

# Estimating unbiased phenological trends by adapting site-occupancy models

TOBIAS ROTH,<sup>1,2,3,4</sup> NICOLAS STREBEL,<sup>1,2</sup> AND VALENTIN AMRHEIN<sup>1,3</sup>

<sup>1</sup>University of Basel, Zoological Institute, 4051 Basel, Switzerland

<sup>2</sup>Hintermann and Weber AG, 4153 Reinach, Switzerland

<sup>3</sup>Research Station Petite Camargue Alsacienne, 68300 Saint-Louis, France

**Abstract.** As a response to climate warming, many animals and plants have been found to shift phenologies, such as appearance in spring or timing of reproduction. However, traditional measures for shifts in phenology that are based on observational data likely are biased due to a large influence of population size, observational effort, starting date of a survey, or other causes that may affect the probability of detecting a species. Understanding phenological responses of species to climate change, however, requires a robust measure that could be compared among studies and study years. Here, we developed a new method for estimating arrival and departure dates based on site-occupancy models. Using simulated data, we show that our method provided virtually unbiased estimates of phenological events even if detection probability or the number of sites occupied by the species is changing over time. To illustrate the flexibility of our method, we analyzed spring arrival of two long-distance migrant songbirds and the length of the flight period of two butterfly species, using data from a long-term biodiversity monitoring program in Switzerland. In contrast to many birds that migrate short distances, the two long-distance migrant songbirds tended to postpone average spring arrival by ~0.5 days per year between 1995 and 2012. Furthermore, the flight period of the short-distance-flying butterfly species apparently became even shorter over the study period, while the flight period of the longer-distance-flying butterfly species remained relatively stable. Our method could be applied to temporally and spatially extensive data from a wide range of monitoring programs and citizen science projects, to help unravel how species and communities respond to global warming.

**Key words:** *Aphantopus hyperantus*; *Bayesian analysis*; *breeding bird census*; *butterfly monitoring*; *long-term monitoring programs*; *Melanargia galathea*; *Muscicapa striata*; *phenological shifts*; *site-occupancy models*; *Sylvia borin*.

## INTRODUCTION

Shifts in phenology are conspicuous responses of animal and plant populations to climate warming (Parmesan 2006). During the last decades, studies reported seasonal advances in dates of plant flowering (Bai et al. 2011), appearance of insects (Diamond et al. 2011), reproduction of mammals (Moyes et al. 2011), spring arrival of migrating birds (Jonzen et al. 2006), or laying date of the first egg in birds (Crick et al. 1997). Furthermore, shifts in phenology were found to vary depending on the region studied (Primack et al. 2009, Hurlbert and Liang 2012), habitat (Altermatt 2012), or ecology of a species (Altermatt 2010). Taken together, these shifts are likely to have profound effects on population dynamics, for instance, through disruption of the annual cycle, in that a species gets out of synchrony with its environment (Crick 2004).

Traditionally, studies on phenological shifts are based on observations of first appearance per season, which is usually given by the date of the first observation (Mason 1995, Primack et al. 2009), the mean date of first observations among several sites (Roy and Sparks 2000), or the date when the first 25% of all observations during a study season have been made (Van Strien et al. 2008). However, observations of first appearance are probably not very suitable measures for investigating shifts in phenology of populations because they are likely to be strongly influenced by several factors. For example, if population size increases, early observations of individuals become more abundant, even if average arrival of individuals in the population remains constant (Tryjanowski and Sparks 2001, Van Strien et al. 2008). Likewise, first observation dates were found to be influenced by the starting date of the observation period (Van Strien et al. 2008), by changing sampling frequencies or other instances of varying observational effort (Miller-Rushing et al. 2008), or by variation in detection probability (Moussus et al. 2010). Nonetheless, useful inferences on long-term phenological change have been drawn also from traditional analyses using

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<sup>4</sup> E-mail: roth@hintermannweber.ch

first arrival dates (Altermatt 2012, Hurlbert and Liang 2012).

However, it seems likely that climate warming will not only affect phenology but also affect detection probability, population size, or study effort. For example, due to climate warming, average song post height of birds may increase (Møller 2011), and birds might thus be more easily detected during the surveys. Yet in phenological studies, the effect of changing detection probabilities has hardly been considered. Important exceptions are studies on stopover duration of migrating birds using capture–recapture techniques. For instance, Schaub et al. (2001) developed a method to estimate stopover duration by combining recruitment analysis with survival analysis, by deducing arrival and departure rates from estimating recruitment and survival rates. However, to our knowledge, this method has never been used to estimate phenological trends of arriving individuals at breeding grounds, possibly because marking individual animals over a larger spatial scale is time and labor intensive (Vögeli et al. 2008, Roth and Amrhein 2010).

