ORIGINAL ARTICLE

Estimation of adult butterfly longevity using long-term citizen-science count data

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1. 75% of butterfly species within the UK have declined in the past 4 decades, whether in terms of abundance, distribution or both. To mitigate against this it is important to understand aspects of species' life histories. One such aspect, which is little understood, is adult longevity. Shorter adult longevities have been shown to increase conservation risk due to temporal fragmentation causing reduced productivity.
2. In this paper we show the plausibility of using long-term citizen-science count data to estimate butterfly adult longevity. Using a stopover type model fitted to the UK Butterfly Monitoring Scheme data we investigated the effect of temporal scale on adult longevity estimates.

In addition temporal trends in adult longevity were estimated using multiyear models.

3. From simulation studies we found that accuracy of longevity could be improved by modelling data at the daily level, which was particularly apparent for species with a longevity of less than seven days. We also showed that multiyear models can be used to obtain trends in lifespans, before then demonstrating how variable lifespans can impact abundance trends, especially in cases of a strong trend in lifespan over time.

4. *Synthesis and applications*: Citizen-science count data can be used to produce robust adult longevity estimates for a variety of butterfly species at national level scales. Accounting for adult longevity in abundance models can have an impact on abundance trends and therefore it is integral to enhancing the understanding of populations and hence lead to more targeted conservation actions. Although this has been demonstrated using UK butterflies the methods have the potential to be used with similar datasets.

KEYWORDS

abundance trends, citizen-science, Generalized Abundance Index, lifespan, multiyear model, stopover model, survival

1 | INTRODUCTION

To protect threatened species, it is important that we understand aspects of species life histories that are pertinent to their protection. This is true especially for insect species which provide both ecosystem functions and act as an early warning system for biodiversity declines (Brereton et al., 2011). One of the best studied groups of insects are butterflies. However, even this group presents unknowns in terms of life-history characteristics. Specifically adult longevity, or adult lifespan, is poorly understood for butterfly species, and could help explain conservation declines.

Adult longevity has been shown to be an important indicator of conservation status of butterfly species (Bubova et al., 2016). This is due to a concept known as temporal fragmentation. This stems from protandry, the reproductive strategy by which the seasonal emergence of male butterflies is earlier than females, increasing the likelihood of mating (Nowicki et al., 2005b). However, due to changes in phenology in response to climate change, an earlier emergence of males could lead to a potential mismatch in flight times between the two sexes (Nowicki et al., 2005b; Bubova et al., 2016). With a minimal overlap in flight times the productivity of the species will decline, leading to decreased population sizes. This effect is expected to be most significant for species that have a shorter adult longevity, making these species of greater conservation concern (Bubova et al., 2016).

A potential method for the estimation of adult butterfly longevity is through analysis of mark-release-recapture (MRR) data (Nowicki et al., 2005a; Bubova et al., 2016). However, collecting these data is time and labour intensive as individuals require to be caught and marked across a limited timeframe. Subsequently, this would only provide a spatial and temporal snapshot of that population (Nowicki et al., 2008). An alternative to MRR when monitoring butterflies is to simply count individuals whilst on transect walks. The simplicity of this methodology allows sampling on larger temporal and spatial scales by utilising citizen-scientists.

The UK Butterfly Monitoring Scheme (UKBMS) is a citizen-science project which started in 1976 with the aim of determining abundance trends of UK butterfly species (Pollard and Yates, 1993). The scheme has grown in popularity since its inception and is, as of 2018, performed at over 1700 sites across the UK. The survey involves the completion of a transect walk once a week across a 26 week season from April to September each year (Pollard and Yates, 1993). During each transect walk, butterflies are counted at the species level when encountered within a $5\mathrm{m}^2$ area ahead of the surveyor. These data have been used in a variety of ways, including for Red Listing (Fox et al., 2022), official biodiversity indicators (Brereton et al., 2011), and for research, such as into climate change effects (Pateman et al., 2012; Woodcock et al., 2012). The scheme also currently provides national level abundance trends for 58 of the 59 species classed as resident or regular migrants in the UK (Fox et al., 2023).

The analytical methods used to produce these trends involve a framework known as the Generalized Abundance Index (GAI) (Dennis et al., 2016a). This framework is used as a means to impute data across the field season during missing weeks at each site that performed the survey. The GAI accounts for the seasonality of butterfly species and uses a concentrated likelihood to improve computational time. The counts can either be modelled using a Poisson, zero-inflated Poisson or negative binomial distribution, whilst also flexibly modelling seasonal variation either as a Normal distribution, a spline or a stopover model, depending on the quality and quantity of the species' data. The stopover model produces ecologically informative parameters that allows for the estimation of adult longevity.

Stopover models were developed to estimate total abundances of birds at stopover sites of migrating birds as well as the duration of time that individual birds remained at these sites (Pledger et al., 2009; Matechou et al., 2013; Schwarz and Arnason, 1996). This was later developed for use in describing seasonal patterns of insects whilst determining the survival probability of individuals across the field season (Matechou et al., 2014).The utility of stopover models to describe seasonal patterns of insects has the advantage of being parametric, allowing for the estimation of ecologically informative parameters (Matechou et al., 2014). In particular, estimation of survival probability allows the longevity of adult butterflies to be derived.

If the GAI stopover model can be used to analyse the UKBMS data to provide accurate estimates of adult butterfly longevity, then we can obtain estimates for many species across a long time period and over many sites. The stopover model has previously been used for UKBMS data but either for single species in a single year (Matechou et al., 2014; Dennis et al., 2016b)) and without further validation or exploration of the robustness of the survival probability estimates. Validation of this method will allow for species of conservation concern to be highlighted, and account for year-to-year variability and estimated trends in lifespan. Accounting for this variability is important as it could have implications for the accuracy of species' abundance trends.

A potential disadvantage to using the GAI stopover model compared to MRR data is the temporal scale used. When designing citizen-science projects for widespread use it is important to account for the time constraints of the volunteer surveyors. For a successful uptake of volunteers a trade-off is often made between the amount of data collected per individual and the amount of time an individual must commit to the project (Dickinson et al., 2010; Isaac et al., 2014; Johnston et al., 2023). Therefore, during the UKBMS season, surveys are carried out once per week, weather permitting. As weather is a major determinant in the performance of the survey there is a degree of flexibility in the survey day each week. It is advised that it is performed on the first occasion in the week that conditions are suitable (Pollard and Yates, 1993). This results in a non-uniform spread of survey occasions, which means that if a survey is performed on consecutive weeks, the true temporal difference between these surveys could be within an interval of 1 to 13 days. When obtaining abundance estimates it is deemed that this is not important and, therefore, this finer-scale temporal information has so far been ignored, with data analysed at a weekly scale. However, estimation of adult longevity may benefit from using this finer-scale information, especially for species with an adult longevity of less than seven days (Mattoni et al., 2001).

We are also interested in analysing data across multiple years, which will allow us to determine trends in adult longevity over time. If there is a temporal decrease in lifespan for a species then this may indicate that this species could be of future conservation concern. Previous studies investigating adult longevity of a species over several years have demonstrated variation between years and sites, such as due to weather conditions, but allowing for a linear trend in adult longevity should demonstrate any overall patterns (Boggs, 1987; Hodgson et al., 2011).

