Using first arrival dates to infer bird migration phenology

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Understanding phenological responses to climate change requires explicit quantitative estimation of phenological distributions. First arrival dates (FAD) are frequently used, but biased, noisy and qualitative metrics of migration phenology. Despite critique against the use of FAD, better understanding of the risks and possible usefulness of this readily available data type is needed. I here present a stochastic model for the number of observed migrating birds during a given season. Firstly, I simulate data according to the model to quantify and describe how FAD are affected by population size, observation effort and observability, and provide some guidelines for interpreting earlier results and doing statistical correction. Secondly, I describe principles for how FAD and complementary daily migration data can be combined to fit phenological distribution functions, providing coherent quantitative measures of phenology. Using data on tree pipits (*Anthus trivialis*) I demonstrate how this can be done using generalized linear models.

Introduction

Many species of migratory birds adjust their timing of migration to climate variation and have during the last decades advanced their arrival profoundly (Ahola *et al.* 2004, Lehikoinen *et al.* 2004, Vähätalo *et al.* 2004, Jonzén *et al.* 2006, Tøttrup *et al.* 2008, Filippi-Codaccioni *et al.* 2010). These responses show extensive variation between ecological groups, species and regions (Both and te Marvelde 2007, Rubolini *et al.* 2007, Thorup *et al.* 2007), potentially having serious population-level consequences (Visser *et al.* 2004, Both *et al.* 2006, 2009, Møller *et al.* 2008). Unravelling the mechanisms of the responses and predicting possible population consequences requires quantitative information about the temporal distributions of phenological events (phenophases) at different trophic levels (Sparks *et al.* 2005, Visser and Both 2005, Jonzén *et al.* 2007).

First arrival dates (hereafter FAD) are the most common type of data in studies relating climate variation to timing of bird migration (Knudsen *et al.* 2007, 2011). Typically FAD are included in statistical analyses as the response variable, to represent some early phase of the distribution of arrival (e.g., Sparks and Tryjanowski 2007). However, in addition to phenology itself, population size, observation effort and observability affects observed FAD, which consequently are likely to be poor metrics for inference on phenology (Sparks *et al.* 2001, 2008, Tryjanowski and Sparks 2001, Mills 2005, Tryjanowski *et al.* 2005, Miller-Rushing *et al.* 2008a, 2008b, Moussus *et al.* 2010). Even if population size and observation effort would be constant, FAD are usually very noisy metrics of phenology (Knudsen *et al.* 2007, 2011, Moussus *et al.* 2010).

Despite the recognized problems, lots of studies use FAD, probably due to the availability of long time series, often representing the only existing phenological data for a certain period, species or location. While obviously other types of data are preferable in phenological research, there is a need for constructive assessment of whether the information in FAD can be reliably used under any circumstances and whether we can trust any earlier results based on FAD. There are only a few simulation based studies assessing the bias in FAD: Moussus *et al.* (2010) concluded that FAD are bad metrics of phenology and usage should be avoided, while Zduniak *et al.* (2010) quantified the bias present in their own study to relate it to their results. In order to recognize situations where FAD are heavily biased, or to be able to statistically correct for sources of bias, a more general simulation based quantitative assessment of the issue is needed.

Another problem with using FAD as a response variable is that the results are cryptic and qualitative, describing some arbitrary measure of start of migration, with little explicit quantitative information about the phenological distribution (Knudsen *et al.* 2011). The fact that FAD are affected by both phenology and population size implies that they contain some information on both aspects. Consequently, an alternative to use FAD as a response variable could be to use them as data to estimate the phenological distribution, including its height (population size).

In this study, I seek to gain a deeper understanding of the limitations, information content and possibilities for sound use of FAD in phenological studies. I present a stochastic model for seasonal variation in the numbers of phenological events, which is applied here for two purposes. Firstly, I use simulation techniques to show how and how much FAD are related to population size, observation effort and observability in some simple settings. This will help to better assess the reliability of earlier studies and to potentially correct for bias in studies using FAD as the response variable. Secondly, I propose an approach for using FAD as data to obtain quantitative estimates of the underlying phenological distributions, which in turn are likely to be useful in further analyses. FAD are then combined with more accurate daily migration count data, which

is complementary by containing more information about the shape and height of the phenological distribution. To illustrate, I show an example using data on tree pipits (*Anthus trivialis*), how such a model might be fitted in the framework of generalized linear models (GLM).

Material and methods

In the first section, I start by describing a stochastic model for seasonal variation and daily numbers of observed migrating birds from a specific population. The model is here described for one season, but can be extended over years and/or space. In the latter sections, I describe how the simulation study was implemented and how FAD can be combined with daily migration counts to fit phenological distribution functions. The latter sections are based on the model described first.