Here, we developed a new method for estimating phenological trends based on the framework of site-occupancy models. Site-occupancy models are flexible and powerful tools for estimating the proportion of occupied sites while accounting for varying detection probabilities (MacKenzie et al. 2002, Tyre et al. 2003, MacKenzie et al. 2006). As site-occupancy models implicitly account for the number of times a site is visited (i.e., observational effort), these models could be useful to obtain unbiased estimates on phenological trends. So far, however, only few efforts have been made to apply site-occupancy models to studies of phenological trends (but see Kendall et al. 2013), probably because site-occupancy models assume that populations are closed within a study period, meaning that no species arrive or disappear between sampling events (Kéry et al. 2009). Clearly, this assumption of population closure is violated in phenological studies where the species arrives at and departs from the study plot, thus apparently impeding the application of site-occupancy models to ecological studies of phenological trends.

Recently, however, a statistical model was presented that relaxes the closure assumption of site-occupancy models by permitting staggered entry and exit times for the species of interest at each site (Kendall et al. 2013). The authors essentially added two new parameters to traditional site-occupancy models. The first is the probability that the species enters the study area between sampling occasions, and the second is the probability that the species will depart from the site before the next sampling occasion. Based on simulations, Kendall et al. (2013) show that their open site-occupancy model provides more robust estimates of occupancy than do closed site-occupancy models. Although this work was based on simulated and real data from only a single study season, we agree with

Kendall et al. (2013) that the approach is attractive and could be useful for studies comparing phenology of species arrival and departure across multiple seasons, e.g., for investigating effects of climate change.

However, we think that one possible shortcoming of the approach by Kendall et al. (2013) for use in phenological studies is that the interpretation of their arrival and departure parameters is difficult, because arrival and departure is estimated as the probability that the species enters or departs from the study area between two sampling occasions. Using the approach by Kendall et al. (2013), the expected arrival and departure dates could possibly be derived as a function of the arrival and departure probabilities; however, we find it desirable to obtain direct estimates of arrival and departure dates. In our model, we thus used a different approach by directly modeling arrival and departure dates of species at the study plots. As a consequence, our approach needs an explicit statement about the distribution of arrival dates of the species at the different study plots, which is a further difference to the Kendall et al. (2013) approach that does not require a particular distributional form of the arrival and departure of species. In our model, we describe the arrival of species on the study plots using an overdispersed Poisson distribution with the average population arrival as its mean. Note, however, that other distributions of the arrival of species on the study plots could also be implemented, such as normal or  $t$  distributions.

We start by developing a model that estimates average arrival and departure dates from data of a single breeding season. Similar to traditional site-occupancy models, this model assumes population closure once a species has arrived and has not yet departed from a site. Using simulated data, we show that this model is able to estimate the average appearance and departure date of a species in a given year, and that the estimate is virtually not affected by variation in detection probability, number of occupied sites, or starting date of the observation period. In a second step, we extend the model for estimating shifts in arrival dates over years. For simplicity and also because departure dates will usually be missing, e.g., in breeding bird surveys, this model only includes the arrival process. We illustrate the performance of this arrival model under three different scenarios using simulated data. Finally, we applied our method to real data from a long-term biodiversity monitoring program in Switzerland. We used the arrival model to compare the trends of spring arrival dates in different habitats of two long-distance migrating bird species, the Garden Warbler (*Sylvia borin*) and the Spotted Flycatcher (*Muscicapa striata*). We estimated habitat-specific average arrival dates and site occupancies, and tested for trends in arrival dates, site occupancies, and detection probabilities over years. Further, we used the full model for estimating both arrival and departure dates, to infer changes in habitat-specific lengths of flight period for butterflies over time.

We applied this model to data on two common butterfly species from the same monitoring program as in the bird study, the marbled white (*Melanargia galathea*; see Plate 1) and the ringlet (*Aphantopus hyperantus*). We estimated habitat-specific arrival dates, departure dates, and site occupancies, and tested for trends in arrival dates, departure dates, site occupancies, and detection probabilities over years.

## MATERIAL AND METHODS

### Model description

Suppose that at the beginning of a breeding season, a number of  $i = 1, \dots, N$  study plots are sampled during  $j = 1, \dots, J$  visits for the presence of a species. Such a sampling situation is similar to the sampling situation of single-season site-occupancy models (MacKenzie et al. 2002, Guillera-Aroita et al. 2010). In our sampling situation, however, the study period should cover a major part of the arrival and/or departure period of the species studied, while in a traditional site-occupancy model, the study period usually covers the time after arrival and before departure of the species, to meet the assumption of population closure (Kendall et al. 1997). Let us define the true occupancy state  $x[i]$  of study plot  $i$  such that  $x[i] = 0$  if plot  $i$  is never occupied during the entire season, and  $x[i] = 1$  otherwise. We assume that the true occupancy state  $x[i]$  is a Bernoulli random variable with site occupancy  $\psi_i$  as its parameter

$$x[i] \sim \text{Bernoulli}(\psi_i).$$

The study plots are assumed to become occupied at different dates within the season. We assume that the species occupies most of the study plots close to an average date of arrival, while some plots are occupied a few days earlier or later. Thus, it seems convenient to describe the arrival process with an average arrival date  $\phi$  and a standard deviation  $\sigma$ . Since arrivals are discrete events, we described the arrival times of the species at the study plots according to an overdispersed Poisson distribution (Kéry 2010). If  $a[i]$  is defined as the arrival date of the species at study plot  $i$  then

$$a[i] \sim \text{Poisson}(\mu_i) \text{ with } \mu_i \sim \text{Normal}(\phi, \sigma).$$