We have several aims for this study. The first is to validate the use of the GAI stopover model fitted to UKBMS data for the estimation of butterfly adult longevity. We will do this in two ways. Firstly, by keeping the data in the weekly format, and secondly, by converting the data into the daily format to account for the exact date of each count. Initially, the potential of using the GAI stopover model will be checked using simulated data, then we will analyse UKBMS data for selected species. The second aim is to determine if creating a multiyear model, in which data are analysed across multiple years, will allow us to determine trends in adult longevity. Finally, we will investigate if accounting for lifespan impacts the abundance trend estimates produced.

2 | MATERIALS AND METHODS

2.1 | GAI stopover model

The GAI stopover model used within this paper is developed from Matechou et al. (2014) and Dennis et al. (2016a). We let S denote the number of sites and T the number of survey occasions. Suppose counts $y_{s,v}$ denote the number of individuals recorded in site $s = 1, \ldots, S$ during visit $v = 1, \ldots, T$. We treat $y_{s,v}$ as realisations from a Poisson distribution, with expectation $\lambda_{s,v}$. We define N_s to be the superpopulation size at site s, with the superpopulation defined as the total number of individuals at a site across the field season. We write

$$\lambda_{s,v} = N_s \sum_{d=1}^{v} \beta_{s,d-1} \Big(\prod_{k=d}^{v-1} \phi_{k,c} \Big), \tag{1}$$

where $\beta_{s,d-1}$ represents the arrival of individuals into a population and we express this through a Normal distribution, or a mixture of Normals, dependent on the number of broods, b. This arrival term is described through Eq (2), where d is a possible time of entry of an individual into the population.

$$\beta_{s,d-1} = \sum_{b=1}^{B} \omega_{s,b} \Big\{ F_{s,b}(t_{s,d}) - F_{s,b}(t_{s,d} - 1) \Big\}, \tag{2}$$

with $F_{s,b}(t_{s,d}) = Pr(X \leq t_{s,d})$, for $X \sim N(\mu_{s,b}.\sigma^2_{s,b})$, with $\mu_{s,b}$ being the mean emergence time at site s for brood b, and $\sigma_{s,b}$ being the associated standard deviation.

The survival probability, $\phi_{k,c}$, denotes the probability that individuals that have been at the site for c occasions and are present on occasion k, will remain until occasion $k+1$. The likelihood for the Poisson case is given by:

$$\mathrm{L}(\mathbf{N}, \phi, \mu, \sigma; \mathbf{y}) = \prod_{s=1}^{S} \prod_{v=1}^{T} \frac{e^{-\lambda_{s,v}} {\lambda_{s,v}}^{y_{s,v}}}{y_{s,v}!}, \tag{3}$$

Although it is possible to optimise Equation 3 to obtain maximum-likelihood estimates of N, ϕ, μ and σ, when the number of sites is large, optimisation can be very slow. Dennis et al. (2016a) demonstrated that it is possible to use a concentrated likelihood to reduce computational time.

It is also possible to treat the counts as a realisation of a negative binomial distribution in cases of overdispersed data. The likelihood for that case is given by:

$$\mathrm{L}(\mathbf{N}, \phi, \mu, \sigma; \mathbf{y}) = \prod_{s=1}^{S} \prod_{v=1}^{T} \frac{\Gamma(y_{s,v} + r)}{\Gamma(r)\, y_{s,v}!} \left(\frac{N_s a_{s,v}}{r + N_s a_{s,v}}\right)^{y_{s,v}} \left(\frac{r}{r + N_s a_{s,v}}\right)^{r}, \tag{4}$$

with dispersion parameter r. An iterative procedure is needed for optimising the concentrated likelihood for the negative binomial, which is described in Dennis et al. (2016a).

2.2 | Simulation study

The purpose of the simulation study is three-fold:

1. To demonstrate the robustness of the GAI stopover model for the estimation of survival probability and subsequently lifespan.

2. To determine if using the data at a daily level impacts the estimation of life span.

3. To determine if reliable trends in life span can be obtained from multiple years of data and if trends in lifespan impact abundance trends.

The simulation study has been designed to mimic the UKBMS data as closely as possible. In the UKBMS, although only one survey is conducted per week, a week is defined as the period from Monday to Sunday. One survey is then conducted within this period, and it is advised that this should occur on the first day in this period with suitable weather conditions. To complete the survey a minimum temperature of 13°C is required and it must be sunny for 60% of the transect walk. Often these conditions are not met and, therefore, the majority of surveys are not conducted at exact seven-day intervals, but at intervals varying from 1 to 13 days, if a survey is conducted on consecutive weeks. We account for this when simulating the daily level data and demonstrate this property in the UKBMS data in the Supporting Information. Once the data are simulated at the daily level we can then choose whether to compress to a weekly format, as has typically been undertaken for analysis of the UKBMS data, or to keep counts in the daily format. If the model is in the daily format then missing observations are added randomly whilst ensuring one day per week contains a count. Then, regardless of format, missing counts are assigned to 30% of non-missing data to match the proportion from the raw data (Dennis et al., 2016a).

We assume that all counts are realisations of a Poisson random variable and consider a univoltine structure with only a single brood per season. Detection is assumed constant, as by design of the UKBMS data collection.

For each comparison, 250 data sets were simulated, and 5 random starts were used for each optimisation to ensure the global optimum was reached. For each simulation run we obtained a single maximum likelihood estimate for the survival probability, $\hat{\phi}$, as ϕ is assumed to be constant over time and age, i.e. $\phi_{k,c} = \phi \forall_{k,c}$.

If the data were compressed to a weekly format then the $\hat{\phi}$ MLE represents weekly survival, which we will denote as $\hat{\phi}_w$. However, if the count data were kept in the daily format $\hat{\phi}$ MLE represents daily survival and was denoted as $\hat{\phi}_d$.

It is more intuitive to think of lifespan in terms of days as the majority of adult lifespans will be in a range of 2-14 days (Bubova et al., 2016). If lifespan was derived using $\hat{\phi}_w$ then lifespan would be derived in terms of weeks. Therefore, we assumed a constant daily survival probability and converted $\hat{\phi}_w$ to $\hat{\phi}_d$ before deriving a lifespan estimate, $\hat{\Lambda}$, in terms of days. To convert $\hat{\phi}_w$ to $\hat{\phi}_d$ we used $\hat{\phi}_d = \hat{\phi}_w^{\frac{1}{7}}$. As lifespan follows a geometric distribution, we obtained a derived estimate of $\Lambda = \frac{1}{1-\hat{\phi}_d}$.

2.3 | Application to UKBMS data

The GAI stopover model analyses data from separate species in separate years. To assess the use of the GAI stopover model for estimation of lifespan we used data from univoltine (single-brooded) species and limited sites to those with at least two non-zero counts throughout the season. We compared outputs to MRR estimates from the literature. Overdispersion of the fitted Poisson model was checked for each species and, if needed, counts were treated as a realisation of a negative binomial distribution.