A stochastic model for seasonal variation in the number of migrating birds

The number of phenological events throughout a season, e.g. observed numbers of migrating birds of a given population, can be modelled as a parametric function for the expected number of observed individuals and a stochastic part defining how the actual observed numbers are scattered around the expectation (*see* e.g., Jonzén *et al.* 2006, Knudsen *et al.* 2007). Here, I present an extension of this approach, also including observation probability.

Here, I denote the day-specific number of observed birds by Z_i, where i is an index for the days of a predefined season in focus (e.g. in the example introduced later, $i = 1$ for 1 April). For a particular season, I modelled the conditional expectation of the number of observed birds on day i as

$$\lambda_i = E_\theta\left(Z_i \middle| v, i, p_i\right) = v f\left(i; \theta\right) p_i, \qquad (1)$$

where v is the constant adjusting for the total number of birds, $f(i; \theta)$ is the parametric function with the vector of parameters θ, describing the relative temporal distribution of migrating

birds throughout a particular season, and p_i is the probability that a bird is observed on day i. I chose $f(i ; \boldsymbol{\theta})$ such that it approximately sums to one over all days (shaped like a probability distribution function). Consequently, ν will closely correspond to the total number of birds and be proportional to population size. Assuming that all observers are equally skilled, I modelled the probability that at least one of m_i observers finds a bird with probability q_i as

$$p_i = 1 - \left(1 - q_i\right)^{m_i}. \qquad (2)$$

If observation effort and detectability can be assumed to be approximately constant throughout the season, or if there is no information regarding those aspects, it is difficult to distinguish between observation effort and relative population size. In such cases, the terms ν and p_i are not identifiable, and their product can be treated as a constant (i.e., $p_i = 1$), which might ease some technical aspects of estimating the empirical phenological distribution statistically.

In this paper, I used a skew normal function for the seasonal variation in migration intensity

$$f\left(i;\boldsymbol{\theta}\right) = \frac{2}{\sigma\sqrt{2\pi\sigma^2}} \exp\left[-\frac{\left(i-\mu\right)^2}{2\sigma^2}\right] \Phi\left[\alpha\frac{\left(i-\mu\right)}{\sigma}\right]. (3)$$

This function has three parameters: the location parameter (μ), the scale parameter (σ) and the shape parameter for skewness (α), and has the same shape as the skew normal probability distribution (Azzalini 1985). Values of $\alpha > 0$ give a right-skewed function, while $\alpha < 0$ gives a left-skewed function. If $\alpha = 0$, then $f(i ; \boldsymbol{\theta})$ is a symmetric Gaussian function. The symbol $\Phi(\dots)$ denotes a function identical in shape to the standard normal cumulative probability distribution. Some earlier studies used Gaussian functions as a rough but fairly good approximation to model the phenological distribution of a single population (Miller *et al.* 2002, Jonzén *et al.* 2006, Lindén and Mäntyniemi 2011; see also Knudsen *et al.* 2007). However, the choice of function is worth to consider carefully and a more complex model, such as a mixture of several functions, might be desirable (Lehikoinen *et al.* 2010, Lindén *et al.* 2011). For very complex phenological patterns, smoothing functions and the use of generalized additive models (GAM)

can be viable options (Knudsen *et al.* 2007, Moussus *et al.* 2009, 2010).

I assumed that the actual counted numbers of observed birds (Z_i) are spread around the model expectation (λ_i) according to some discrete probability mass function that is defined for zero and positive integers. To model the lower bound of variation, I used the Poisson distribution

$$Z_i \sim \text{Pois}\left(\lambda_i\right), \qquad (4)$$

which also can be used for fitting the model statistically, as long as standard errors are corrected for overdispersion (ver Hoef and Boveng 2007). As a more realistic alternative I here used the negative binomial distribution, which can be seen as a Poisson–Gamma mixture (*see* e.g., Lindén and Mäntyniemi 2011). The data are then distributed as

$$Z_i \sim \text{NegBin}\left(\frac{1}{w}, \frac{1}{1+w\lambda_i}\right), \qquad (5)$$

such that the variance increases quadratically with the mean, depending on the overdispersion parameter w, as

$$V\left(Z_i\right) = \lambda_i + w\lambda_i^2. \qquad (6)$$

Simulating effects of population size and observation effort on FAD

To assess the effects of population size, observation effort and observability on FAD, I simulated four different scenarios of the model described by Eqs. 1–5, with different shape of the phenological distribution, error structures and parameter values (Table 1). The scenarios applied were: (i) a Gaussian function with Poisson error, (ii) a Gaussian function with negative binomial error, (iii) a clearly right-skewed function with negative binomial error, and (iv) a clearly left-skewed function with negative binomial error.

