each session were summed before analysis. The number of monitored sites varied across the study period: 178 sites in 2001, 616 in 2002, 774 in 2003, 856 in 2004, 886 in 2005 and 873 in 2006.

In order to address statistical problems due to data over-dispersion, we fixed a threshold for the number of birds seen at the same time at ten individuals on the scale of the count point (Julliard *et al.* 2006). Wetland birds were excluded from the study because they are not well monitored by this protocol (Jiguet *et al.* 2007).

Seasonal abundance variation modelling

The purpose for this study was to determine the differences in phenological timing of a species between two years. The BBS data provide us with a count distribution across time within a year of the survey. Thus, for a given species it would be possible to estimate its phenological shifts between two years by using mean or median count dates weighted by abundance (Knudsen *et al.* 2007). However, it is not possible to use such measures, to compare the shifts of different species displaying different shapes of count distributions. Indeed, the sign of the shifts of mean and median dates depends on the type of count distribution the species displays (see Fig. 1 for an example based on two different theoretical abundance

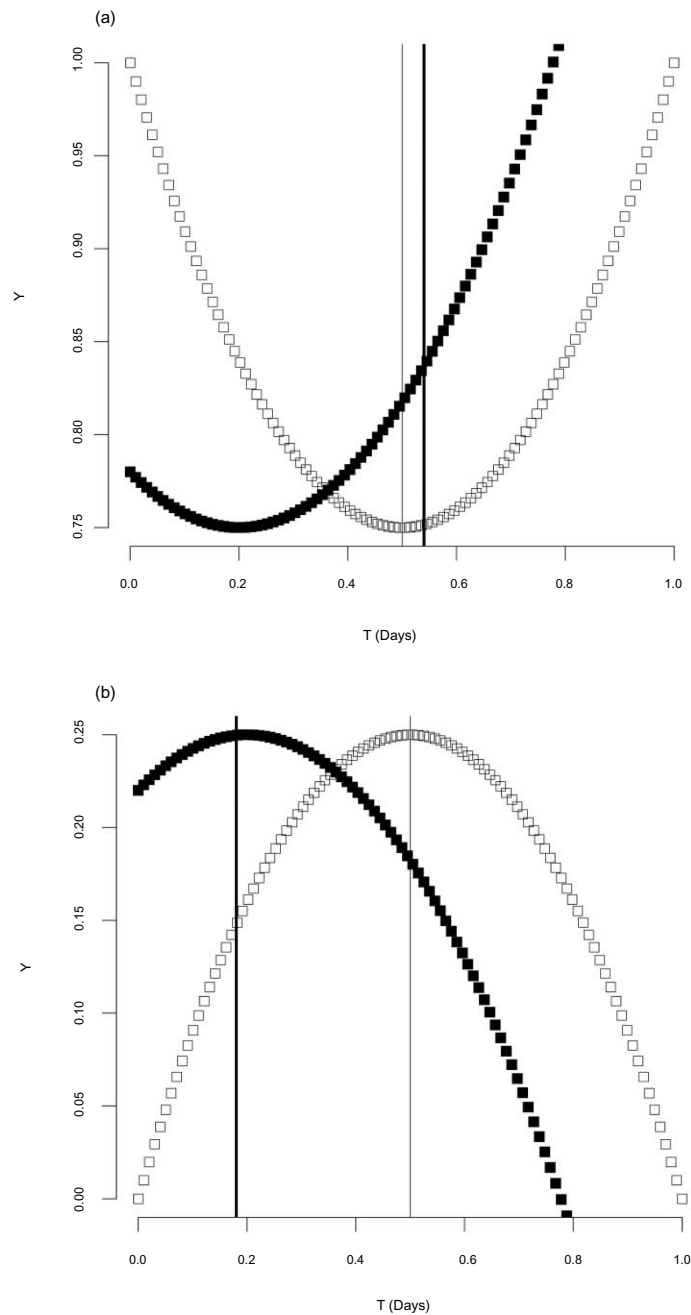


Figure 1. Mean shifts reflecting the same effective phenological shift, depend on the shape of the seasonal count distribution. (a) Two equations representing two theoretical seasonal abundance trends identical in their shape but delayed in their timing: $Y = T^2 - T + 1$ (open squares) and $Y = 0.75T^2 - 0.3T + 0.78$ (representing a 0.3-unit time advance; filled squares). Their means are drawn respectively in slim and thick lines. This 0.3-unit time advance in the effective timing results for this particular seasonal pattern (bell curve) in a counterintuitive +0.04-unit time shift for the mean T weighted by Y . (b) Two seasonal count distributions also identical in their shape (which is different from the shape in a) but delayed in their timing (same delay as in a): Equations $Y = -(T^2 - T + 1) + 1$ (open squares) and $Y = -(0.75T^2 - 0.3T + 0.78) + 1$ (representing a 0.3-unit time advance; filled squares) are represented as well as their mean dates respectively in slim and thick lines. This time, for this shape of distribution the 0.3-unit time advance in the effective timing results in an intuitive -0.32-unit time shift in the mean T weighted by Y . Thus, mean date shifts computed for different species showing different shapes of seasonal abundance patterns (either bell or U curves) are not comparable since the same biological change makes the weighted mean change in opposite ways.

distributions). For this reason it was not possible to use mean dates or given quantile dates as did Sparks *et al.* (2005) or Jonzen (2006). To address this issue we developed a method yielding phenological shifts and from which the signs do not depend on the species life-history traits. The first step is the modelling of a species' annual phenology using the count data. Birds were counted twice a year at a given site. This provides an estimation of the species' seasonal abundance variation for this site. As each species was detected on numerous sites at various dates, then for a given species, pooling data originating from all sites yields a continuous estimation of the species' seasonal abundance variations. We assumed that variation in estimated abundance using raw counts was a proxy for a species' phenology. Indeed, detection probability which determines this count is a function of two variables. First, the number of birds that are to be counted and second, the probability of counting a bird knowing it is actually present (MacKenzie *et al.* 2002, Royle *et al.* 2005). The number of birds to be counted varies with a species' phenology. The probability of detecting a certain bird that is present is a function of its behaviour and of the observer's skill. Behaviour is also highly dependent on phenology (Best & Petersen 1982, Hegelbach & Spaar 2000, Amrhein *et al.* 2004, Kunc *et al.* 2007). Both variables could be to some extent confounded, but this has no major impact on the method. Indeed it is very likely that, for a given species, if detection probability increases with abundance throughout the sampling season, this should happen evenly every year. As under these assumptions, we expected non-linear abundance variations, we fitted a generalized additive model (GAM) to the count data across time using the following model: Counts~(Counting site) + spline function (Counting date) with a Poisson error. The non-linear part of the model (spline function) was assigned three degrees of freedom. Smoothing abundance data to model phenology has recently been suggested (Knudsen *et al.* 2007). For each species and each annual model, relevance was tested and the significance of the smoothed term (Counting date) was recorded.

Repeatability in different abundance patterns in different years is a prerequisite for computation of phenological shifts because year-to-year comparisons require that both annual abundance distributions can be matched. Therefore, this method can only be applied to the species under the assumption that the shape of the seasonal distribution does not change between years. This is also true for any other tested dataset. For this reason, we only calculated temporal shifts for the species for which the counting date had a significant

effect on seasonal abundance and similar shapes in abundance distributions in at least 3 years. Thus, 46 species out of 93 were retained.