The species investigated using the GAI stopover model were the Orange-tip (*Anthocharis cardamines*), Marbled White (*Melanargia galathea*), and Dark Green Fritillary (*Speyeria aglaja*). These species are a mixture of wider country-side species (Orange-tip) and habitat specialists (Marbled White and Dark Green fritillary). The Orange-tip and the Dark Green Fritillary were chosen because we have corresponding lifespan estimates from MRR studies.

Table 1 summarises the studies used for comparison to the lifespan estimates from the GAI Stopover model. Details of the region of study and year of study are included as these could influence the lifespan estimates produced from these studies.

The Marbled White was chosen as it is limited to the south of the UK and, therefore, may show less variation in lifespan estimates due to a reduced spatial variability in climatic conditions. Each of these species were analysed initially using data from three separate years from 2016-2018. 95% confidence intervals for lifespan estimates were obtained via the Hessian matrix and the associated δ-method calculation. The negative binomial structure of the GAI stopover model was used as the Poisson model was determined to be too restrictive.

TABLE 1 Summary of the literature used to obtain adult lifespan estimates from mark-recapture studies.

Species	Literature	Lifespan (days)	Region of study
DGF	Zimmermann et al. (2009)	8.2	Czech Republic
	Warren (1994)	3.5-4.3	UK
OT	Dempster (1997); Courtney and Duggan (1983)	6.95 (5.60-8.30)	UK
	Courtney and Duggan (1983)	4.5-8.3	UK

DGF, Dark Green Fritillary; OT, Orange-tip.

2.4 | Multiyear model

The GAI model is typically fitted to data separately for each year. To jointly analyse data from multiple years we formed an integrated likelihood, multiplying likelihood components corresponding to each individual year. This forms a global likelihood for the chosen time-span. We refer to this as the multiyear model and instead of assuming a constant lifespan over all years it is possible to estimate trends in lifespan across multiple years. After an initial investigation we determined that to ensure accuracy in the lifespan estimate in the multiyear model both σ and μ parameters should be allowed to vary with year.

For each of the three considered species we analysed data from 1994-2018. The chosen time-frame of 25 years ensured a sufficient trade-off between the quality and quantity of the data, which is lower in earlier years of the UKBMS. This analysis was performed using both the daily and weekly formats and a comparison was made between the two. As with the single year analyses, a negative binomial GAI stopover model was used.

2.5 | Abundance trends

The UKBMS dataset is primarily used to produce estimates of the trends in abundance of UK butterfly species. Currently abundance trends produced do not account for lifespan as they are not estimated using the GAI stopover model. We, therefore, wished to compare the abundance trends produced for the three species when accounting for lifespan and when not. Abundance trends were calculated by placing a linear regression over the yearly abundance indices obtained from a Poisson GLM fitted to the superpopulation size estimates with both fixed year and site effects, as well as a weighting based on the proportion of the flight period sampled. From this annual growth rates were calculated, which are the yearly changes in the linear trend, set relative to 1, with 1 indicating no trend. We also calculated overall percentage changes which are the percentage changes in index values from the first year to the last year analysed. We compared the GAI stopover models with a model that does not account for lifespan by modelling seasonal variation in the form of a Normal distribution ('No ϕ'). The options for the multiyear GAI stopover models were either with a fully time-varying lifespan ('Year-dependent ϕ') or with a linear temporal trend over lifespan ('Year covariate ϕ'). 95% confidence intervals were calculated by sampling the MLEs from a multivariate Normal 250 times and refitting the GLM, a process which is described in greater detail in the Supporting Information.

3 | RESULTS

3.1 | Simulation study

Figure 1 shows that as the value of the daily survival probability, ϕ_d, increases there is an improvement in accuracy of the lifespan estimates. As the minimum interval between counts is seven days for the weekly model, the decrease in accuracy of the lifespan estimates was expected for the weekly format model. However, unlike the weekly format model which tends to overestimate lifespan when true lifespan is less than seven days, under the daily format. Figure 1 shows that for true lifespans of less than seven days accurate estimates of adult lifespan were obtained. This would suggest that for lifespans of less than seven days the daily format model should be used to improve the accuracy of lifespan estimates.

An additional simulation (Supporting Information) was run that investigated the effect of sampling multiple days per week on lifespan estimates and showed a large improvement in precision of lifespan estimates with just one additional survey per week. However, increasing the number of surveys beyond 2 a week did not have a substantial impact on the estimates of lifespan.

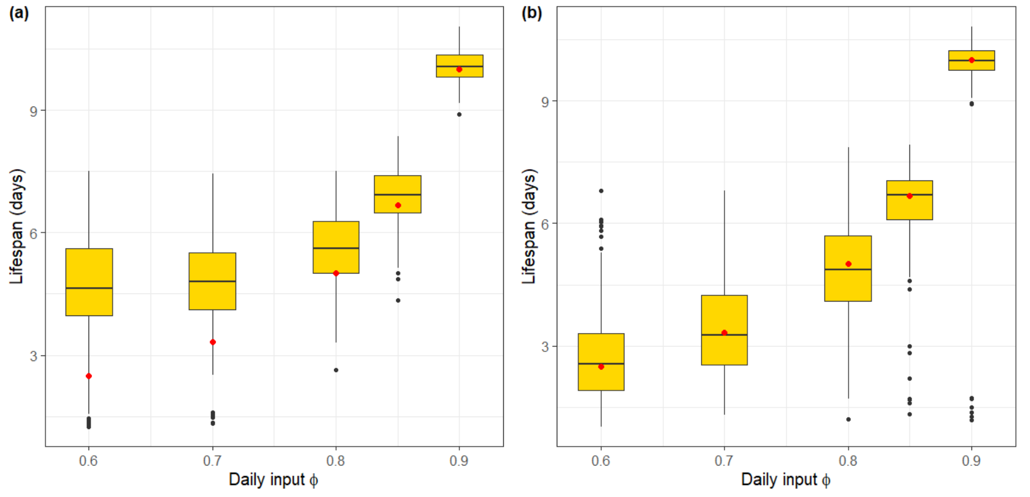

FIGURE 1 Derived lifespan estimates from 250 simulation runs of the a) weekly and b) daily model for varying values of $\phi_d = \{0.6, 0.7, 0.8, 0.85, 0.9\}$. The relationship $\hat{\phi}_w = \hat{\phi}_d^7$ was used for (a), and the relationship $\hat{\Lambda} = \frac{1}{1-\hat{\phi}_d}$ was used for both plots. The true value of the lifespan Λ based on the input is shown by the red dot.

3.2 | Application to UKBMS data

Figure 2 summarises the estimated lifespans for the Dark Green Fritillary, Marbled White and Orange-tip for each year from 2016-2018 which were fitted under both the weekly and daily formats.

The estimated lifespans for the Dark Green Fritillary match for the two formats across the three years considered and this could be due to the lifespans being greater than seven days, with the simulation studies suggesting that the two formats should match on these occasions. The Marbled White consistently had an estimated lifespan of less than seven days and this was the likely cause for a mismatch between the two formats in two of the three years, with the only match being with the largest estimated daily lifespan of the three years. However, the Orange-tip produced daily estimates greater than seven days but still resulted in mismatches between the two formats.