The potential migration season ranged from day 1 to 99. The effect of population size was investigated by varying the expected total number of observed birds (ν) from 40 to 960, with and interval of 10 birds, and assuming that all birds were detected perfectly ($p_i = 1$). The simulation was done once for each population size. I used a

log-linear curve to describe the relationship, such that the observed FAD is linearly related to $\ln \nu$. The curve was however plotted on the original scale, along with the simulated data points.

To investigate effects of observation effort and observability (*see* Eq. 2), I let the number of observers (m) range from 1 to 11 with an interval of 0.5. The detection probability for one person (q) was set to range from 0.05 to 0.95, with an interval of 0.05. While Eq. 2 presents the parameters m_i and q_i as day-specific values, I assumed in the simulations that these are constant over the season. Here expected population size (ν) was fixed to 1000. For all parameter combinations (of m and q) the simulation was repeated 10 000 times and the average FAD are presented in the results.

All simulations and analyses were implemented in the MATLAB® (ver. 7.6.0, R2008a, The MathWorks Inc.) environment.

The principle of including FAD data in seasonal distribution models

An alternative to use FAD as a response variable in regression type models is to use them as data for fitting phenological functions, i.e. models similar to that described in Eqs. 1–5. To date, these kinds of models have been fitted only to daily migration counts from a particular place, typically a bird observatory, being a robust way to handle missing and truncated data (Jonzén *et al.* 2006, Knudsen *et al.* 2007, Moussus *et al.* 2010). FAD can be seen as special cases of truncated and right-censored data sets on the number of daily counted birds. The number of observed birds is zero before the first arrival, non-zero

(possibly a known count) on the first day of arrival, and missing after that.

To make use of FAD in this context, they must be combined with complementary day-specific migration count data that contain more information about the shape of the phenological distribution. The FAD might on the other hand contribute to describe temporal location of the estimated phenological distributions for time periods and sites with no other data available. In order to make effective use of the information in FAD, the model must also be extended over years and preferably also space, with restrictive assumptions about some parameters. When fitting these models to several seasons and data sets, annual variation in population size and site-specific observation effort is explicitly accounted for by letting the parameter ν (Eq. 1) vary. Effects of year and site (or data type) on ν should be modelled as multiplicative main effects i.e., on log-scale additive main effects similar to a two-way ANOVA without interactions. Depending on species ecology, any of the parameters μ, σ and α can be assumed to be constant over time, be treated as separate parameters for each year, or be allowed to vary between years and/or sites according to some model.

The model can be fitted using Bayesian methods as well as based on a maximum likelihood approach, where the sum of all log-likelihoods from different data sources is maximized (Hilborn and Mangel 1997). For any parameter combination (of ν, p_i, $\boldsymbol{\theta}$, w), the log-likelihood of any parameter combination given a particular FAD (day of season at first sighting; denoted by x), without information on the number of seen birds is

$$\ell\left(\nu, p_i, \boldsymbol{\theta}, w \mid x\right) = \sum_{i=1}^{x-1} \ln \varphi_i + \ln\left(1 - \varphi_x\right), \quad (7)$$

Table 1. The four simulated scenarios used to study effects of population size and observation effort on FAD. In all scenarios I described phenology of migration intensity as skew normal functions (parameters μ, σ and α), and assumed that the number of observed birds are Poisson or negatively binomially distributed (overdispersion parameter w).

Scenario	Phenology	Error distr.	μ	σ	α	w
i	Gaussian	Poisson	50	10	0	–
ii	Gaussian	NegBin	50	10	0	0.8
iii	Right skewed	NegBin	30	20	4	0.8
iv	Left skewed	NegBin	70	20	–4	0.8

where φ_i and φ_x are the probabilities of observing zero birds on days i and x, respectively. Information about the number of observed birds on the first day of arrival should be used, whenever available. In such a case, FAD correspond to truncated count data without censored values, and can be included as data in the model fitting procedure without modifying the likelihood separately.

Example: using FAD of tree pipits

As an example of combining FAD and daily migration count data in the same model, I analysed data on the tree pipit (*Anthus trivialis*). The species is a common breeding bird in Finland, with a rather distinct unimodal pattern of migration. Furthermore, it is a long-distance migrant wintering in Africa and south Asia. Consequently, there is not likely to be outliers in the data due to wintering in areas close to the study site.