In sampling situations with study periods covering parts of the departure period of the studied species, the model could optionally also account for the departure process of the species from the study plots. We assume that the species departs from the study plots at different dates within the season. Like the arrival process, we describe the departure process with an overdispersed Poisson distribution with average departure date  $\lambda$  and a standard deviation  $\xi$ . If  $d[i]$  is defined as the departure date of the species from study plot  $i$  then

$$d[i] \sim \text{Poisson}(\omega_i) \text{ with } \omega_i \sim \text{Normal}(\lambda, \xi).$$

In a traditional site-occupancy model, it is assumed that a study plot that was observed to be occupied at any visit was also occupied during all other  $j = 1, \dots, J$  visits (i.e., the closure assumption); further, it is assumed that some of the occupied plots might falsely be recorded as not being occupied due to imperfect detection (MacKenzie et al. 2002). Thus, in a traditional site-occupancy model, the observed occupancy state  $y[i, j]$  of study plot  $i$  at visit  $j$  would be Bernoulli distributed with probability  $x[i] \times p_{i,j}$ , where  $p_{i,j}$  is the probability that the species present at a study plot is observed. In our phenological site-occupancy model, we relaxed the closure assumption by allowing species to arrive at and depart from the study plots between the visits by the observer. Similarly to traditional site-occupancy models, we assume population closure after a study plot has been occupied by a species but before the species has departed again from the study plot. Note that in areas where a species both breeds and occurs on passage during migration, there will be cases where sites are temporarily occupied by transients. Similar to capture–recapture and traditional site-occupancy models, transients may be problematic because they bias capture probability or detection probability to a lower level (Pradel et al. 1997). We here assume that transients do not occur in our data; further work is needed to explicitly incorporate transients into arrival models, for instance using a strategy similar to that used for capture–recapture data (Saracco et al. 2010).

Denote the variable DATE[ $i, j$ ] as the date when plot  $i$  was visited for the  $j$ th time. Then in our phenological site-occupancy model, the observed occupancy state  $y[i, j]$  (i.e., the data) is given as

$$y[i, j] \sim \text{Bernoulli}(x[i] \times p_{i,j} \times I[i, j])$$

with

$$I[i, j] = \begin{cases} 1 & \text{when } a[i] \leq \text{DATE}[i, j] \text{ and } d[i] > \text{DATE}[i, j] \\ 0 & \text{when } a[i] > \text{DATE}[i, j] \text{ or } d[i] \leq \text{DATE}[i, j] \end{cases}.$$

Thus, during a visit  $j$ , study plot  $i$  is observed to be occupied (i.e.,  $y[i, j] = 1$ ) only if it is ever occupied during the field season (i.e.,  $x[i] = 1$ ), if the species has already arrived to plot  $i$  at the time of visit  $j$  (i.e.,  $a[i] \leq \text{DATE}[i, j]$ ), if the species has not yet departed from plot  $i$  at the time of visit  $j$  (i.e.,  $d[i] > \text{DATE}[i, j]$ ), and if the species is also observed. In all other cases, i.e., when a plot is not occupied (i.e.,  $x[i] = 0$ ), when the species has not arrived at the time of the visit  $j$  (i.e.,  $a[i] > \text{DATE}[i, j]$ ), when the species has departed from the plot at the time of the visit  $j$  (i.e.,  $d[i] \leq \text{DATE}[i, j]$ ), or when the species is not observed due to imperfect detection,

study plot  $i$  is not observed to be occupied (i.e.,  $y[i,j] = 0$ ).

### *Simulation studies*

In a first simulation study, we tested the performance of our single-season phenological model using simulated data. Appendix A contains the description of how the data were simulated and how estimates were obtained based on Markov-chain Monte Carlo methods and gives the results of the simulation studies: such a single-season phenological model was able to accurately estimate average appearance date  $\phi$  and average departure date  $\lambda$  of a species in a given year when detection probability ( $p_i$ ) and site occupancy ( $\psi_i$ ) was varying among study plots. Further, we used a single-season phenological model that only accounted for the arrival process and compared the performance of our model with three traditional estimators for spring arrival, namely the first observation date, the mean of the first observations from all study plots (Roy and Sparks 2000), and the day when 25% of all observations during a study have been made (Van Strien et al. 2008). We found that estimates based on our model were virtually not affected by variation in detection probability, site occupancy, or starting date of the observation period (see Appendix A).