For the Dark Green Fritillary and the Orange-tip the GAI stopover estimates were compared to MRR estimates obtained from previous studies (Bubova et al., 2016; Warren, 2021; Zimmermann et al., 2009; Dempster, 1997; Courtney and Duggan, 1983; Warren, 1994). For the Dark Green Fritillary the MRR estimates are 8.2 days for one study (Zimmermann et al., 2009) and 3.5-4.3 days for another (Warren, 1994) and these failed to overlap with those produced by the GAI stopover model for all but the 2018 data.

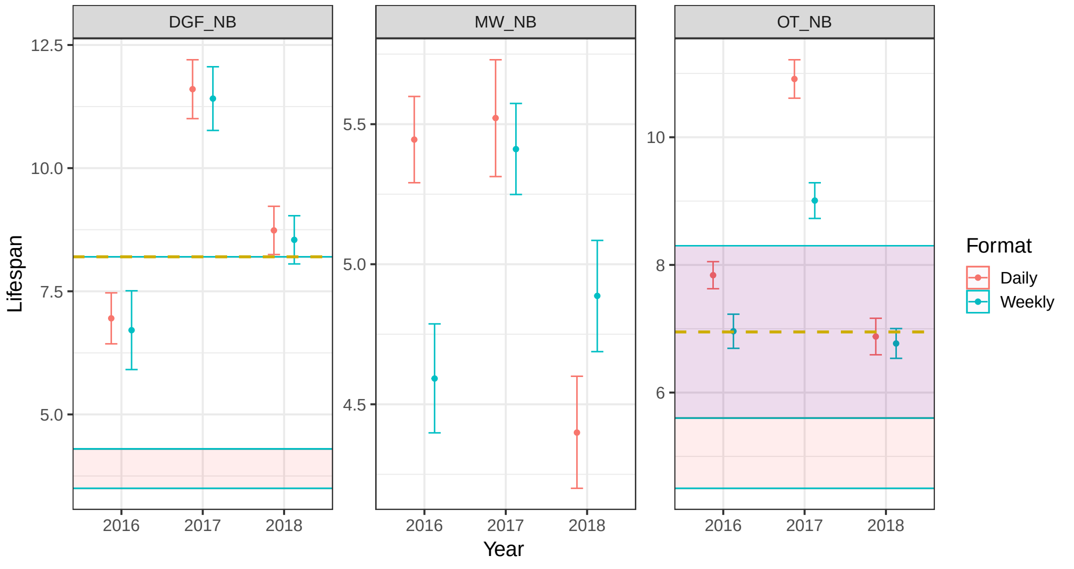

FIGURE 2 Estimated lifespan estimates for 2016-2018 negative binomial models for the Dark Green Fritillary (DGF_NB), Marbled White (MW_NB) and Orange-tip (OT_NB) data. The model is fitted either in the daily or weekly format and the 95% confidence intervals are calculated using the Hessian with associated δ-method calculation. The yellow dashed line indicates the median capture-recapture estimate for this species from Bubova et al. (2016). The blue region indicates the range of mark-release-recapture estimates as calculated in Bubova et al. (2016), where available. The red region indicates the range of mark-release-recapture estimates as calculated in Warren (2021).

A much wider interval is available for the Orange-tip as more MRR studies have been carried out on this species. This includes a lifespan of 6.95 (5.60-8.30) days, based on two studies (Dempster, 1997; Courtney and Duggan, 1983) from Bubova et al. (2016). Whereas the estimate that appeared in Warren (2021) was based upon Courtney and Duggan (1983) only, which gave a range of 4.5-8.3 days. The GAI stopover estimates overlap with these for both the 2016 and 2018 data, however there is no overlap with either in 2017.

3.3 | Multiyear model

Figure 3 shows the individual year lifespan estimates alongside the estimated trend line for the multiyear model in the weekly and daily formats. For the Dark Green Fritillary and Marbled White outputs the trends in lifespan estimates overlap between the daily and weekly format of the model. For the daily format the slope coefficients are 0.217 (0.185, 0.249) and -0.0180 (-0.0342, -0.00182) for the two species respectively and for the weekly format these are

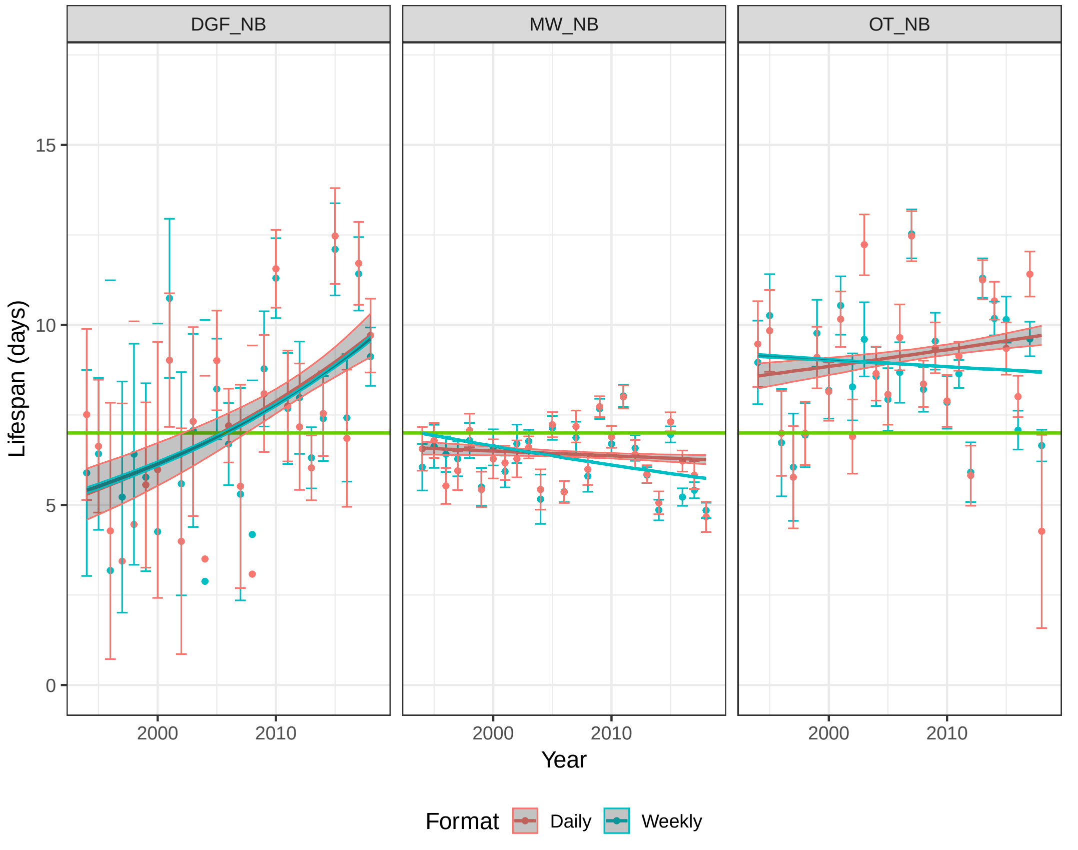

FIGURE 3 Points showing the derived lifespan estimates for the fully year-dependent multiyear GAI stopover negative binomial model for the Dark Green Fritillary (DGF_NB), Marbled White (MW_NB) and Orange-tip (OT_NB) for each year of analysis and the lines showing the corresponding time trend when survival probability is fitted with a time trend. Results for both the daily (blue) and weekly (red) formats. The green line references a lifespan of seven days. 95% confidence intervals obtained from the Hessian and associated δ-method calculation.