I used daily data on actively migrating birds, counted during the four first hours of daylight at the Hanko bird observatory (59°49´N, 22°54´E) during the years 2006–2009. I defined the spring migration season to start on 1 April and end on 31 May (i = 1 to 61). From the same period, I also used FAD data collected by three different local ornithological societies: Hakki, Apus and Tringa. These societies collect observations from separate areas located close to the south coast of Finland, within approximately 200 km from the Hanko bird observatory. For each society, I also used the numbers of birds observed on the first day of arrival (Table 2). To illustrate the information content of FAD, I fitted the model with and without including FAD.

Under the assumption that a Gaussian function describes the phenology ($\alpha = 0$ in Eq. 3), I used a generalized linear model (GLM) with a logarithmic link function and Poisson error distribution (with quasi-Poisson type correction for overdispersion). This approach is possible, because the Gaussian function can be written as a second order polynomial on the log-scale

$$\ln \lambda_i = ai^2 + bi + c. \qquad (8)$$

In practice, I included the daily index i and

its square (i^2) as explanatory variables in the model, and main effects (different intercepts) of 'year' and 'data type' using dummy variables. Further, to allow between-year variation in the shape and timing of the migration distribution, I included an interaction between the dummy variables 'year' and i, as well as 'year' and i^2. Except from the height (parameter c), I hence assumed that the distribution timing and shape is the same for all data sets for a particular year. O'Hara (2009) provides a good introduction of how main effects and covariates can be included in this type of models, as fixed or random effects, e.g. using dummy variables.

The estimated parameters a, b and c for each year (c also separate for all data sets) were transformed to more meaningful Gaussian function parameters (*see* Eq. 1 and 3) as

$$\mu = \frac{-b}{2a} , \qquad (9)$$

$$\sigma = \frac{-1}{2a} , \qquad (10)$$

$$\nu = \sqrt{\frac{-\pi}{a}}\, a \exp\left(\frac{-b^2}{4a} + c\right). \qquad (11)$$

I approximated the standard errors of the Gaussian function parameters by: (i) drawing 10 000 pseudorandom multinormal vectors with mean and covariance given by the estimated parameters (a, b and c) and their estimated covariance matrix, respectively, (ii) applying Eq. 9–11 for each trial separately, and (iii) calculating standard deviations of the transformed values over all trials.

Table 2. First arrival dates (FAD) and associated numbers of observed tree pipits (in parenthesis), during the spring migration periods 2006–2009. I used FAD from three local ornithological societies (Hakki, Apus and Tring*a*) in Uusimaa (southern Finland).