For a second simulation study, we extended our single-season phenological model to cover multiple years by modeling the parameters with an additional index for the  $t = 1, \dots, T$  years of the study. For simplicity and also because departure dates will usually be missing, e.g., in breeding-bird surveys (Kéry and Schmid 2006), we included the arrival process only. Each of the three main parameters, i.e., site occupancy ( $\psi_t$ ), detection probability ( $p_t$ ), and mean arrival of the species ( $\phi_t$ ), were described as linear models with intercepts (i.e.,  $a_0$ ,  $b_0$ , and  $c_0$  for the linear model of  $\psi_t$ ,  $p_t$ , and  $\phi_t$ , respectively) and slope parameters for the temporal trends (i.e.,  $a_1$ ,  $b_1$ , and  $c_1$ ). The linear regression models for site occupancy ( $\psi_t$ ) and detection probability ( $p_t$ ) were described on the logit scale.

We simulated data for three different scenarios (see the following paragraphs). For each scenario we simulated 100 data sets with  $N = 100$  study plots,  $T = 10$  years of study duration, and  $J = 6$  yearly visits to the study plots. The study period was set to 50 days, and the six visits to the study plots were performed at day 1, 10, 20, 30, 40, and 50, respectively. For all simulations we set site-occupancy at year 5 to  $\psi_5 = 0.8$ , detection probability at year 5 to  $p_5 = 0.5$ , and average arrival at year 5 to  $\phi_5 = 30$ . The temporal trend of these three parameters depended on the simulation scenarios (see the following paragraphs). Furthermore, in all simulated scenarios the mean arrival advanced over the years with a temporal trend of  $c_1 = -0.5$  days per year, which corresponds to an average arrival of day 32 during the first year and of day 27.5 during the last year. The simulated data were analyzed using a Bayesian analysis based on Markov-chain Monte Carlo (MCMC) meth-

ods (Link et al. 2002). MCMC simulations were conducted using OpenBUGS 3.2.1 (Thomas et al. 2006), executed in R using the R add-on library R2OpenBUGS (Sturtz et al. 2005). For the Bayesian analyses of the simulated data, we used noninformative prior distributions for the intercepts and temporal slopes of the three parameters site occupancy ( $\psi_t$ ), detection probability ( $p_t$ ), and mean arrival of the species ( $\phi_t$ ), which all were Normal with mean = 0 and SD = 100. To summarize the performance of the multi-season arrival model to estimate temporal trends in average arrival, we summarized the 100 simulations by giving the number of times the true trend was contained in the 95% credible interval (i.e., the coverage), the number of times the 95% credible interval did not contain "0" (i.e., the power), and the difference between the true trend and the estimated temporal trend (i.e., the bias).

In the first simulation scenario, we aimed to test whether our method is able to retrieve earlier arrival accurately even though decreasing detection probability is resulting in a later first observation date over the years. We thus simulated detection probability  $p_t$  to decrease over the years with a linear trend of  $b_1 = -0.1$ , which corresponds to a detection probability of 0.62 during the first year and a detection probability of 0.40 during the last year. In the second scenario, we aimed to test whether our method is able to retrieve earlier arrival even though site occupancy is decreasing over the years, and thus, first observations are becoming later over the years. We simulated site occupancy  $\psi_t$  to decrease over the years with a linear trend of  $a_1 = -0.1$ , which corresponds to a site-occupancy of 0.86 during the first year and a site occupancy of 0.71 during the last year. In the third scenario, we aimed to test whether our method is able to retrieve accurate arrival estimates if the numbers and dates of the visits differ among study plots and years. Therefore, for each plot and each year we simulated different numbers and dates of visits. For each plot, a random number of between 2 and 10 visits were conducted, and the date of each survey was randomly chosen.

### *Case studies: bird and butterfly monitoring program*

To illustrate the flexibility of our method, we applied it to bird and butterfly monitoring data from a long-term biodiversity monitoring program in the canton of Aargau in northern Switzerland (Roth et al. 2008, Altermatt 2012). Aargau has a total area of 1404 km<sup>2</sup>, of which 46% is in agricultural use, 37% is forest, and 15% is urban area, and it covers an altitudinal range from 260 m to 908 m above sea level. In the monitoring scheme, breeding birds and butterflies are two of five species groups investigated on a systematic grid with random origin, covering ~520 study plots. We analyzed data collected between 1995 and 2012 for birds and between 1998 and 2010 for butterflies. The field methods for the birds and butterfly surveys are given in Appendices B and C, respectively.



Using our method, we aimed to analyze arrival times for the long-distance migrants Garden Warbler (*Sylvia borin*) and Spotted Flycatcher (*Muscicapa striata*). These species arrived sufficiently late to the breeding area so that the monitoring scheme covered most of their arrival events. We estimated independent intercepts and temporal trends across years for the four main habitat categories, i.e., residential areas, forests, agriculture, and mixed land-use plots. Furthermore, we added a random plot effect for site occupancy to account for the independence of data, since all plots were surveyed every five years. Further, since each examined plot was visited once during each of five consecutive two-week periods, we estimated separate intercepts and temporal trends across years for detection probabilities for each of the five visits that were formulated as random intercepts and random slopes. For the average arrival of the species, we also estimated different intercepts and temporal trends across years for the four main habitat categories, which were formulated as random intercepts and random slopes.