0.310 (0.275, 0.325) and -0.114 (-0.132, -0.0956) respectively. The uncertainty in the lifespan estimates was greatest for the Dark Green Fritillary. However, this species showed a clear positive trend in lifespan from 1994-2018. The Marbled White showed a decline over this time-frame but this was not a strong trend in terms of magnitude. The Orange-tip exhibited a disagreement in the direction of the trend of the lifespan, although neither trend was strong, with daily having a slope of 0.0423 (0.0243, 0.0604) and weekly a slope of -0.0247 (-0.0477, -0.00168). Figure 3 also demonstrates the amount of stochastic temporal variation within lifespans of butterflies, especially for the Dark Green Fritillary and the Orange-tip.

TABLE 2 Annual growth rates obtained when using the GAI Normal model (No ϕ), fully year-dependent model (year-dependent ϕ), and model with a time trend on ϕ (year covariate ϕ) for negative binomial models from 1994-2018 for the Dark Green Fritillary (DGF), Marbled White (MW) and Orange-tip (OT) in the weekly and daily format. 95% confidence intervals are obtained through sampling MLEs from a multivariate Normal 250 times and refitting the GLM. Bold font highlights significant trends.

Annual Growth Rate			
Species	Model	Weekly	Daily
DGF	No ϕ	**1.016 (1.006-1.036)**	**1.018 (1.008, 1.034)**
	Year-dependent ϕ	1.000 (0.991-1.030)	0.991 (0.973, 1.012)
	Year covariate ϕ	1.001 (0.990-1.020)	0.992 (0.981, 1.008)
MW	No ϕ	0.999 (0.992-1.007)	1.002 (0.994, 1.009)
	Year-dependent ϕ	1.002 (0.994-1.010)	1.004 (0.996, 1.011)
	Year covariate ϕ	1.004 (0.997-1.012)	1.004 (0.996, 1.012)
OT	No ϕ	**1.010 (1.004-1.016)**	**1.009 (1.004, 1.015)**
	Year-dependent ϕ	**1.008 (1.002-1.014)**	**1.008 (1.000-1.016)**
	Year covariate ϕ	**1.011 (1.004-1.016)**	1.003 (0.998, 1.009)

DGF, Dark Green Fritillary; MW, Marbled White; OT, Orange-tip.

3.4 | Abundance trends

The annual growth rates and percentage changes were calculated for the three analysed species to determine if accounting for lifespan when modelling seasonal variation results in a change the abundance trend produced and whether this varies based upon whether the lifespan is allowed to vary completely with year or by adding a linear trend to lifespan over time.

The tables show that on the majority of occasions there is an overlap in the trends produced for both the daily and weekly formats in the abundance trends across the three formulations of the model. For the Dark Green Fritillary there was a significant increase in the abundance from 1994-2018 when lifespan is not accounted for, but there is no significant trend for the daily or weekly formats for both models with a linear trend in lifespan and with a fully time-varying lifespan. The Dark Green Fritillary showed the strongest trend in lifespan of the three example species as shown in Figure 3. For the Marbled White no significant trend is estimated regardless of temporal scale or modelling methodology. For the Orange-tip there is a significant positive trend for all model formulations under the

TABLE 3 Percentage changes obtained when using the GAI Normal model (No ϕ), fully year-dependent model (year-dependent ϕ), and model with a time trend on ϕ (year covariate ϕ) for negative binomial models from 1994-2018 for the Dark Green Fritillary (DGF), Marbled White (MW) and Orange-tip (OT) in the weekly and daily format. 95% confidence intervals are obtained through sampling MLEs from a multivariate Normal 250 times and refitting the GLM. Bold font highlights significant trends.

		Overall percentage change	
Species	Model	Weekly	Daily
DGF	No ϕ	**46.91 (14.28-134.67)**	**53.03 (22.25, 121.92)**
	Year-dependent ϕ	0.72 (-19.75, 101.51)	-19.77 (-47.58, 33.27)
	Year covariate ϕ	2.87 (-20.96, 61.48)	-17.36 (-36.21, 20.10)
MW	No ϕ	-1.70 (-17.47,19.00)	4.51 (-13.06, 24.98)
	Year-dependent ϕ	3.89 (-13.39, 27.50)	9.47 (-8.47, 31.16)
	Year covariate ϕ	9.80 (-7.42, 33.92)	10.13 (-8.79, 31.98)
OT	No ϕ	**26.23 (9.78, 44.92)**	**23.20 (8.86, 42.00)**
	Year-dependent ϕ	**21.57 (4.80, 40.15)**	**22.41 (0.65-46.34)**
	Year covariate ϕ	**29.85 (11.57, 48.97)**	8.41 (-4,52, 23.80)

DGF, Dark Green Fritillary; MW, Marbled White; OT, Orange-tip.

weekly format and also for the daily format for models not accounting for lifespan and with fully time-varying lifespan. However, there is no significant trend when lifespan is restricted to a linear temporal trend.

4 | DISCUSSION

The aim of this paper was to demonstrate the use of the GAI stopover model for obtaining adult lifespan estimates from long-term citizen science data, whether temporal scale of counts mattered for this and then whether temporal trends in lifespans could be determined. Simulation studies investigated the potential of using the GAI stopover model to obtain lifespan estimates for butterfly species. From this it was discovered that for lifespans of more than seven days the weekly format estimated the lifespans well. However, for shorter lifespans using the weekly format resulted in biased estimates. This was expected, as for the weekly format there is a minimum time difference of seven days between counts. When accounting for the daily level data we found that the accuracy improved for shorter lifespans as the shorter time differences between counts were accounted for. Due to the amount of variation in length of adult longevity with year it is difficult to predict the occurrence of longevities under seven days, therefore we recommend the use of the daily format if the aim of the anlysis is to estimate adult longevity. Additionally, simulations showed that performing one extra count per week could lead to improved lifespan estimates. As with any citizen science scheme the potential benefits of increased surveys has to be balanced with volunteer time commitment. Therefore as a compromise, it could be suggested to surveyors of species of particular interest or focus to perform an additional count per week during their flight period if estimating a lifespan was of interest.

The proposed models were fitted to UKBMS data from which it was discovered that lifespan estimates matched between the two spatial scales when the daily estimate of lifespan was greater than seven days, with the exception of the 2016 and 2017 data for the Orange-tip. The Orange-tip is the most-common of the three species analysed and it may be due to the increased amount of data that we obtained tight confidence intervals for this species. Additionally, it was found that using alternative methods for obtaining confidence intervals were less conservative than deriving these from the Hessian (Moerbeek et al., 2004; Zhou, 2002; Datta and Ghosh, 2014). Similarly like-for-like data was not being compared for the two formats. If there were multiple counts in a week then these could be included for the daily format, whereas for the weekly format the largest count was chosen. As the Orange-tip was a more common species there were more double counts in a week for this species than the other two, which could result in mismatches.