| Orn. Society	2006	2007	2008	2009
Hakki	24 Apr (3)	24 Apr (1)	19 Apr (1)	11 Apr (1)
Apus	13 Apr (1)	24 Apr (1)	18 Apr (1)	16 Apr (2)
Tringa	17 Apr (1)	14 Apr (1)	15 Apr (1)	4 Apr (1)
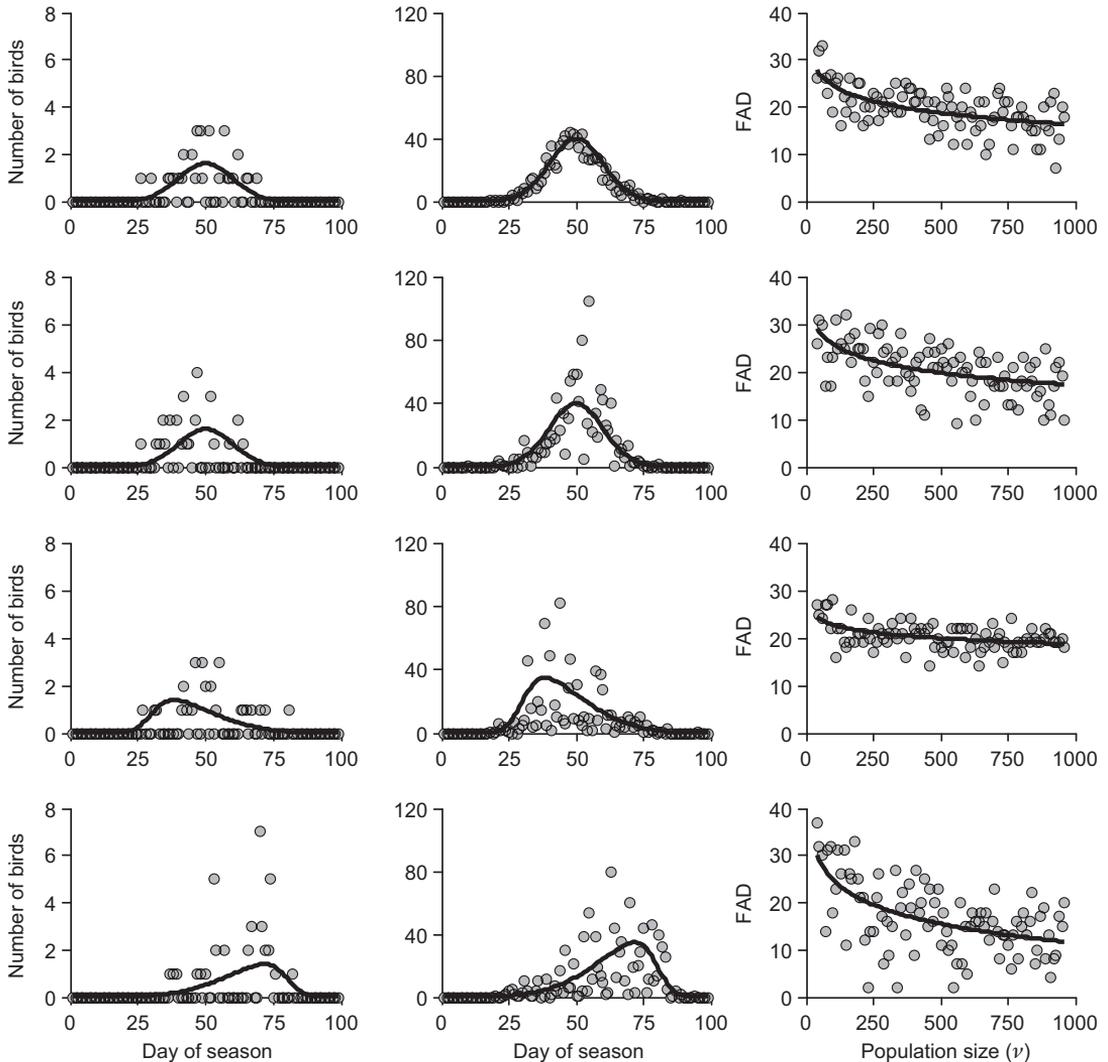
Fig. 1. Simulated scenarios of counted migration numbers with expected population size (parameter v) 40 individuals (left-hand-side column of figure panels), 960 individuals (middle column), and the fitted log-normal relationships between FAD and population size when the phenological distributions are kept constant (right-hand-side column). The rows of panels, from top downwards, represent scenarios with different parameter values (Table 1): (i) Gaussian distribution with the Poisson error, (ii) Gaussian distribution with the neg. bin. error, (iii) right-skewed function with the neg. bin. error, and (iv) left-skewed function with the neg. bin. error.

Results

Simulations approve clear effects of population size on FAD, when the underlying temporal distribution of migration is kept constant (Fig. 1). While population size increases, FAD are strongly advanced. However, this relationship decreases in steepness as the number of birds increases. Here the expected FAD conditional on population size [E(FAD | v) = y] is

described as linearly related to ln v. The slope of the fitted regression reports the change in days, when the population size grows with 272% (i.e. is multiplied with Euler's constant).