Estimation of inter-annual temporal shifts

For those species for which seasonal trends in abundance were significantly related to time measured by the counting date, we estimated temporal shifts of the phenology. In order to achieve this we propose a method based on maximum likelihood: the main picture of this method is to compare the timing of two smoothed seasonal abundance trends by setting one as a reference and by shifting the other one temporally until it best matches the first one. In order to achieve this, all estimated temporal shifts were computed between each one of the survey's within-year seasonal trend for each species, and the trend for 2005. This year was set as the reference year because it had the most monitored sites and therefore yielded most data. The algorithm employed the following steps:

- (a) Both the tested year's and the reference year's abundance data were pooled into a common dataset comprising dated abundance data.
- (b) Onto this dataset we fitted the following GAM: Counts~(Counting site) + spline function (Counting date + t) with a Poisson error, where t was equal to 0 for all the data gathered during the reference year (the trend that remains fixed) and ranged from -15 to +15 days with 0.1-day intervals for the tested year (the trend that is translated temporally until it matches the reference trend). We limited the time interval to 30 days to remain within biologically relevant values. As the survey period only covers an 80-day period, a 30-day interval avoided estimating shifts referring to these situations in which both seasonal trends are completely separate. Moreover, phenological changes mostly occur within such a time frame. The choice of such narrow intervals (0.1 days) was made to optimize further estimation of the minimal AIC (Akaike 1981). This algorithm looks for the best temporal translation that makes two seasonal abundance trends match, using an iteration on the elementary translation (t) applied to one trend. It then tests whether this elementary translation reduces the difference between both trends: for each t we measured the model's AIC. In this case the AIC is a measure of how two different annual abundance distributions can be fitted

under the same model by correcting timing differences using t . As for one comparison all the 301 models corresponding to the 301 different t s (t ranging between -15 and $+15$ with 0.1 intervals) had the same number of parameters, AIC was equivalent to the negative of the log likelihood so that minimizing AIC was the same as maximizing likelihood in this framework.

- (c) Eventually, to estimate the temporal shift (t) corresponding to the minimal AIC we modelled for each species and each year-to-year comparison, the relationship between t and AIC. To do so, we used a quadratic regression: $AIC \sim t + t^2$. We only applied this model to the ten t s around the minimum AIC that we obtained during the iteration phase because the estimation of a minimum and its standard error are more accurate locally. Using the regression coefficients, the temporal shift between both years was estimated as $-b/2a$, where a is the second-degree coefficient of the quadratic regression and b the first-degree coefficient. We computed the standard estimation error of t as $1/a$, which is equal to the negative inverse of the log likelihood's second derivative. If there was no local minimum AIC within the $-15/+15$ days interval, the method was considered inefficient for this particular species and this particular year (see Fig. 2 for an illustration of the computation of the shifts). Statistical analyses were performed using the R software (R Development Core Team 2006).

Robustness tests

We compared the phenological shifts with a classical phenological measure. We chose the mean count date because it is widespread in phenological studies (Sparks *et al.* 2005). We computed mean count date shifts by estimating for each year, the mean date weighted by abundance. Mean shifts were then calculated as the difference between this mean and the mean weighted by counts for the reference year (2005). In order to test the relationship between this mean shift and the phenological shifts, we had to subset the dataset into sedentary species, long-distance migrants and short-distance migrants. Indeed, for each of these categories, mean shift sign is not expected to be the same, given the different shapes of the count distributions (see Fig. 1).

We looked at the relationships between the relative standard deviation (rsd) of the phenological

shifts and various variables concerning the migratory status of the included species. Rsd was defined as the absolute value of the variation coefficient of the phenological shifts (standard deviation/mean). Migratory index (Migind) was defined as the log-transformed mean distance between breeding and wintering grounds of ringed individuals. This was determined using data from the French ringing database and only considering birds ringed in France between April and July and subsequently recorded anywhere, alive or recently dead, between November and February (Jiguet *et al.* 2006). Migratory status (Mig stat), was defined as a discrete variable (3 for sedentary species (Migind < 300km), 2 for short-distance migrants (300km < Migind < 1500km) and 1 for long-distance migrants (Migind > 3000km). The gap in migration distances between short-distance migrants and long-distance migrants is due to the crossing of the Sahara desert by these species.

It has been reported that long-distance migrants travelling by night are influenced by moon cycles (Pyle *et al.* 1993, James *et al.* 2000). Yet, these cycles do not occur on the same date each year, so the phenological shifts for these species could only reflect the differences between one year's moon cycles and 2005's cycles. Thus, for long-distance migrants we tested the relationship between moon cycles and the estimated phenological shifts (shift). To achieve this, we calculated the temporal delay (Moonshift) lying between April 2005's full moon and the other years' April full moon in order to remain relevant with the way we had estimated the phenological shifts (2005 as the reference year). To test all these relationships we used linear mixed-effects models with species as a random effect. Migind was log-transformed.

RESULTS

Seasonal abundance modelling

We modelled variation in seasonal abundance using GAMS for each species ($n = 93$) and each year ($n = 6$). Abundance was significantly influenced by the counting date in at least one year for 89% of the studied species and in at least three different years for 49% of the species. The percentage of species for which abundance was significantly related to counting date for all six study years dropped to 13% which represented 12 species out of the 93 initially considered in the study. If 2001 (when only 178 sites were monitored) was excluded, the percentage of species that showed a significant effect of