When comparing the results obtained from these models to MRR estimates for two species it can be seen that on 3 of the 6 datasets there was not a match for either format to the corresponding MRR estimate. This could be due to such studies being a spatial and temporal snapshot of the population studied in that research. In addition, the lifespan of butterflies can be variable from year-to-year, as is also seen in Figure 2, and this can be due to weather conditions (Boggs, 1987; Hodgson et al., 2011).

We have demonstrated that it is possible to obtain estimated trends in lifespan through the development of a multiyear model. It was found that when there is a strong trend in lifespan, as was found with the Dark Green Fritillary, that this could result in changes to abundance trends. In the case of the Dark Green Fritillary, whose lifespan was estimated to be increasing over time, this increased time for each individual could have been taken as more individuals, and this could influence the abundance trend if lifespan was not included within the model.

We have considered only univoltine species here, but the GAI multivoltine stopover model could be used in the same way to obtain estimates of lifespan. This could also be used to determine whether lifespans can vary between different broods in a single year. In addition, investigating how lifespan varies with habitat and climatic covariates may be of interest and could be naturally incorporated through our statistical framework.

Additionally, to obtain greater confidence in lifespan estimates, it may be possible to integrate data from smaller scale MRR studies to help inform lifespan estimates at these larger spatial and temporal scales, see for example Dennis et al. (2021).

There are various assumptions of the model that could also be further tested, such as the validity of the emergence distribution being modelled as a Normal distribution. It has been shown that emergence may follow more skewed distributions due to mass emergence events Calabrese (2012). Therefore, specifying the model with alternative distributions may be of future interest.

Overall, we have demonstrated the potential of using the GAI stopover model to estimate lifespan from citizen-science data. This has the potential to provide greater insights into adult butterfly lifespans and how they could be changing over time. It could also be used for similar datasets such as the European Butterfly Monitoring Scheme (eBMS) or the National Moth Recording Scheme (van Swaay et al., 2008; Fox et al., 2011). This will thus provide us with a greater knowledge of species of either current or future conservation concern.

Author contributions

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Conflict of interest statement

The authors declare no conflict of interest associated with this study.

Data availability statement

ORCiD

REFERENCES

Boggs, C. L. (1987) Within Population Variation in the Demography of Speyeria mormonia (Lepidoptera: Nymphalidae). *Holarctic Ecology*, **10**, 175–184.

Brereton, T., Roy, D. B., Middlebrook, I., Botham, M. and Warren, M. (2011) The development of butterfly indicators in the United Kingdom and assessments in 2010. *Journal of Insect Conservation*, **15**, 139–151.

Bubova, T., Kulma, M., Vrabec, V. and Nowicki, P. (2016) Adult longevity and its relationship with conservation status in European butterflies. *Journal of Insect Conservation*, **20**, 1021–1032.

Calabrese, J. M. (2012) How emergence and death assumptions affect count-based estimates of butterfly abundance and lifespan. *Population Ecology*, **54**, 431–442.

Courtney, S. P. and Duggan, A. E. (1983) The population biology of the Orange Tip butterfly Anthocharis cardamines in Britain. *Ecological Entomology*, **8**, 271–281.

Datta, J. and Ghosh, J. K. (2014) Bootstrap—An exploration. *Statistical Methodology*, **20**, 63–72.

Dempster, J. P. (1997) The role of larval food resources and adult movement in the population dynamics of the orange-tip butterfly (Anthocharis cardamines). *Oecologia*, **111**, 549–556.

Dennis, E. B., Kéry, M., Morgan, B. J. T., Coray, A., Schaub, M. and Baur, B. (2021) Integrated modelling of insect population dynamics at two temporal scales. *Ecological Modelling*, **441**, 109408.

Dennis, E. B., Morgan, B. J. T., Freeman, S. N., Brereton, T. M. and Roy, D. B. (2016a) A Generalized Abundance Index for Seasonal Invertebrates. *Biometrics*, **72**, 1305–1314.

Dennis, E. B., Morgan, B. J. T., Freeman, S. N., Roy, D. B. and Brereton, T. (2016b) Dynamic Models for Longitudinal Butterfly Data. *Journal of Agricultural Biological and Environmental Statistics*, **21**, 1–21. WOS:000374695400001.

Dickinson, J. L., Zuckerberg, B. and Bonter, D. N. (2010) Citizen Science as an Ecological Research Tool: Challenges and Benefits. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 149–172. URL: https://www.jstor.org/stable/27896218. Publisher: Annual Reviews.

Fox, R., Dennis, E. B., Brown, A. F. and Curson, J. (2022) A revised Red List of British butterflies. *Insect Conservation and Diversity*, **15**, 485–495.

Fox, R., Dennis, E. B., Purdy, K. M., Middlebrook, I., Roy, D. B., Noble, D. G., Botham, M. S. and Bourn, N. A. D. (2023) The State of the UK's Butterflies 2022. *Tech. rep.*, Butterfly Conservation, Wareham, Dorset, UK. URL: https://butterfly-conservation.org/state-of-uk-butterflies-2022.

Fox, R., Randle, Z., Hill, L., Anders, S., Wiffen, L. and Parsons, M. S. (2011) Moths count: recording moths for conservation in the UK. *Journal of Insect Conservation*, **15**, 55–68.

Hodgson, J. A., Thomas, C. D., Oliver, T. H., Anderson, B. J., Brereton, T. M. and Crone, E. E. (2011) Predicting insect phenology across space and time. *Global Change Biology*, **17**, 1289–1300.

Isaac, N. J. B., van Strien, A. J., August, T. A., de Zeeuw, M. P. and Roy, D. B. (2014) Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods in Ecology and Evolution*, **5**, 1052–1060.

Johnston, A., Matechou, E. and Dennis, E. B. (2023) Outstanding challenges and future directions for biodiversity monitoring using citizen science data. *Methods in Ecology and Evolution*, **14**, 103–116.

Matechou, E., Dennis, E. B., Freeman, S. N. and Brereton, T. (2014) Monitoring abundance and phenology in (multivoltine) butterfly species: a novel mixture model. *Journal of Applied Ecology*, **51**, 766–775.

Matechou, E., Morgan, B. J. T., Pledger, S., Collazo, J. A. and Lyons, J. E. (2013) Integrated Analysis of Capture-Recapture-Resighting Data and Counts of Unmarked Birds at Stop-Over Sites. *Journal of Agricultural Biological and Environmental Statistics*, **18**, 120–135.

Mattoni, R., Longcore, T., Zonneveld, C. and Novotny, V. (2001) Analysis of Transect Counts to Monitor Population Size in Endangered Insects The Case of the El Segundo Blue Butterfly, Euphilotes Bernardino Allyni. *Journal of Insect Conservation*, **5**, 197–206.

Moerbeek, M., Piersma, A. H. and Slob, W. (2004) A Comparison of Three Methods for Calculating Confidence Intervals for the Benchmark Dose. *Risk Analysis*, **24**, 31–40.

Nowicki, P., Richter, A., Glinka, U., Holzschuh, A., Toelke, U., Henle, K., Woyciechowski, M. and Settele, J. (2005a) Less input same output: simplified approach for population size assessment in Lepidoptera. *Population Ecology*, **47**, 203–212. URL: `http://doi.wiley.com/10.1007/s10144-005-0223-2`.