In the scenarios using a symmetric Gaussian function, the relationship between population size and FAD is very similar when the daily numbers are Poisson ($y = 41.1 - 3.59\ln v$) and negatively binomially distributed ($y = 42.9 - 3.72\ln v$), respectively (Fig. 1). The shape of
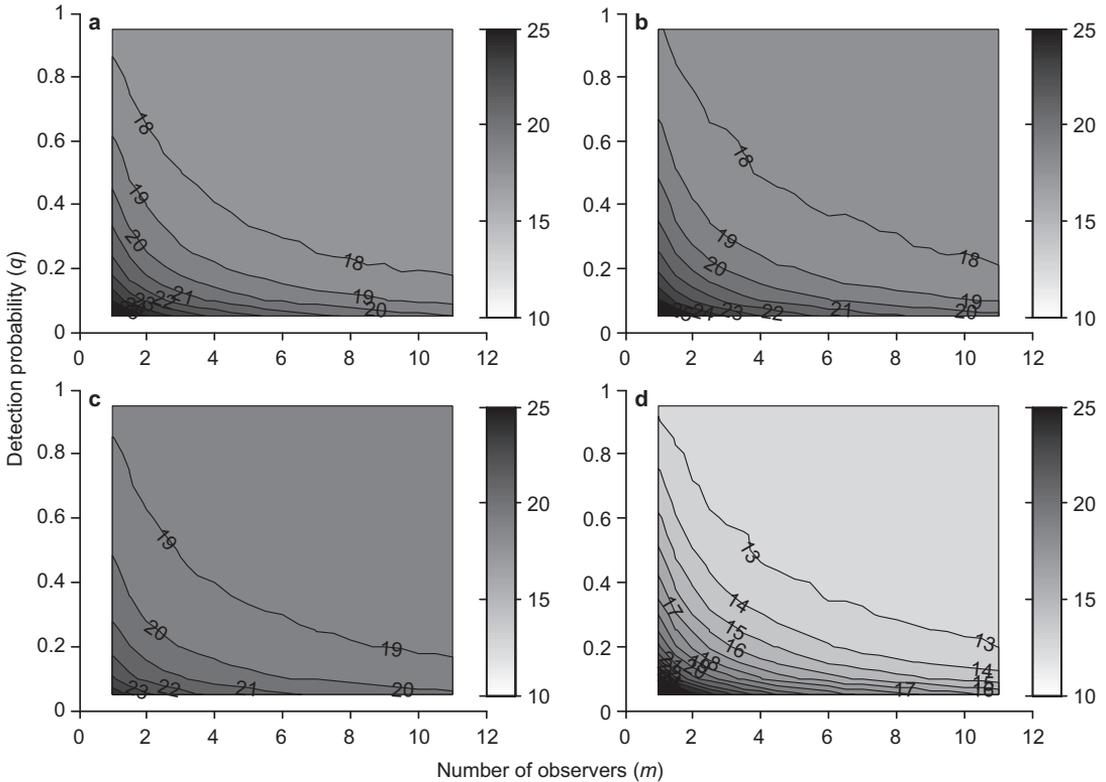
Fig. 2. Average FAD under the four investigated scenarios (a–d) with varying number of observers (*m*; *x*-axis) and detection probability (*q*; *y*-axis). Population size (*v*) is fixed to 1000. The average FAD is illustrated both as shades of grey and with contour lines.

the phenological function is clearly of greatest importance for determining how strong effects population size has on FAD. The scenario with a right-skewed function show very small effects of population size ($y = 30.8 - 1.75 \ln v$), while the scenario with a left skewed function show strong effects ($y = 51.8 - 5.84 \ln v$). Intuitively enough, FAD are more robust against all sources of bias with a steep start of migration (Fig. 1). Not only right skewness, but also a short and intensive migration period (small σ) will increase the steepness of migration start.

The average effects of counting effort and observability are similar to those of population size (Fig. 2). Bias in FAD is strongest with low observation effort and observability. Actually, what seems to matter the most in terms of bias, is the numbers of observed birds, regardless of the reason: true population size or the observation process. The shape of phenological distributions is also in this analysis a very strong determinant of the amount of bias.

The Gaussian functions fitted with GLM methodology fit the data reasonably well, despite the huge day-to-day variation that is typically present in this kind of data (Fig. 3). The fitted curves and parameter estimates are very similar with and without including FAD in the analyses (Fig. 3 and Table 3). However, the standard errors of the parameter estimates are clearly smaller when FAD are included (Table 3), suggesting that the information of FAD is successfully used to decrease the uncertainty of estimates. Not only the point estimates, but also measures of uncertainty of estimates can and should be used whenever further analyses of phenological patterns are done.