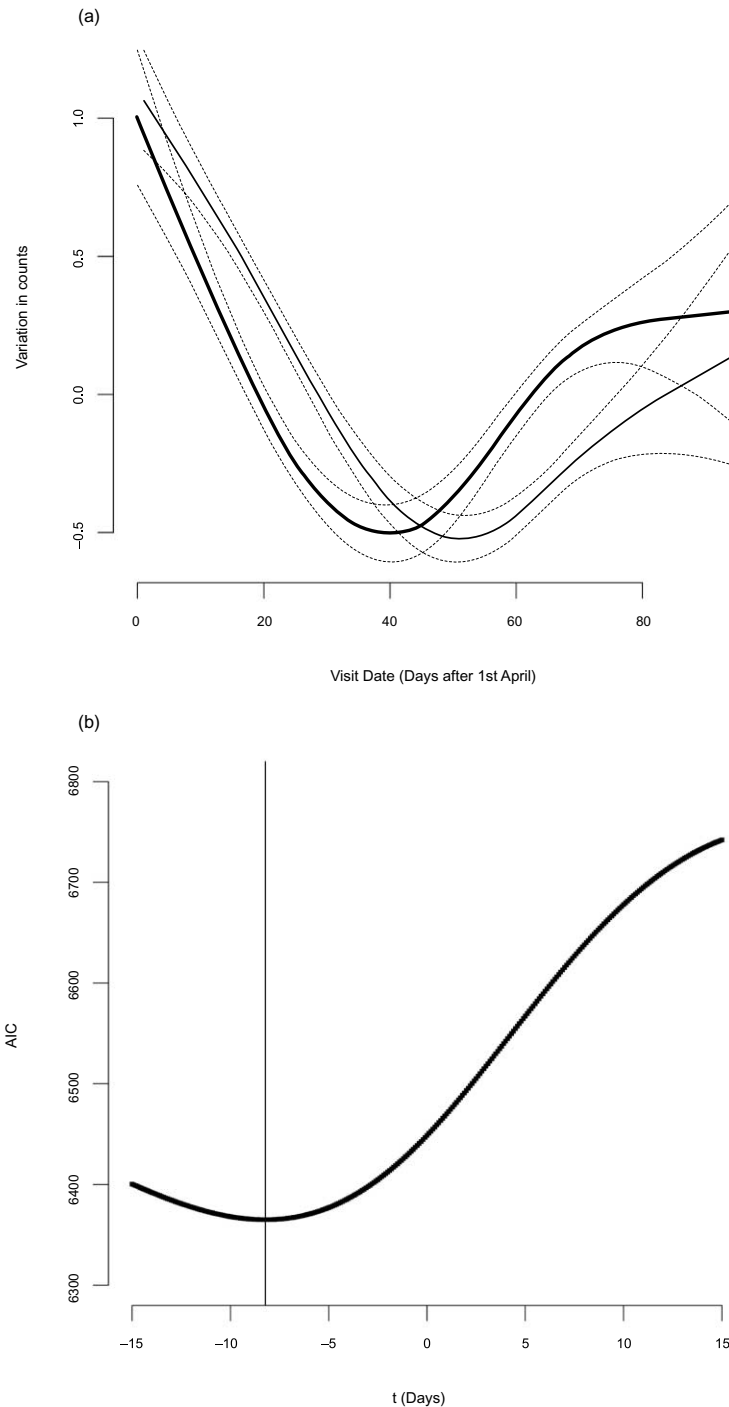


Figure 2. (a) Seasonal abundance distributions for the Wood Nuthatch *Sitta europaea* in 2005 (thick line) and 2006 (slim line). Smoothing was done using a generalized additive model (GAM): Counts+spline function (visit date) with three degrees of freedom assigned to the smoothing term. Ninety-five percent confidence intervals are shown in dotted lines. The figure shows a phenological shift of about 8 days between both curves, 2006 being late compared with 2005. (b) Computed Akaike Information Criterion values for the following GAM: Counts+(Counting site)+spline function (Counting date + t) in relation to t. Three hundred and one different t-values ranging from -15 to +15 days with 0.1 intervals were tested. The relation between AIC and t can be modelled using a quadratic regression: $AIC = t + t^2$. The phenological shift (vertical line) is estimated by $-b/2a$, where a is the second-degree coefficient of the quadratic regression and b the first-degree coefficient. It is worth -8.32 days in this example. Thus, the phenology of abundance of the Eurasian nuthatch was 8.32 days late in 2006 compared to 2005.

counting date on abundance reached 29%. A plot of abundance against counting date for the species for which abundance was significantly related to counting date for all six study years yielded two clearly different patterns. One type consisted of a decrease, with abundance reaching a minimum and afterwards showing a secondary increase. This pattern was displayed only by sedentary species breeding in France (see Fig. 3a). The other pattern type consisted in an increase in counts at the beginning of the study period followed either by stabilization in counts or a decrease. This type of curve applied mainly to long-distance migrants (see Fig. 3b).

Phenological shift estimation

In all the species for which counting date had a significant effect on abundance for at least five out of the six study years (taking the 2001 issue into account) we observed very similar seasonal abundance year-to-year patterns. Species for which counting date was not important in determining seasonal abundance in more than three study years often displayed various different but non-significant seasonal abundance curves. Examples of such species are Goldcrests *Regulus regulus*, Firecrests *Regulus ignicapillus*, and all the tested Bunting species (*Emberiza schoeniclus*, *E. cirrus*, *E. citrinella*, *E. calandra*). This illustrates heterogeneity in detection through point counts, especially for the Goldcrest and the Firecrest. Their song is difficult to detect which produces heterogeneity in the abundance data. Species like the buntings do not show significant variations of abundance during the season. This feature makes them not suitable for this method.

We applied the method designed for the computation of inter-annual phenological shifts to 46 species (see Table 1). For 34 species, phenological shift computation yielded five relevant estimates (temporal shift estimation lying between -15 and +15 days). This represented 72% of the sedentary species included in the 46 tested species, 77% of the short-distance migrants and 87.5% of the long-distance migrants. The computed phenological shifts have a mean of 0.16 and are distributed around 0. The method's ability to produce a phenological shift varies among species. Thus, more long-distance migrants than sedentary species or short-distance migrants had five annual estimations of the phenological shift. Within these groups failures of the method to compute phenological shifts are most likely due to detectability issues during counts. For species such as European Goldfinches *Carduelis carduelis*, Rooks *Corvus frugilegus* and Grey Partridges *Perdix perdix* the method only yields a single

effective estimation. The detection of such species on point counts is highly variable and stochastic depending on the movement of a group. Surprisingly, two very common species of songbirds are unsuited for this method, namely Great Tits *Parus major* and Common Chiffchaffs *Phylloscopus collybita*. When we looked at the values of the shifts in relation to the different years of the study period, we did not find any statistically significant differences. Yet, means of the shifts for the years 2001 and 2003 were positive, unlike the means of the shifts for 2002, 2004 and 2006. This is in accordance with the fact that 2001 and 2003 were among the hottest ever years experienced in France in the past 100 years. Moreover, 2005 was also very hot, so we expected the phenological shifts to be negative for the years 2002, 2004 and 2006 compared with 2005, which was set as the reference year.

Robustness tests

We found a highly significant positive relationship between the phenological shifts computed using the method described in this study and the mean date shift for long-distance migrants (16 species) ($F_{1,92} = 34.67$, $P < 0.001$, species as a random effect; Fig. 4a). A highly significant negative relationship was found between these same variables in sedentary species (18 species) ($F_{1,88} = 16.67$, $P = 0.001$, species as a random effect; Fig. 4b). We observed a weak negative relationship between the phenological shifts and the mean date shifts in short-distance migrants (seven species) ($F_{1,35} = 3.59$, $P = 0.07$) which could also be due to a small sample size. We found no relationship between the shifts' relative standard deviation and the species migratory index ($F_{1,178} = 1.06$, $P = 0.31$). Therefore, migratory status had no significant effect on the phenological shifts' relative standard deviation either ($F_{2,177} = 0.32$, $P = 0.73$). There were no differences between standard deviations of the phenological shifts between sedentary species and short-distance migrants ($P = 0.54$) or between sedentary species and long-distance migrants ($P = 0.49$).

We tested the robustness of the phenological shifts of long-distance migrants to full-moon shifts by looking for a possible relationship between them (difference in abundance timing between one year and 2005) and the moon cycle shifts (difference between April full moon date for one year and April full moon date in 2005). We did not find any significant relationship between both shifts ($F_{1,76} = 0.0002$, $P = 0.99$), thus showing that the phenological shifts clearly do not depend on moon cycles.