Nowicki, P., Settele, J., Henry, P. and Woyciechowski, M. (2008) Butterfly Monitoring Methods: The ideal and the Real World. *Israel Journal of Ecology & Evolution*, **54**, 69–88.

Nowicki, P., Witek, M., Skórka, P., Settele, J. and Woyciechowski, M. (2005b) Population ecology of the endangered butterflies Maculinea teleius and M. nausithous and the implications for conservation. *Population Ecology*, **47**, 193–202.

Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R. and Thomas, C. D. (2012) Temperature-Dependent Alterations in Host Use Drive Rapid Range Expansion in a Butterfly. *Science*, **336**, 1028–1030. Publisher: American Association for the Advancement of Science.

Pledger, S., Efford, M., Pollock, K., Collazo, J. and Lyons, J. (2009) Stopover Duration Analysis with Departure Probability Dependent on Unknown Time Since Arrival. In *Modeling Demographic Processes In Marked Populations.*, vol. 3 of *Environmental and Ecological Statistics*, 349–363. Boston, MA: Springer.

Pollard, E. and Yates, T. J. (1993) *Monitoring Butterflies for Ecology and Conservation: The British Butterfly Monitoring Scheme*. Conservation Biology. Springer Netherlands.

Schwarz, C. J. and Arnason, A. N. (1996) A General Methodology for the Analysis of Capture-Recapture Experiments in Open Populations. *Biometrics*, **52**, 860–873.

van Swaay, C. A. M., Nowicki, P., Settele, J. and van Strien, A. J. (2008) Butterfly monitoring in Europe: methods, applications and perspectives. *Biodiversity and Conservation*, **17**, 3455–3469.

Warren, M. (1994) Autecology and conservation needs of the high brown fritillary: Annual report for 1993/1994. *Tech. rep.*, Butterfly Conservation, Wareham, Dorset, UK.

— (2021) Butterflies in the landscape. In *Butterflies: A Natural History*, 61–81. London: Bloomsbury Publishing.

Woodcock, B. A., Bullock, J. M., Mortimer, S. R., Brereton, T., Redhead, J. W., Thomas, J. A. and Pywell, R. F. (2012) Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment. *Biological Conservation*, **155**, 50–58.

Zhou, S. (2002) Estimating Parameters of Derived Random Variables: Comparison of the Delta and Parametric Bootstrap Methods. *Transactions of the American Fisheries Society*, **131**, 667–675.

Zimmermann, K., Konvicka, M., Fric, Z. and Čihaková, V. (2009) Demography of a common butterfly on humid grasslands: Argynnis aglaja (Lepidoptera: Nymphalidae) Studied by Mark-Recapture. *Polish Journal of Ecology*, **57**, 715–727.

SUPPORTING INFORMATION

| Simulation study

Table 4 contains the fixed parameter values for the simulation study described in Section 2.2.

TABLE 4 Parameter values used in the simulations

Parameter	Description	Value
μ	Mean flight date (days)	55
σ	Standard deviation of flight date (days)	20
ϕ_d	Survival probability (daily)	$\{0.6, 0.7, 0.8, 0.85, 0.9\}$
N_i	Average superpopulation size at each site	150
T	No. of days	175
S	No. of sites	200

| Days between counts

To demonstrate the relationship in the UKBMS data for the true interval between counts if counts are obtained on consecutive weeks we have used the Orange-tip (*Anthocharis cardamines*) data from 2018. This is summarised in the histogram in Figure 4. In this figure we can see the interval between counts centering around 7 days, but with extremes of 1 and 13 days, when the data is limited to counts occurring on consecutive weeks.

We then checked the simulated counts would match this pattern when using the daily level format. Therefore, the simulated counts $\lambda_{s,v}$ will be made at the daily level and then a single count is selected for each week, before setting all other values within the week to NA. The probability of choosing a day of the week is determined through the probabilities obtained from the complete UKBMS dataset. The number of occasions that a survey was undertaken for each day per week in the UKBMS data is summarised in Figure 5.

Thus we can see that through simulating the data in this way we are producing counts mimicking those seen in the UKBMS data, shown in Figure 4, which is demonstrating a similar pattern to Figure 6.

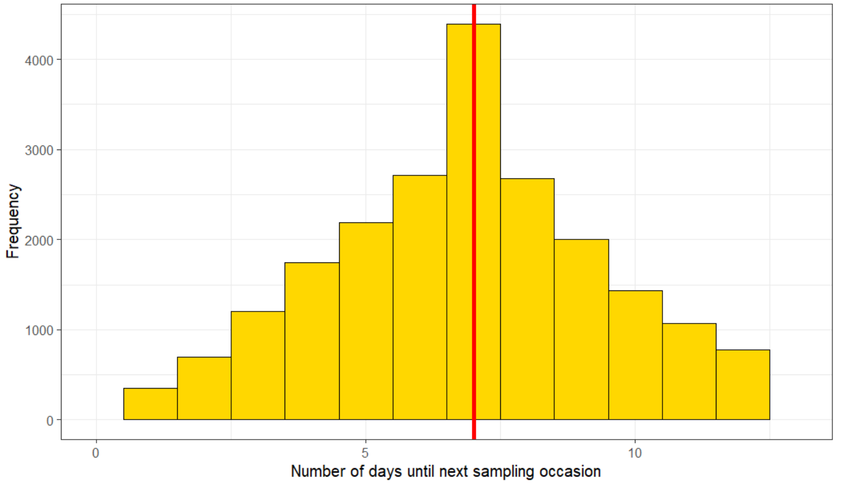

FIGURE 4 Histogram of number of days between counts for the 2018 Orange-tip data across all sites. The plot only takes into account counts made on consecutive weeks. A red line indicates 7 days between counts, which was what was originally assumed to be the length of time between counts.

We again see a centering around 7 days, although, this is not as pronounced as Figure 4. However, we are simulating data across 50 sites compared to over 1500 in the raw data for *A. cardamines*, which could account for this discrepancy.

| Days per week simulation

We simulated the count data as was done in the main text but changed the number of counts per week included within the dataset. The days chosen were based upon probabilities from the complete UKBMS dataset.

As the model was struggling to estimate lifespans of less than 7 days we decided to set $\phi_d = 0.8$, equivalent to $\Lambda = 5$, and set $S = 200$ to determine if increasing the number of days sampling per week will improve estimates of these shorter lifespans. All other values were as Table **??**. We also ran the weekly model for use in this comparison.

Figure 7 shows that increasing the number of sampling days per week does, as expected, improve the accuracy of lifespan estimates, even with only increasing to 2 days per week. It may not be possible to implement this change in sampling effort in the UKBMS, however, if there was a particular species of interest then it may be possible to increase effort during the flight period of this species.