Discussion

This study shows that population size, observation effort and observability affect FAD significantly. Especially with thick-tailed distributions
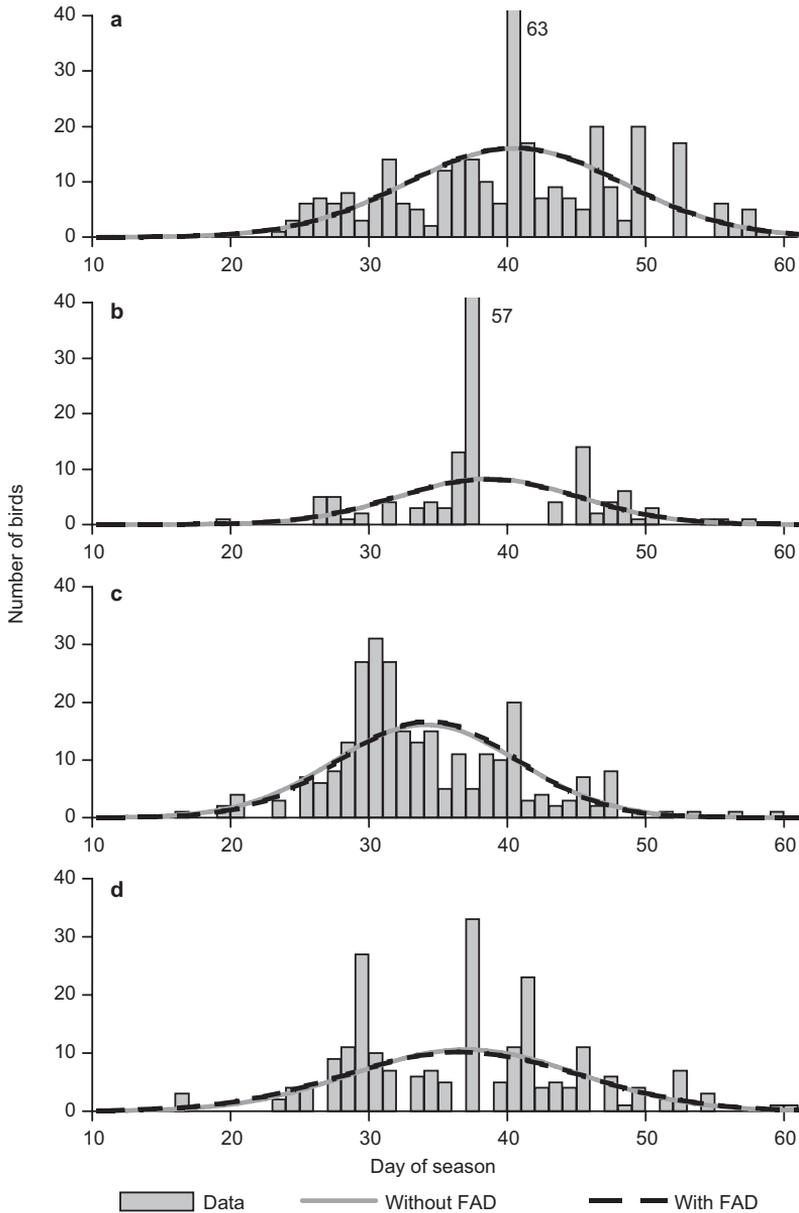
Fig. 3. Number of observed tree pipits at the Hanko Bird Observatory (grey bars), for the years (**a**) 2006, (**b**) 2007, (**c**) 2008 and (**d**) 2009. A Gaussian functions fitted without FAD and with FAD included as data are shown as grey solid and black dashed lines, respectively.

— in our case a left-skewed skew-normal function — the magnitude of bias in FAD is huge, when population sizes are small and/or observability or observation effort is poor. Studies typically relate annual variation in phenology to explanatory variables such as weather or climate (e.g. mean temperature, rainfall, the North Atlantic Oscillation), often accounting for temporal trends. All of these variables are potentially correlated with population size, observation effort or observation probability. Whenever ignored in the analyses, such effects might give spurious results and cause biases.

Using FAD as response variables

Typically, the focus of studies using FAD is on phenology as a population-level life-history trait that is modified by environmental conditions

though phenotypic plasticity. In such cases, the actual number of arrived birds is not of primary interest, but population size is a source of noise when investigating FAD. Sometimes, temporal variation in the actual number of birds throughout the season might be of explicit interest, e.g. when studying interspecific interactions, such as predation pressure by a migratory predator (Lehikoinen *et al*. 2011, interspecific competition, or the availability of host nests for brood parasites (Saino *et al*. 2009). In such cases, FAD can in fact be of greater interest, since they summarize information about both phenology and population size — something often neglected in studies addressing the relationship between FAD and population size. A good starting point in all phenological research is to distinguish between phenology as a life history trait (shape and timing of the distribution) and the absolute number of events early in the season, and to specify which is of interest.

In any setting, FAD are qualitative measures, providing information only about some arbitrary early phase of migration. It is, therefore, difficult to interpret the magnitude of phenological change based on FAD, for example in meta-analyses. When no daily count data are available, using long time series of FAD as a response variable might still be the best option available. Tryjanowski and Sparks (2001) proposed that FAD can prior to analysis be corrected for population size, by regressing FAD against some measure of population density and then use the residuals for further analyses. According to the results presented here, the negative relationship is non-linear, with a slope approaching zero with increasing population size, observation probability or observation effort. For example, including a log-transformed measure of population density and/or observation effort as a covariate in models of interest would be a better approximation for statistical correction of possible bias, compared to using residuals of linear regression.