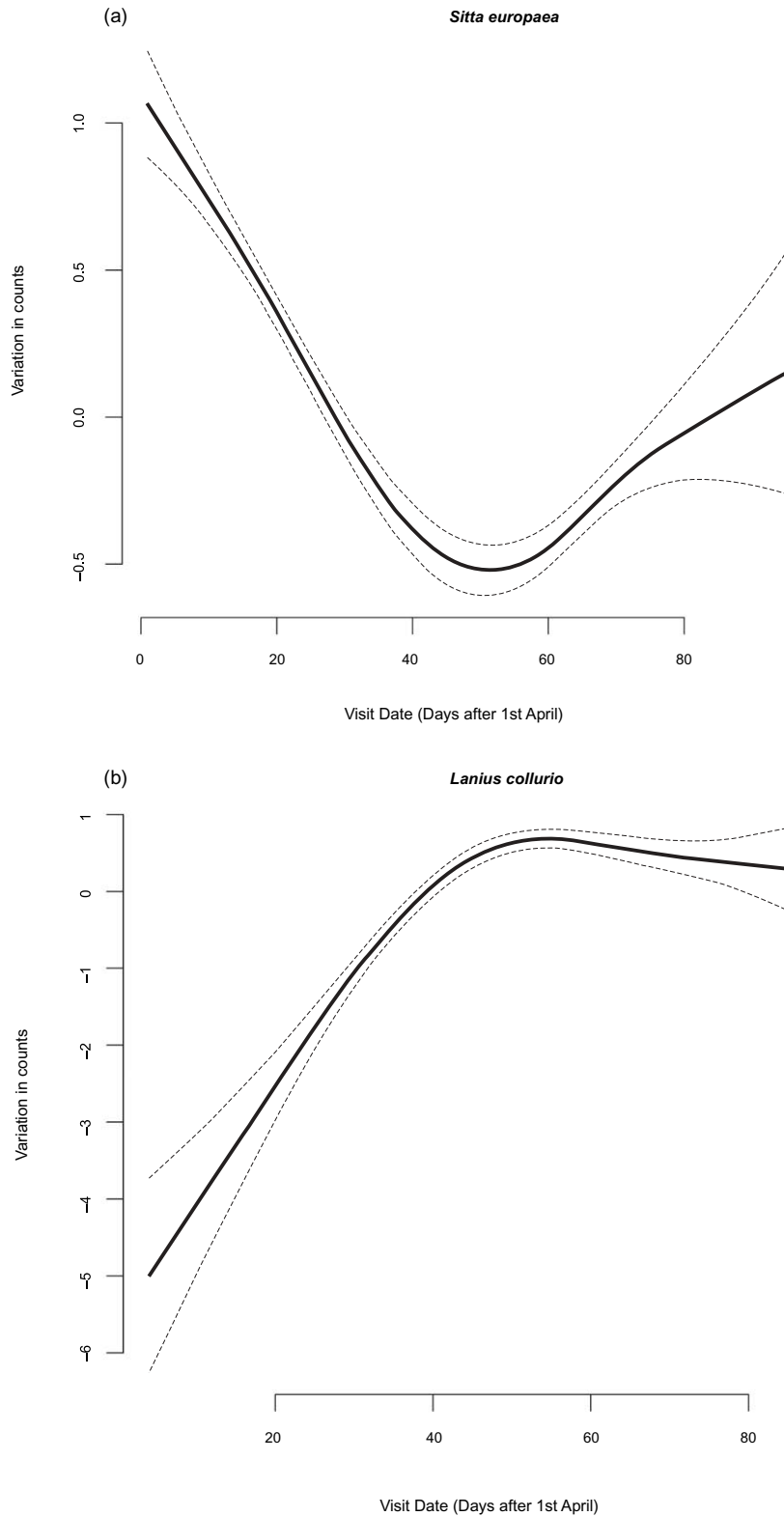


Figure 3. Relationship between abundance and counting date modelled by a generalized additive model with counting date as a smoothing function. (a) example of a sedentary species, Wood Nuthatch; (b) example of a long-distance migrant, Red-backed Shrike. Ninety-five percent confidence intervals are displayed in dotted lines.

Table 1. Phenological shifts estimates computed using the maximum likelihood method. Estimated phenological shifts (in days \pm se) between a given year and 2005 for 46 species monitored by the French Breeding Bird Survey. 2005 was chosen as the reference and so is not included in the table because the shift is obviously 0.