While the bird surveys were conducted in spring covering the arrival period and the start of the breeding season, but not the period of departure, the butterfly surveys were conducted from April to September and covered entire flight periods of most butterfly species. For butterflies, it therefore seemed not sensible to assume closed populations once a species had arrived at the study plots, and thus, both arrival and departure needed to be accounted for in the model. Note that in the case of butterflies, arrival and departure refer to the beginning and the end of the flying period of imagines on the study plots.

For butterflies, we used a similar model as for the analysis of bird data, which included habitat-specific intercepts and temporal trends for site occupancy, and average arrival date and visit-specific detection probabilities. Additionally, however, we also included the departure from the study plots as a further process in the model. Applying this extended model to data on two common summer-flying butterfly species, the marbled white (*Melanargia galathea*) and the ringlet (*Aphantopus hyperantus*), we aimed to estimate habitat-specific flight period lengths that are not sensitive to population size and sampling effort and thus could be used in phenological studies that usually should be interpreted accounting for habitat types (Altermatt 2012).

A more detailed description of the models in BUGS language and of the Bayesian analyses is given in Appendix B for the bird study and in Appendix C for the butterfly study. We used the means of the simulated values of the posterior distributions as point estimates of the parameters and the 2.5% and 97.5% quantiles as estimates of the credible intervals. We speak of a “clear” effect (which, in a frequentist terminology, may be similar to a significant effect) if zero was not included in the 95% Bayesian credible interval of an estimate, or of a “clear” difference, e.g., between two land-use categories

if the point estimate for the first land-use category was not within the credible interval of the estimate for the second land-use category (Amrhein et al. 2012).

## RESULTS

### Simulation studies

According to the simulation study, our arrival model succeeded well in uncovering temporal trends of appearance dates of a species under three different scenarios. In the first scenario, we aimed to test whether our method was able to detect earlier arrival if decreasing detection probability is resulting in a later first observation date over the years; in the second scenario, we aimed to test whether our method is able to detect earlier arrival if site occupancy is decreasing over the years; and in the third scenario, we aimed to test the effect of varying numbers and dates of survey visits on the ability of our method to detect earlier arrival. Estimation bias, expressed as the difference between estimated and true temporal trends for each of the 100 simulated data sets, was 0.003, 0.022, and 0.007 for scenario 1, 2, and 3, respectively, corresponding to a bias of <5% of the true value in all scenarios. Further, credible interval coverage, which is the number of times the true value is contained in the 95% credible interval, was close to the nominal level of 95% (0.93, 0.97, and 0.89 for scenario 1, 2, and 3, respectively), suggesting that model assumptions were met and that our model provided estimates of temporal trends in arrival with reasonable precision. Also, the power to detect the temporal trend was reasonable in all scenarios (0.92, 0.92, and 0.90 for scenario 1, 2, and 3, respectively). The results of the three simulation scenarios are given in more detail in Appendix D. Taken together, the simulation results on three scenarios suggested that our multi-season arrival model was able to accurately estimate temporal trends of appearance dates of a species. For the simulation results on the single-season arrival model, see Appendix A.

### Case studies

In the canton of Aargau, the average spring arrival of the long-distance migrating Garden Warblers (30 April) was about three days earlier than that of Spotted Flycatchers (3 May; Fig. 1a). Although there was considerable variation in site occupancies among habitats (Appendix B: Fig. B2) and in detection probability among visits (Appendix B: Fig. B3), in both bird species, average arrival was not found to differ among land-use categories (Fig. 1a). While there were no clear differences among land-use categories in how the two bird species changed their average arrival over the period of 18 years, over all habitats Spotted Flycatchers tended to postpone average spring arrival by 0.9 days per year (CI, −1.6 to 3.6 days per year) and Garden Warblers by 0.5 days per year (CI, −0.1 to 1.3 days per year) (Fig. 1b).

For the two butterfly species we also found considerable variation in site occupancies among habitats