Pros and cons of using FAD in distribution functions

Estimating expected phenology with parametric functions provides an approach to obtain explicit quantitative information about the distribution of phenological events, population size and the nature of day-to-day variability (error structure). It allows combining FAD data with daily migration counts, e.g. from bird observatories. Under proper assumptions and model restrictions, there are potential synergistic effects of the two data sources. FAD are likely to provide temporal and spatial coverage, while daily count data provides more information about distribution shape, population size, day-to-day variability and variation in those traits. Especially using Bayesian modelling, it is possible to make flexible assumptions and restrictions about the variation in the height, shape, and timing of phenological distributions (Jonzén *et al*. 2006, Schleip *et al*. 2006), and

Table 3. Parameter estimates ± SD for all years and parameters, with and without FAD included in the model. The main difference is that the standard errors are smaller when FAD are included in the model. The estimated Gaussian function parameters (μ, σ and ν) are calculated from the estimated second order polynomial coefficients (a, b, c in Eq. 8) according to Eq. 9–11.

	2006	2007	2008	2009
Without FAD				
Mean (μ)	40.1±1.09	38.1±3.03	33.6±0.98	36.5±1.41
SD (σ)	7.86±0.84	6.51±1.32	6.62±0.72	8.14±1.08
Population (ν)	316.0±42.2	135.0±30.1	268.0±39.0	216.2±35.9
Overdispersion	2.26	2.26	2.26	2.26
With FAD				
Mean (μ)	40.1±0.83	38.1±1.10	33.8±0.71	36.2±1.11
SD (σ)	7.83±0.59	6.65±0.75	6.34±0.47	8.59±0.79
Population (ν)	316.2±33.4	135.2±22.6	265.3±30.7	218.7±28.2
Overdispersion	1.84	1.84	1.84	1.84

thus the information contained by the FAD can be used even more efficiently. For example, the height of the functions could be modelled further with a population dynamical model, which in turn could be linked to complementary monitoring data.

While fitting distribution functions is an effective way to account for missing days of observation and truncated data, a problem is that days without observations are not always missing at random, but e.g. due to bad weather. Assuming that migration follows the same process during missing days can be misleading and cause overestimation of the number of birds and underestimation of the day-to-day variation. Replacing missing days with zeros could then be closer to the truth, although applying such a solution would have to be very well grounded. Inclusion of important weather effects, e.g. rainfall, wind speed and direction (*see* Sinelschikova *et al.* 2007, Kemp *et al.* 2010), could greatly improve the model performance. A natural way to include such covariates is to assume log-linear multiplicative effects, i.e. regular covariates if included in a GLM with a logarithmic link function.

Another problem with the proposed approach is that independence of data sets is not guaranteed. The daily variation in migration intensity not explained by the fitted curve is likely to be correlated between sites located nearby due to weather effects. This can lead to underestimated uncertainty of the estimates, which might be the case also in the example presented here. A false assumption of independence between data sets can still give unbiased point estimates (Abadi *et al.* 2010). Again, including environmental covariates in the phenological models is likely to reduce the problem. Further, Poisson mixed models (GLMM and GAMM) provide a solution. The extra Poisson day-to-day variation (overdispersion) and the dependence between data sets (different sites) can be treated as a nuisance variable, modelled as a multinormal random effect on the log-scale (O'Hara 2009).

Finally, the suitability and quality of FAD data should be considered before use. Firstly, if observation effort varies a lot in time and/ or show temporal trends, FAD data can be very misleading. If information about observation effort is available the model in Eq. 2 can be integrated in the analysis, but that requires a Bayesian-, or more advanced maximum likelihood approach (GLM-methodology would be difficult to apply). Secondly, the distributions of migrants at bird observatories (and the functions used here) describe migration passage. FAD might often be more closely related to the distribution of territory holding birds at the breeding grounds, which is a cumulative function related to the former. If FAD are mainly collected at migration or stopover sites, there should be no problems. The two kinds of distributions are also likely to be similarly shaped in the very beginning of the migration season, which reduces the problem.

Concluding remarks

Population size, as well as observation effort and observability all have negative relationships with observed FAD. The steepness of the relationship decreases with bigger population sizes, higher observation effort and observability. Usually these effects can be regarded as bias that makes any inference on phenology difficult based on FAD, but whenever the start of organism presence is of primary interest (e.g., food resources, predators, parasites) FAD can actually be useful summaries of population size and phenology. However, using FAD as a response variable in statistical analyses is never really desirable, because the answers obtained from such analyses are very qualitative in nature. However, if there are no other options, it is worth to correct for effects of population size, e.g. by including the logarithm of some measure of population density as a covariate in the model. FAD can be used as complementary data when estimating phenological distribution functions, but for successful results also more detailed daily data on migration or stopover counts is needed in the analyses. From the fitted functions, quantitative measures of phenology can be extracted for further analyses, along with suitable measures of estimation uncertainty.

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