Species	2001	2002	2003	2004	2006
Meadow Pipit <i>Anthus pratensis</i> (2)	-1.77 \pm 3.44	-2.8 \pm 1.2	1.03 \pm 1.05	-0.48 \pm 1.26	2.57 \pm 1.27
Common Swift <i>Apus apus</i> (1)	-1.42 \pm 1.06	0.45 \pm 0.62	0.78 \pm 0.58	2.6 \pm 0.5	-1.61 \pm 0.49
Common Buzzard <i>Buteo buteo</i> (na)	-9.35 \pm 4.55	-0.06 \pm 3.66	0.85 \pm 2.63	-5.41 \pm 3.22	-1.82 \pm 2.1
Common Linnet <i>Carduelis cannabina</i> (2)	-0.78 \pm 4.28	1.9 \pm 1.9	-9.48 \pm 2.81	-4.68 \pm 1.79	4.43 \pm 2.2
European Goldfinch <i>Carduelis carduelis</i> (2)	11.32 \pm 9.71	-	-	-	-8.99 \pm 4.66
European Greenfinch <i>Carduelis chloris</i> (3)	1.74 \pm 3.14	1.43 \pm 2.09	1.48 \pm 1.93	-1.25 \pm 2.19	7.13 \pm 2.67
Cetti's Warbler <i>Cettia cetti</i> (na)	-4.38 \pm 5.89	-1.45 \pm 5.13	-	0.52 \pm 5.64	-14.44 \pm 4.05
Hawfinch <i>Coccothraustes coccothraustes</i> (2)	-0.83 \pm 4.34	-	-0.79 \pm 3.24	-12.11 \pm 4.87	-5.49 \pm 2.3
Common Wood Pigeon <i>Columba palumbus</i> (3)	-	-	-	-4.85 \pm 3.73	-
Carrion Crow <i>Corvus corone</i> (3)	14.83 \pm 3.15	6.72 \pm 2.3	4.39 \pm 1.5	-1.23 \pm 1.23	-3.62 \pm 1.63
Rook <i>Corvus frugilegus</i> (3)	-	0.89 \pm 2.32	-	2.61 \pm 2.52	8.96 \pm 2.85
Common Cuckoo <i>Cuculus canorus</i> (1)	-2.31 \pm 1.92	3.68 \pm 1.06	4.86 \pm 1.04	-4.92 \pm 1.23	2.6 \pm 1.07
House Martin <i>Delichon urbicum</i> Linnaeus (1)	1.75 \pm 2.67	-13.15 \pm 2.14	-0.81 \pm 1.27	14.65 \pm 1.87	5.03 \pm 1.76
Great Spotted Woodpecker <i>Dendrocopos major</i> (3)	1.76 \pm 5.07	-4.48 \pm 2.37	0.96 \pm 1.66	-4.5 \pm 1.88	-6.44 \pm 1.83
Lesser Spotted Woodpecker <i>Dendrocopos minor</i> (na)	1.68 \pm 5.7	-4.87 \pm 4.05	3.21 \pm 2.91	-4.83 \pm 2.39	-1.2 \pm 3.06
European Robin <i>Eriothacus rubecula</i> (2)	-11.2 \pm 6.32	-3.66 \pm 2.48	-1.71 \pm 1.68	-2.81 \pm 2.05	4.69 \pm 2.24
Eurasian Jay <i>Garrulus glandarius</i> (3)	-	7.94 \pm 2.05	11.2 \pm 2.11	-0.96 \pm 1.58	-8.83 \pm 1.44
Melodious Warbler <i>Hippolais polyglotta</i> (1)	-3.12 \pm 1.24	-2.43 \pm 0.89	-0.71 \pm 0.83	-0.67 \pm 0.76	1.37 \pm 0.78
Barn Swallow <i>Hirundo rustica</i> (1)	-1.09 \pm 1.38	-4 \pm 1.03	-7.82 \pm 1.09	1.95 \pm 0.66	5.34 \pm 0.82
Red-backed Shrike <i>Lanius collurio</i> (1)	4.08 \pm 2.51	3.27 \pm 1.35	1.44 \pm 1.04	-0.2 \pm 1.36	4.25 \pm 1.09
Common Nightingale <i>Luscinia megarhynchos</i> (1)	-3.84 \pm 1.2	-4.44 \pm 0.71	-2.99 \pm 0.72	-3.96 \pm 0.58	1.15 \pm 0.62
Yellow Wagtail <i>Motacilla flava</i> (na)	8.87 \pm 9.86	4.37 \pm 2.27	4.17 \pm 2.98	11.58 \pm 2.95	5.85 \pm 2.35
Eurasian Golden Oriole <i>Oriolus oriolus</i> (1)	-3.75 \pm 1.08	0.54 \pm 0.66	2.52 \pm 0.54	1.13 \pm 0.54	2.62 \pm 0.54
Blue Tit <i>Cyanistes caeruleus</i> (3)	-1.12 \pm 2.76	0.91 \pm 1.65	5.21 \pm 1.38	0.78 \pm 1.96	-3.72 \pm 1.26
Great Tit <i>Parus major</i> (3)	-	-	12.94 \pm 1.95	-	-3.17 \pm 2.05
Marsh Tit <i>Parus palustris</i> (3)	13.95 \pm 20.9	10.92 \pm 5.59	7.37 \pm 6.71	-5.99 \pm 5.46	5.91 \pm 3.61
House Sparrow <i>Passer domesticus</i> (3)	-7.81 \pm 4.8	-13 \pm 4.35	-	0.64 \pm 1.66	-1.12 \pm 1.61
Grey Partridge <i>Perdix perdix</i> (3)	-	-	-	-	9.12 \pm 3.02
Black Redstart <i>Phoenicurus ochruros</i> (2)	11.41 \pm 9.85	7.81 \pm 3.42	7.07 \pm 4.78	-1.95 \pm 5.21	2.48 \pm 3.37
Common Redstart <i>Phoenicurus phoenicurus</i> (1)	11.87 \pm 6.44	-1.71 \pm 2.79	-2.95 \pm 3.51	-1 \pm 2.62	3.74 \pm 2.82
Common Chiffchaff <i>Phylloscopus collybita</i> (2)	3.51 \pm 5.42	-	-	-	-
Wood Warbler <i>Phylloscopus sibilatrix</i> (1)	-4.21 \pm 4.23	-4.87 \pm 2.7	-5.37 \pm 5.29	-5.67 \pm 3.05	-1.24 \pm 2.34
Willow Warbler <i>Phylloscopus trochilus</i> (1)	-	-3.99 \pm 2.61	0.34 \pm 5.15	-0.78 \pm 2.85	-2.24 \pm 2.55
Black-billed Magpie <i>Pica pica</i> (3)	-0.89 \pm 1.99	-2.14 \pm 2.06	-4.01 \pm 2.5	-4.17 \pm 1.8	-0.89 \pm 1.99
Green Woodpecker <i>Picus viridis</i> (3)	10.3 \pm 5.79	9.78 \pm 2.63	0.56 \pm 2.65	-1.11 \pm 1.96	-4.38 \pm 1.89
Whinchat <i>Saxicola rubetra</i> (1)	-5.61 \pm 2.58	1.53 \pm 1.71	3.5 \pm 2.64	-	-2.18 \pm 3.3
Stonechat <i>Saxicola torquatus</i> (2)	-1.02 \pm 4.42	7.97 \pm 3.58	11.9 \pm 3.26	3.99 \pm 3.37	-7.29 \pm 4.47
Wood Nuthatch <i>Sitta europaea</i> (3)	-8.7 \pm 2.58	-1.64 \pm 1.31	0.54 \pm 1.15	-9.32 \pm 1.18	-8.23 \pm 0.98
European Turtle Dove <i>Streptopelia turtur</i> (1)	1.53 \pm 0.83	-0.25 \pm 0.61	0.43 \pm 0.58	-0.25 \pm 0.57	0.35 \pm 0.58
Common Starling <i>Sturnus vulgaris</i> (3)	-6.37 \pm 2.34	-6.83 \pm 2.1	-7.93 \pm 1.67	-3.02 \pm 1.53	-10.65 \pm 1.5
Garden Warbler <i>Sylvia borin</i> (1)	0.31 \pm 1.72	1.43 \pm 1.18	4.31 \pm 1.15	2 \pm 1.13	3.99 \pm 1.23
Common Whitethroat <i>Sylvia communis</i> (1)	7.14 \pm 2.61	7.08 \pm 1.35	4.07 \pm 1.22	9.9 \pm 1.27	9.16 \pm 1.37
Lesser Whitethroat <i>Sylvia curruca</i> (1)	-5.64 \pm 6.39	1.09 \pm 2.93	1.35 \pm 2.61	7.24 \pm 3.52	-0.19 \pm 5.56
Common Blackbird <i>Turdus merula</i> (3)	4.58 \pm 6.54	-4.34 \pm 3.52	-12.43 \pm 3.57	-9.1 \pm 3.27	-7.35 \pm 2.79
Song Thrush <i>Turdus philomelos</i> (2)	-0.66 \pm 5.11	4.62 \pm 2.64	9.39 \pm 2.96	2.46 \pm 2.35	1.51 \pm 2.26
Fieldfare <i>Turdus pilaris</i> (na)	2.73 \pm 7.02	6.4 \pm 3.26	-1.97 \pm 2.65	-0.42 \pm 3.73	1.15 \pm 2.64

The migratory strategy of the species is presented in the species column: 1, long-distance migrant; 2, short-distance migrant; 3, sedentary species; na, information on the mean migration distance not available.