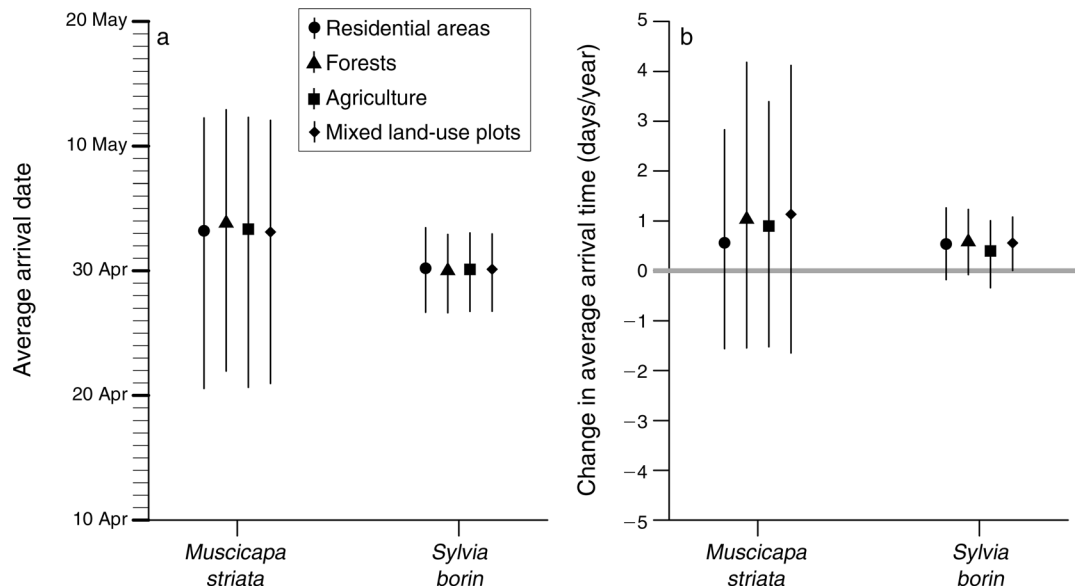


FIG. 1. Average arrival dates of the long-distance migrating songbirds Spotted Flycatcher (*Muscicapa striata*) and Garden Warbler (*Sylvia borin*), estimated from bird surveys of a long-term monitoring program of the canton Aargau in Switzerland. Data shown are means and 95% credible intervals of the posterior distributions of (a) average arrival for 2005, and (b) of temporal trends (1995–2012) in average arrival as estimated from our model.

(Appendix C: Fig. C2) and in detection probabilities among visits (Appendix C: Fig. C3), but little evidence for habitat-specific measures of phenology (Fig. 2a–d). However, we found a clear difference in average flight period lengths between the two species (Fig. 2a). Further, over the study period of 13 years, the flight period length of ringlets that already had a much shorter flight period than marbled whites likely decreased (probability of decreased flight period = 0.90; average change of flight period length per year =  $-0.5$  days), while the flight period of marbled whites apparently remained stable or even further increased (probability of decreased flight period = 0.22; average change of flight period length per year =  $0.45$  days; Fig. 2d). The likely decrease in flight period length of the ringlet was due both to a later arrival and an earlier departure of the species at the study plots (Fig. 2b, c).

#### DISCUSSION

By extending classic site-occupancy models (MacKenzie et al. 2002), we developed and illustrated a new model for estimating phenological measures like spring appearance of a population of animals. Simulations for three different scenarios showed that our model provided accurate estimates of temporal trends of mean spring arrival date at the breeding grounds that were virtually not influenced by variation in site occupancies or detection probabilities. Because our model is based on site-occupancy models, it is able to account for imperfect detection and for changes in occupancy probability, which is a major source of bias if spring appearance data are analyzed using traditional methods (Tryjanowski and Sparks 2001, Miller-Rushing et al.

2008, Van Strien et al. 2008). Further, our method is flexible and can be adapted for studying different aspects of phenology. For instance, by accounting for both arrival and departure in the models, we were able to estimate the length of the flight period of butterflies independently of site occupancies and detection probabilities; thus, our estimate of flight period lengths is easier to interpret than traditional estimates (Altermatt 2012).

Our method complements current research to modify the closed site-occupancy models by MacKenzie et al. (2006) to relax the population closure assumption for situations where the species is not always available for detection during the observation period (Rota et al. 2009, Hines et al. 2010, Kendall et al. 2013). We argue that such new site-occupancy models are promising tools to untangle effects of climate change on phenology, on species occurrence, on local rates of extinction, and on colonization across space (Kendall et al. 2013). For example, we could test whether the rate with which species adjust their phenology is related to the rate of change in site occupancy at the latitudinal or altitudinal edges of the species range (Hurlbert and Liang 2012). However, further work is needed to test the limitations of our methods, for instance, by exploring different distributions of arrival dates, which may vary among study plots.

The main question of current phenological studies is usually whether a measure of phenology has changed over time and whether this was related to climate change. Our method estimates arrival dates at multiple sites and thus estimates the expected arrival of a species in a larger study area. This seems to be an intuitive