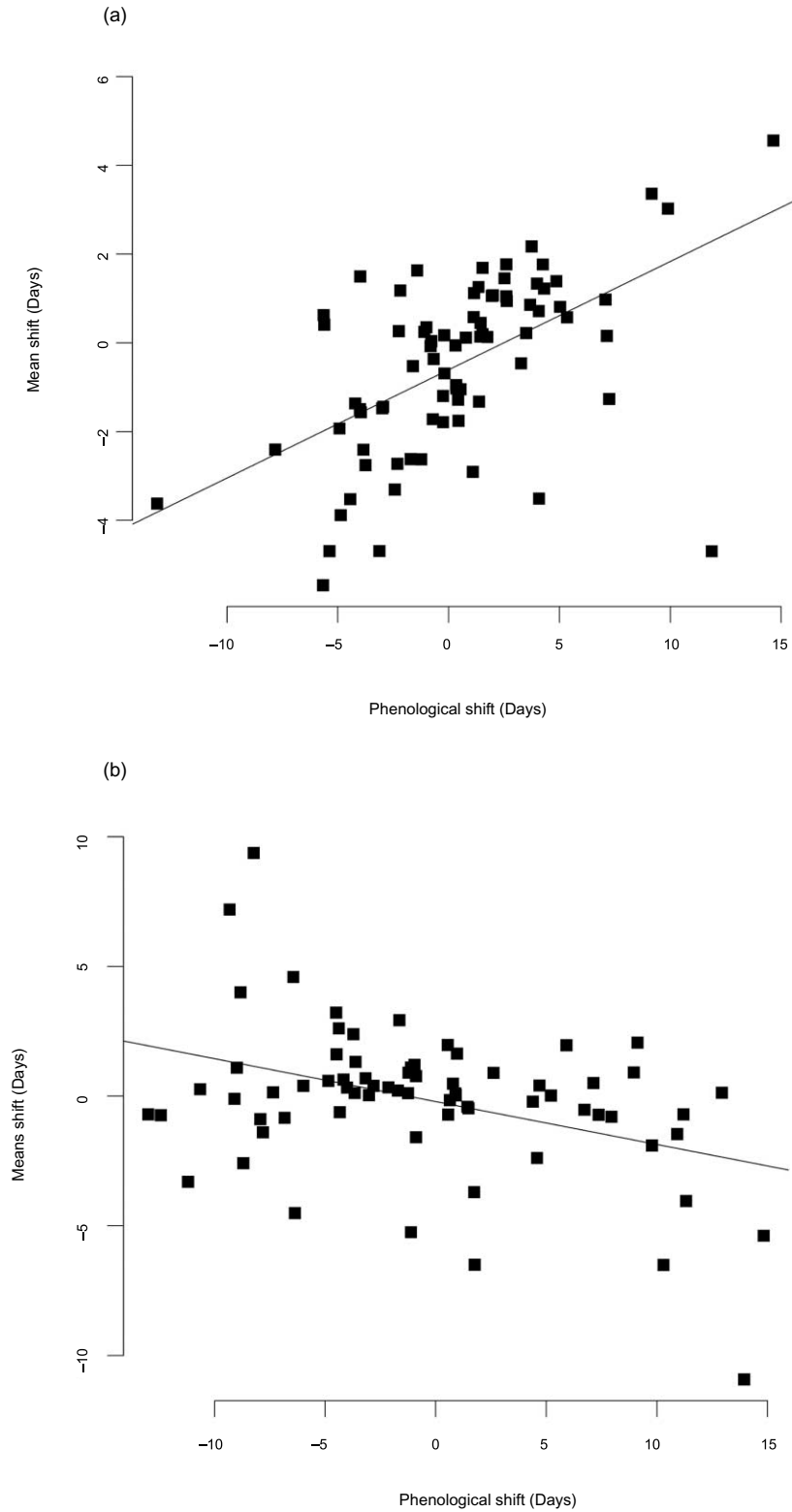


Figure 4. Relationship between the phenological shifts computed using the method described in this study and temporal shifts computed using the mean count date. (a) long-distance migrants; (b) sedentary species.

DISCUSSION

Method novelty and interest in phenological studies

Studies dealing with species phenology are numerous and the field is currently developing rapidly within the context of global climatic change. Proposing a novel approach to these issues would not be very useful if it did not allow new perspectives concerning the data that can be incorporated in phenological studies or the results these studies generate. There are at least two current gaps in the phenological field. First, a gap in the spatial scale. Most works have previously focused on small populations or specific migration monitoring sites. As a consequence, little is known about what happens in the wider countryside. However, the method described here allows very large areas to be studied within the phenological framework. The second gap in our phenological knowledge is due to the particular features of each species, which makes it difficult to include all of them in a single study. Indeed, because species share different life-history traits, the nature of their phenological response is likely to be unclear when combined. Here we have shown that a classical phenological measure, the mean date for a given process, cannot be used on groups of species that include both sedentary species and migrants. Indeed, the same variation in a species' timing results in opposite signs in the behaviour of the measure for these species groups. For this reason such responses could not be combined and included in further studies. The method used in this paper addresses this issue: the shifts in timing are estimated in the same way for all species, which makes them comparable. Nevertheless, as this method should be measuring the same biological process as classical methods, the phenological shifts should somehow relate to the ones yielded by classical measures. One of the most frequently used estimators of a species' phenology is mean date weighted by the intensity of the surveyed biological process (Sparks *et al.* 2005). The issue raised by such estimators is that they do not vary in the same way depending on the shape of the process's distribution across time (Fig. 1). They are relevant only if one is interested in studying a single species or a group of species sharing the same process distributions, but cannot be used in comparisons involving species with different features. We found significant relationships between the phenological shifts and the mean shifts for long-distance migrants and sedentary species breeding in France when taken separately. Moreover, the signs of both relationships were

opposite in consistency with the ones predicted by the interaction of the shape of the distribution and the phenological shift (see Fig. 1); i.e. positive for long-distance migrants and negative for sedentary species. This study shows that by estimating the same processes in different ways does not change the predictions about the estimated phenological shifts and it allows larger spatial scales to be studied as well as the combination of more species. However, these advantages rely on several important assumptions which need further discussion.

Interaction between spatial and temporal replicates and method applicability

We used data originating from many different sites surveyed only twice a year and used this to model abundance variations across the whole study area. However, species' seasonal abundance patterns are influenced by time, space and the interaction between them. Migratory species illustrate this point. They first arrive on the monitoring sites located in the south of France and are therefore detected on these point counts before being detected at more northern point counts. Nevertheless, as they colonize the whole study area, the sum of all counts rises, which explains the increasing pattern observed here. Hence it is likely that this pattern reflects the phenology of their return to breeding sites. For sedentary species, this interaction could be a major issue only if maximal song activity (thus detectability) in northern point counts exactly matched minimal activity in southern sites where the breeding season started earlier. This is very unlikely and not in accordance with the clear abundance variation patterns presented here although it might be one explanation for non-significant abundance variation patterns in some species. On the whole, we may conclude that interactions between time and space represent no major bias in the analysis, at least in frequently detected species. Indeed, since roughly the same sites are monitored each year the interaction between time and space remains roughly constant. This allows interannual comparisons to be made. For these, it is possible to consider all the spatial replicates as temporal replicates without altering the biological message that abundance data encompass. More generally, the method may suit datasets where the intensity of a biological phenomenon is monitored either with few temporal replicates for each site but on many sites, or many temporal replicates but on few sites. Indeed, both cases result in

a well-described seasonal pattern for the monitored phenomenon as long as the number of observations is large enough to support a smoothing term. Issues resulting from the interaction between time and space would be much smaller in cases where there are many temporal replicates on few sites. We can, therefore, safely assume that in such cases this method would be even more efficient and robust.

Relationship between seasonal abundance trends and breeding phenology

It is assumed that abundance estimated through point counts, transects or other monitoring programmes relates strongly to a species phenology (Best & Petersen 1982, 1985). Taking advantage of this relationship is novel, because the main emphasis has been to get rid of heterogeneous detection probabilities to estimate unbiased abundance at a given site (Boulinier *et al.* 1998, Calladine *et al.* 1999, MacKenzie *et al.* 2002, Selmi & Boulinier 2003, Royle *et al.* 2005). Indeed, the actual number of counted individuals can be split into two components. First, the number of birds that are to be counted in the field (true abundance) and second, the conditional probability, knowing the bird is there and is actually counted (true detectability). True abundance relates to the species' phenology, especially in migratory species. Indeed, there are no birds to count before they arrive back from their wintering grounds. As they arrive, their numbers increase and thus their detectability also increases (Huin & Sparks 2000). This component is probably not as important in sedentary species, although we cannot exclude that fledglings add to the number of birds present at the end of spring. True detectability of a species also relates to its particular phenology. In fact, most birds are detected by their song and it is well established that song activity in males varies across the breeding season in many song-bird species (Calladine *et al.* 1999, Hegelbach & Spaar 2000, Poesel *et al.* 2001, Amrhein *et al.* 2002). Relationships have been found between egg-laying by females and song activity in males (Thomas 2002, Amrhein *et al.* 2004, Kunc *et al.* 2005, Amrhein *et al.* 2007, Kunc *et al.* 2007). Moreover, for all bird species, females are far less detectable when incubating, therefore the number of birds susceptible to being counted remains constant but the actual counts decrease.

Therefore, the integration of both true abundance and true detectability into count data originating from large-scale sampling protocols should therefore lead to complex non-linear patterns for estimated abundance

across time. We observed such patterns in this study. For nearly half the studied species, these patterns were significant in at least half the number of years. Nevertheless, the ultimate condition to be able to relate such non-linear curves with each species phenology is their repeatability across years. Indeed, phenology, which consists in the succession of different lifecycle stages, remains qualitatively completely constant across years (females always lay eggs after having mated, which, for migratory species, always occurs after having returned to their summering grounds). Therefore, annual patterns should at least also be repeatable qualitatively (in their shape) from one year to another to prove this relationship. Not surprisingly, species that displayed significant seasonal abundance patterns for more than half of the studied years, also showed obvious repeatability in the shape of the curves.

Moreover, we identified two different curve shapes, the first one displayed by sedentary species and the second one by long-distance migrants. As discussed above, these curves are also consistent with a phenological explanation of estimated abundance variations as they were repeatable and quite easy to interpret. On the one hand, sedentary birds start their breeding cycle early in spring (Poesel *et al.* 2001) when males are easy to detect through song activity. This diminishes during the breeding season but may start again if the species are multi-brooded. Detectability could also, for certain species increase, after having gone down to a minimum during incubation, due to chick feeding or activity of fledged families. This scenario could very well explain the estimated abundance pattern we observed in sedentary species (Fig. 3a). On the other hand, long-distance migrants are not present at the beginning of the study period and arrive from the end of April to May and then start breeding. This scenario is consistent with the abundance pattern we observed in migrants with strong increases (Huin & Sparks 2000) and then either stabilization or decrease (Fig. 3b). Although we noticed some variability in the shape of the pattern between species belonging to a given migratory class, these particular features can be related to well-established behavioural features. For example, Common Nightingales *Luscinia megarynchos* displayed a pattern consisting of an increase reaching a peak followed by a strong decrease well matching song activity (Amrhein *et al.* 2002, Kunc *et al.* 2007).

In conclusion, we propose that measuring birds' abundance across the entire monitored area and across the study period (April to June) can be used to address

phenological issues as an alternative to studies focusing on particular stages of the breeding lifecycle (e.g. Grieco *et al.* 2002, Both *et al.* 2006, Visser *et al.* 2006).

Method robustness to species heterogeneity

We were able to estimate phenological shifts for 34 species, which represents slightly more than 36% of the total number of species in the study area. The distribution of these species between sedentary, short-distance and long-distance migrants, was roughly homogenous with slightly more long-distance migrants. Hence, since a species' counts are significantly influenced by counting date for at least 3 years, the probability that the method is able to compute phenological shifts is high.

A crucial point is the phenological content of these temporal shifts. As emphasized above, the novelty of this method lies in the phenological estimations it provides, but these should be comparable across species. Possible biases could arise, however. One example is that some long-distance migrants rely, in the timing of their journey, on moon phases (Pyle *et al.* 1993, James *et al.* 2000), which do not occur on the same calendar date each year. Therefore, for long-distance migrants, there could be a bias in the estimated shifts towards the shift of the moon phase of the tested year compared with the reference year. We did not find such a relationship for the 16 long-distance migrant species so that such a bias must remain very small. Phylogenetic autocorrelation was not taken into account in the analysis and could lead to potential bias in the results. Nevertheless, in this case, the effect of moon shifts is so insignificant that taking phylogeny into account would not have changed the results. This shows that the accuracy of the estimated phenological shifts does not vary significantly between species which have very different migration strategies. We made the assumption that the phenological shifts resulted from the match of two almost identical annual abundance patterns. This means that the phenological shifts result only from the difference in the timing of detectability. On such a large scale, it is very likely that such differences are driven by climate. Potential biases, such as inter-annual variations of the sex ratio (Donald 2007), which would lead to more or fewer singing individuals, or of nest predation (leading to males restarting to sing) probably remain limited and are unlikely to influence strongly the seasonal abundance patterns and thus the estimated phenological shifts. Indeed, here it is not only the

number of birds that is important but also the moment when they are detectable.

Conclusion

Large-scale abundance monitoring programmes carried out by voluntary observers are a very widespread method to survey common animal and plant populations. These large-scale sampling designs are currently being developed in many countries where there is concern about population trends in response to global change. These data have rarely been used to study phenology, perhaps because the protocol was not designed for this purpose. Nevertheless, the huge amount of dated abundance data collected by programmes such as the BBS has great potential in describing species' phenology and highlighting factors driving their changes. Following Sparks' (2007) wise advice about 'lateral thinking' in the way we should consider data in phenological studies, we demonstrate here that readily accessible data collected in large-scale long-term volunteer monitoring programmes can be used to study phenological shifts on the scale of an entire country. We emphasize that this novel approach can be readily used in other protocols such as constant effort site monitoring in birds to study large-scale variations in the phenology of juvenile captures as a proxy for egg-laying dates or any other taxa as long as the structure of the data meets the one described here i.e. a temporal distribution of counts reflecting phenology. The next step will be to use the computed temporal shifts to create indices which would indicate how species phenology varies across years. It would also be of great interest to test whether phenological plasticity is linked to long-term trends or to the ability of a species to adapt locally to climate change.

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REFERENCES

- Akaike, H.** 1981. A new look at the statistical-model identification. *C./Eng. Tech. Appl. Sci.* **22**: 22.