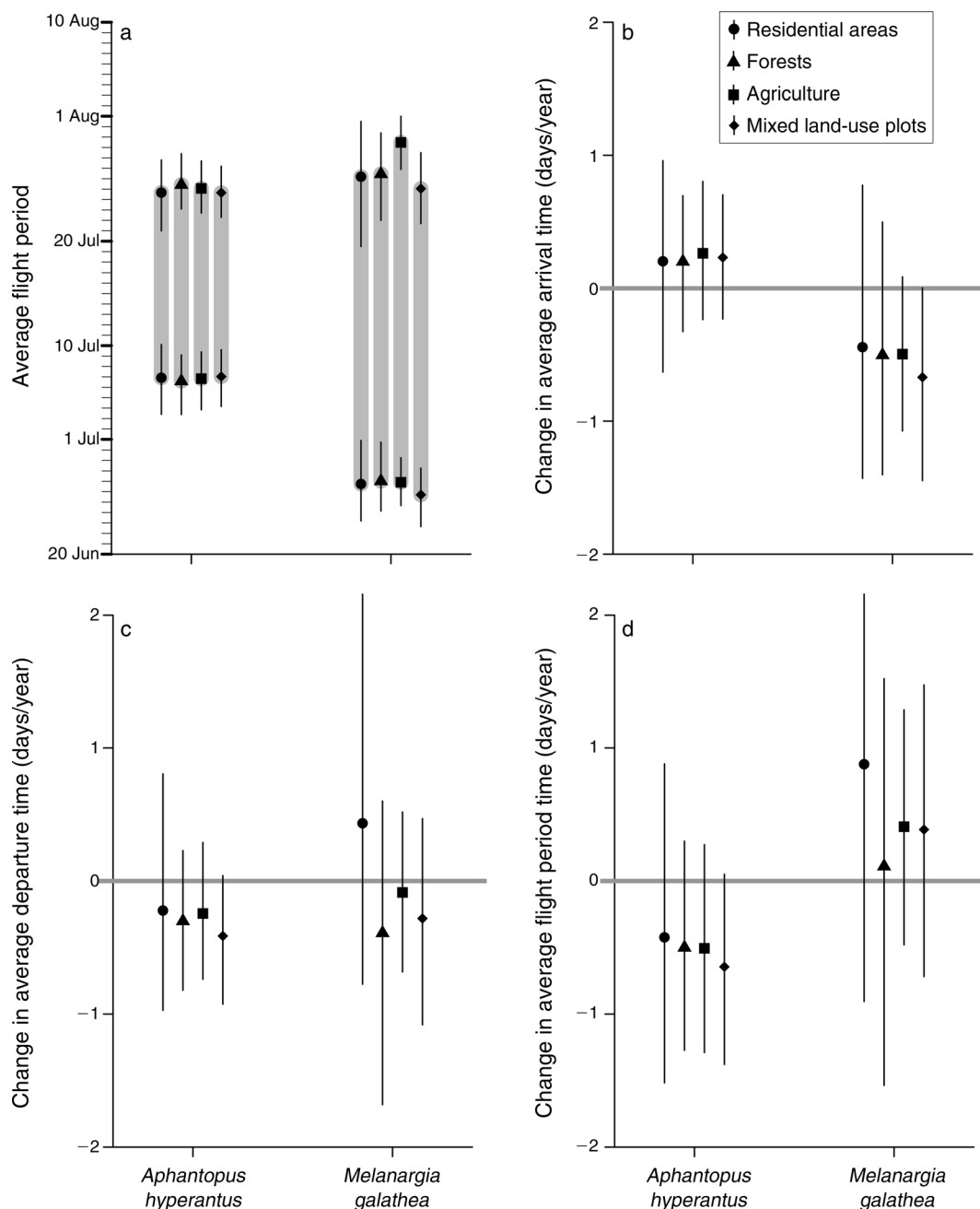


FIG. 2. Flight period of the summer-flying butterflies ringlet (*Aphantopus hyperantus*) and marbled white (*Melanargia galathea*), estimated from butterfly surveys of a long-term monitoring program of the canton Aargau in Switzerland. Data shown in (a) are estimates for the flight period length for 2005 (gray lines), with average arrival (lower symbols) and average departure (upper symbols). Further, estimates from our model are given for the temporal trends (1998–2010) in (b) average arrival and (c) departure, and for (d) the temporal trends of the flight period length. Data represent means and 95% credible intervals of the posterior distributions.

measure of arrival and could easily be compared among studies. A traditional measure that is frequently applied for phenological studies is the average date of the first observations from several sites (Roy and Sparks 2000, Sparks et al. 2005). Apparently, interpretation of this observational measure of arrival is similar to the arrival

as estimated from our model. However, the average date of first observation of a species will usually be later than the true average arrival date of that species; this is because a species that has arrived will not always be detected, e.g., because the sites may not be visited every day (Van Strien et al. 2008). In our simulation study,



PLATE 1. Some individuals of marbled white (*Melanargia galathea*) look quite worn as it is a species with a relatively long flight period. Photo credit: T. Roth.

this led to mean first observations from all study plots that were generally later than the estimated mean dates of population arrivals from our model (Appendix A: Fig. A4).

Although shifts in phenology in response to climate change are well established, the different extents or directions of phenological shifts found in different studies are poorly understood (Knudsen et al. 2011, Hurlbert and Liang 2012). For instance, how species adapt their phenology to climate warming may vary among studies because climate change may differ among study regions or because the studied species differ in ecology (Walther et al. 2002, Marra et al. 2005, Rubolini et al. 2005, Altermatt 2010). However, methodological differences and biased estimates of phenological shifts could also be a main reason for differing results among studies. Although it was acknowledged that traditional methods for estimating phenological shifts are likely biased (Tryjanowski and Sparks 2001, Miller-Rushing et al. 2008, Van Strien et al. 2008), little priority has been given to developing procedures to obtain unbiased estimates of phenological changes (Van Strien et al. 2008). One of the few exceptions is Moussus et al. (2009), who proposed a method that is based on daily count data. In this method, daily count data from one year are set as reference data, and count data from a second year are then laid over the reference data and