- Amrhein, V., Korner, P. & Naguib, M.** 2002. Nocturnal and diurnal singing activity in the Nightingale: correlations with mating status and breeding cycle. *Anim. Behav.* **64**: 939–944.
- Amrhein, V., Kunc, H.P. & Naguib, M.** 2004. Seasonal patterns of singing activity vary with time of day in the Nightingale (*Luscinia megarhynchos*). *Auk* **121**: 110–117.
- Amrhein, V., Kunc, H.P., Schmidt, R. & Naguib, M.** 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*. *Ibis* **149**: 237–244.
- Best, L.B., & Petersen, K.L.** 1982. Effects of stage of the breeding cycle on Sage Sparrow detectability. *Auk* **99**: 788–791.
- Best, L.B., & Petersen, K.L.** 1985. Seasonal changes in detectability of Sage and Brewers Sparrows. *Condor* **87**: 556–558.
- Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E.** 2006. Climate change and population declines in a long-distance migratory bird. *Nature* **441**: 81–83.
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H.** 1998. Estimating species richness: the importance of heterogeneity in species detectability. *Ecology* **79**: 1018–1028.
- Calladine, J., Buner, F. & Aebischer, N.J.** 1999. Temporal variations in the singing activity and the detection of Turtle Doves *Streptopelia turtur*: implications for surveys. *Bird Study* **46**: 74–80.
- Crick, H.Q.P.** 2004. The impact of climate change on birds. *Ibis* **146**: 48–56.
- Crick, H.Q.P. & Sparks, T.H.** 1999. Climate change related to egg-laying trends. *Nature* **399**: 423–424.
- Croxtton, P. J., Sparks, T. H., Cade, M. & Loxton, R.G.** 2006. Trends and temperature effects in the arrival of spring migrants in Portland (United Kingdom) 1959–2005. *Acta Ornithol.* **41**: 103–111.
- Donald, P.F.** 2007. Adult sex ratios in wild bird populations. *Ibis* **149**: 671–692.
- Grieco, F., van Noordwijk, A.J. & Visser, M.E.** 2002. Evidence for the effect of learning on timing of reproduction in Blue Tits. *Science* **296**: 136–138.
- Hegelbach, J. & Spaar, R.** 2000. Annual variation in singing activity of the Song Thrush (*Turdus philomelos*), with comments on high post-breeding song output. *J. Ornithol.* **141**: 425–434.
- Huin, N. & Sparks, T.H.** 2000. Spring arrival patterns of the Cuckoo *Cuculus canorus*, Nightingale *Luscinia megarhynchos* and Spotted Flycatcher *Muscicapa striata* in Britain. *Bird Study* **47**: 22–31.
- James, D., Jarry, G. & Erard, C.** 2000. Influence of the moon on the nocturnal postnuptial migration of the Skylark *Alauda arvensis* L in France. *C. R. Acad. Sci. III-Vie.* **323**: 215–224.
- Jenni, L. & Kery, M.** 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proc. Roy. Soc. B* **270**: 1467–1471.
- Jiguet, F., Gadot, A.S., Julliard, R., Newson, S.E. & Couvet, D.** 2007. Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology* **13**: 1672–1684.
- Jiguet, F., Julliard, R., Thomas, C.D., Dehorter, O., Newson, S.E. & Couvet, D.** 2006. Thermal range predicts bird population resilience to extreme high temperatures. *Ecol. Lett.* **9**: 1321–1330.
- Jonzen, N., Linden, A., Ergon, T., Knudsen, E., Vik, J.O., Rubolini, D., Piacentini, D., Brinch, C., Spina, F., Karlsson, L., Stervander, M., Andersson, A., Waldenstrom, 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.
- Julliard, R., Clavel, J., Devictor, V., Jiguet, F. & Couvet, D.** 2006. Spatial segregation of specialists and generalists in bird communities. *Ecol. Lett.* **9**: 1237–1244.
- Knudsen, E., Linden, A., Ergon, T., Jonzen, N., Vik, J.O., Knape, J., Roer, J.E. & Stenseth, N.C.** 2007. Characterizing bird migration phenology using data from standardized monitoring at bird observatories. *Climate Research* **35**: 59–77.
- Kunc, H.P., Amrhein, V. & Naguib, M.** 2005. Seasonal variation in dawn song characteristics in the common nightingale. *Anim. Behav.* **70**: 1265–1271.
- Kunc, H. P., Amrhein, V. & M. Naguib.** 2007. Vocal interactions in Common Nightingales (*Luscinia megarhynchos*): males take it easy after pairing. *Behav. Ecol. Sociobiol.* **61**: 557–563.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A.** 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecol.* **83**: 2248–2255.
- Møller, A.P., Fiedler W. & Berthold P.** 2004. Birds and climate change. In Caswell, H. (ed.) *Advances in Ecological Research*, Vol. 35: 1–259. Academic Press, USA.
- Parmesan, C.** 2006. Ecological and evolutionary responses to recent climate change. *Ann. Rev. Ecol. Evol.* **37**: 637–669.
- Parmesan, C. & Yohe, G.** 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Poesel, A., Foerster, K. & Kempenaers, B.** 2001. The dawn song of the Blue Tit *Parus caeruleus* and its role in sexual selection. *Ethology* **107**: 521–531.
- Pyle, P., Nur, N., Henderson, R.P. & Desante, D.F.** 1993. The effects of weather and lunar cycle on nocturnal migration of landbirds at southeast Farallon Island, California. *Condor* **95**: 343–361.
- R Development Core Team.** 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>.
- Royle, J.A., Nichols, J.D. & Kery, M.** 2005. Modelling occurrence and abundance of species when detection is imperfect. *Oikos* **110**: 353–359.
- Selmi, S. & Boulinier, T.** 2003. Does time of season influence bird species number determined from point-count data? A capture–recapture approach. *J. Field Ornithol.* **74**: 349–356.
- Sparks, T.H.** 2007. Lateral thinking on data to identify climate impacts. *Trends Ecol. Evol.* **22**: 169–171.
- Sparks, T.H., Bailein, F., Bojarinova, J.G., Huppopp, O., Lehikoinen, E.A., Rainio, K., Sokolov, L.V. & Walker, D.** 2005. Examining the total arrival distribution of migratory birds. *Global Change Biol.* **11**: 22–30.
- Sparks, T.H. & Braslavská, O.** 2001. The effects of temperature, altitude and latitude on the arrival and departure dates of the Swallow *Hirundo rustica* in the Slovak Republic. *Int. J. Biometeorol.* **45**: 212–216.
- Thomas, R.J.** 2002. Seasonal changes in the nocturnal singing routines of Common Nightingales *Luscinia megarhynchos*. *Ibis* **144**: E105–E112.
- Tryjanowski, P. & Sparks, T.H.** 2001. Is the detection of the first arrival date of migrating birds influenced by population size? A case study of the Red-backed Shrike *Lanius collurio*. *Int. J. Biometeorol.* **45**: 217–219.
- van Strien, A., Plantenga, W. Soldaat, L., van Swaay, C. & WallisDeVries, M.** 2008. Bias in phenology assessments based on first appearance data of butterflies. *Oecologia* **156**: 227–235.
- Visser, M.E. & Both, C.** 2005. Review. Shifts in phenology due to global climate change: the need for a yardstick. *Proc. Roy. Soc. B* **272**: 2561–2569.

Visser, M., Holleman, L. & Gienapp, P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**: 164–172.

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.

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