shifted by date until the overlap between the two data sets is maximized; the required shift then represents the phenological shift between the two years. While this technique is a promising method to analyze large data sets, it seems difficult to obtain reliable results if data are relatively sparse. Furthermore, it is not possible to assess how observational effort, site occupancy, detection probability, or shifts in arrival or departure times contribute to the temporal changes in count patterns, and therefore phenological shifts could still be masked, over- or underestimated. In contrast, our method allows us to estimate site occupancy, detection probability, and average arrival of animals independently, and thus allows us to quantify how those variables contribute to the observed temporal changes of phenology in animal populations. Thus, when using our method, results on phenological shifts probably can be compared more reliably among studies.

Although studies that did not account for differences in population sizes between habitats reported habitat-specific phenologies of birds and butterflies (Altermatt 2012, Tryjanowski et al. 2013), for the two birds and the two butterfly species in our study, we found little evidence that their phenologies differed among habitats (residential areas, forests, agriculture, and mixed land use). We found a clear effect of land use on site occupancies, but average arrivals of the two birds and



the two butterfly species were not found to vary with land-use type. This was unexpected, as site occupancies and arrival dates are assumed to be correlated because high site occupancies and early arrival dates are both thought to indicate high habitat suitability (Johnson 2007, Altermatt 2012). Thus, our results add to the evidence that ecologists should be cautious when relying on indirect measures of habitat quality such as site occupancy and arrival dates (Arlt and Pärt 2007, Johnson 2007, Doligez et al. 2008).

We found that detection probability of Spotted Flycatchers tended to increase over the years in the beginning of the season and to decrease over the years later in the season. As singing or calling activity is likely a main predictor of detection probability, this pattern may suggest that Spotted Flycatchers called more over the years early in the season but called less later in the season. We also found that between 1995 and 2012, Spotted Flycatchers and Garden Warblers tended to postpone average spring arrival by about 0.5 days per year. Both species are long-distance migrants wintering in sub-Saharan Africa and are among the last species arriving on the breeding grounds in spring (Maumary et al. 2007). While several studies reported shifts towards an earlier spring arrival date in short-distance migrants, the results of studies investigating phenological responses of long-distance migrants to climate change are usually less clear (Butler 2003, Mills 2005, Hurlbert and Liang 2012). In line with our results, other studies reported shifts towards a later first observation date in the Garden Warbler (Mason 1995, Rubolini et al. 2010). Such a delay in spring arrival could have multiple reasons, for example that suitable wintering grounds are increasingly farther away from breeding grounds because of climate change (Barbet-Massin et al. 2009), or because unfavorable conditions in sub-Saharan foraging areas or in resting areas visited during migration may cause a significant prolongation of stopover time during northward migration (Hüppop and Hüppop 2003, Balbontin et al. 2009, Tottrup et al. 2012). Finally, we found that the flight period of the ringlet, a butterfly species with short flight period, became even shorter over the study period, while the length of the flight period of the longer-flying marbled white remained relatively stable. Indeed, the average flight period length of a butterfly species might be a promising criterion to assess its vulnerability to climate change (Heikkinen et al. 2010), with shorter-flying species tending to be more threatened than longer-flying species.

So far, there is often no mechanistic understanding of how climate warming translates to phenological changes in populations. Therefore, predicting how species or communities will react to climate warming remains challenging (Knudsen et al. 2011). Potentially, studies on phenological responses of populations to climate warming could make use of online tools where amateur naturalists can submit their observations for scientific research (Baillie et al. 2006, Sullivan et al. 2009,

Dickinson et al. 2010, Hurlbert and Liang 2012), or of the numerous long-term monitoring programs implemented all over the world (Lepetz et al. 2009, Couvet et al. 2011). Applying our method to data from online databases would allow accounting for varying observation effort within and among years as well as for varying starting times of observation periods, which are typical for such data sources (Devictor et al. 2010). For long-term monitoring programs that are usually more standardized, our method could also yield estimates of average arrival that are more comparable among programs, because the method accounts for the number of occupied sites and for detection probabilities, which are both likely to vary among monitoring programs (Tanadini and Schmidt 2011). Therefore, we suggest that our method could be applied to temporally and spatially extensive data from large online databases and monitoring programs, to help unravel how species and communities respond to global warming.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Performance of the single-season phenological model ([Ecological Archives E095-190-A1](#)).

### Appendix B

Field methods and analyses of the bird surveys of the Aargau Biodiversity Monitoring Program ([Ecological Archives E095-190-A2](#)).

### Appendix C

Field methods and analyses of the butterfly surveys of the Aargau Biodiversity Monitoring Program ([Ecological Archives E095-190-A3](#)).

### Appendix D

Simulation results of the three simulation scenarios to estimate trends in average arrival across years ([Ecological Archives E095-190-A4](#)).