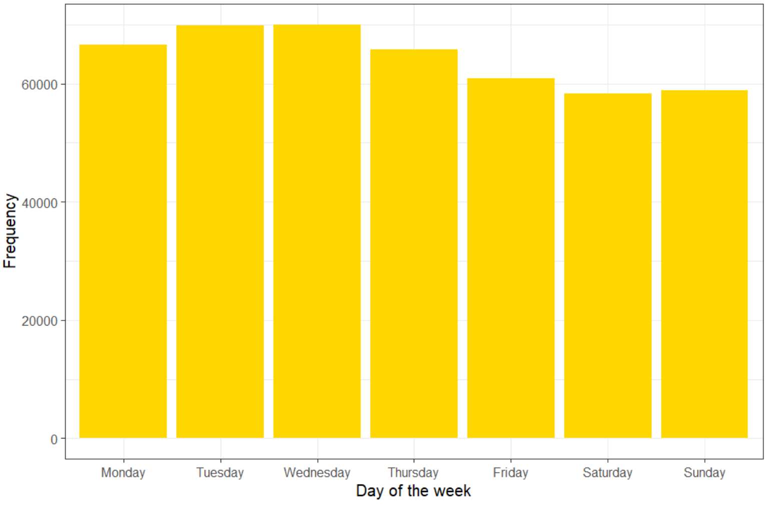

FIGURE 5 The number of occasions that a survey has been conducted on each of the 7 days of a week using data from the complete UKBMS dataset from 1976-2018.

Figure 7 also indicates the improvement in accuracy when using the daily format compared with the weekly format for estimating lifespans.

| Number of sites simulation

In the previous examples we have used a total of 200 sites. However, in the UKBMS data the number of sites can be substantially greater than this. For example, the Meadow Brown (*M. jurtina*) is a common species which in 2018 was counted at a total of 1658 sites across the UK.

Therefore, in these simulations we aim to vary the number of sites within our simulation and determine the effect on the precision of the lifespan estimates. For this simulation study we had the input values set as of Table **??** with $\phi_d = 0.8$, corresponding to an adult lifespan of 5 days. The number of sites will vary and are $S = \{100, 200, 500, 1000\}$.

Figure 8 shows the change in precision of the daily format model when changing the number of sites analysed.

Although accuracy is similar for the daily format across differing numbers of sites the precision greatly increases with the number of sites. To estimate the precision the root mean square error (RMSE) was calculated for each simulation. These were 0.145, 0.0822, 0.0502 and 0.0519 as the number of sites increase from 100 to 1000 respectively.

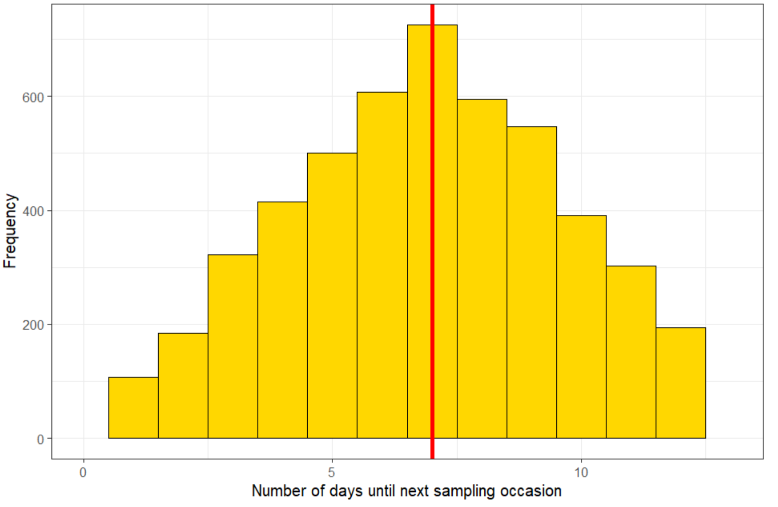

FIGURE 6 Histogram of number of days between counts in the simulated data when one count is made per week for consecutive weeks.

Although the precision does increase this plateaus when there is 500 sites analysed and adding more sites does not result in further improvements in precision.

Similarly, we wished to understand the effect of varying the number of sites within the weekly format. We used the input $\phi_d = 0.8$ and had sites varying such that $S = \{100, 200, 500, 1000\}$. Figure 9 shows how the precision of the lifespan changes with the number of sites.

Again there is an improvement in the precision but as the lifespan is < 7 days the accuracy remains biased. The RMSE was 0.0884, 0.0721, 0.0537 and 0.0532 when increasing the number of sites from 100 to 1000 respectively. As with fitting the daily format model there is a plateau around 500 sites and increasing the number of sites further does not result in improvements to the precision.

| Abundance trend confidence intervals

To obtain the 95% confidence intervals for the abundance indices we can not use the Hessian as we perform multiple stages in the analysis. We instead decided to obtain the 95% confidence intervals by performing a simulation based approach for propagating uncertainty. We used this method instead of the bootstrap as this took a long time to calcu-

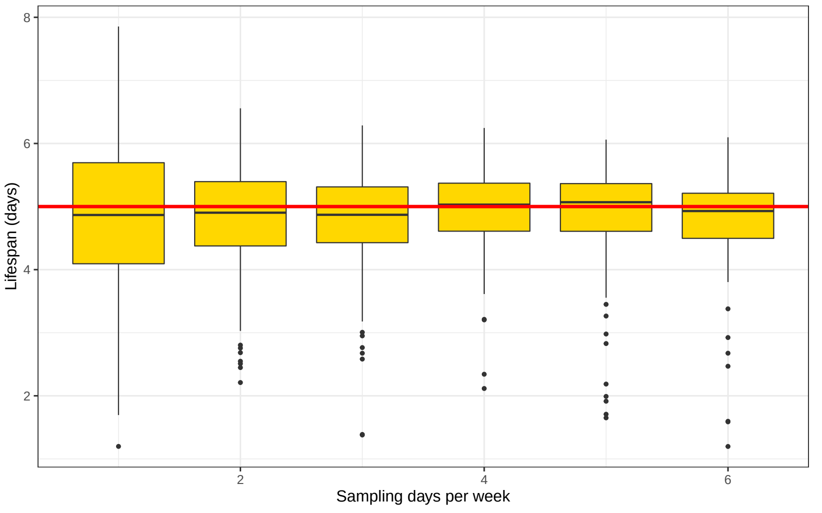

FIGURE 7 Derived lifespan estimates ($\hat{\Lambda}$) across 250 simulation runs when fitting the daily model with input $\phi_d = 0.8$ when varying the number of days per week that sampling occurs. The relationship $\hat{\Lambda} = \frac{1}{1-\hat{\phi}_d}$ was used to obtain lifespan values. The red line indicates the expected lifespan of $\Lambda = 5$.

late with the stages used to obtain the indices, from the GAI and then the GLM. The method makes the assumption that the parameters have a sampling distribution that is Normal, rather than using the bootstrap to obtain the sampling distribution. The stages of the method are detailed below. We carry out 250 iterations of our method to obtain the measure of uncertainty.

1. Obtain the MLEs from GAI model.
2. Obtain the variance-covariance matrix of the estimated parameters by calculating the inverse of the Hessian for the model.
3. Using the MLEs and the variance-covariance matrix from the model we produce 250 new parameter values by randomly sampling from a multivariate Normal distribution, with mean given by the vector of MLEs and variance given by the variance-covariance matrix.
4. Calculate the value of $N_{i,k}$ for each set of parameter values computed at stage 3.
5. Fit the GLM to the estimated $N_{i,k}$ values.
6. Obtain the abundance indices for each set of parameter values from the estimated year coefficients.

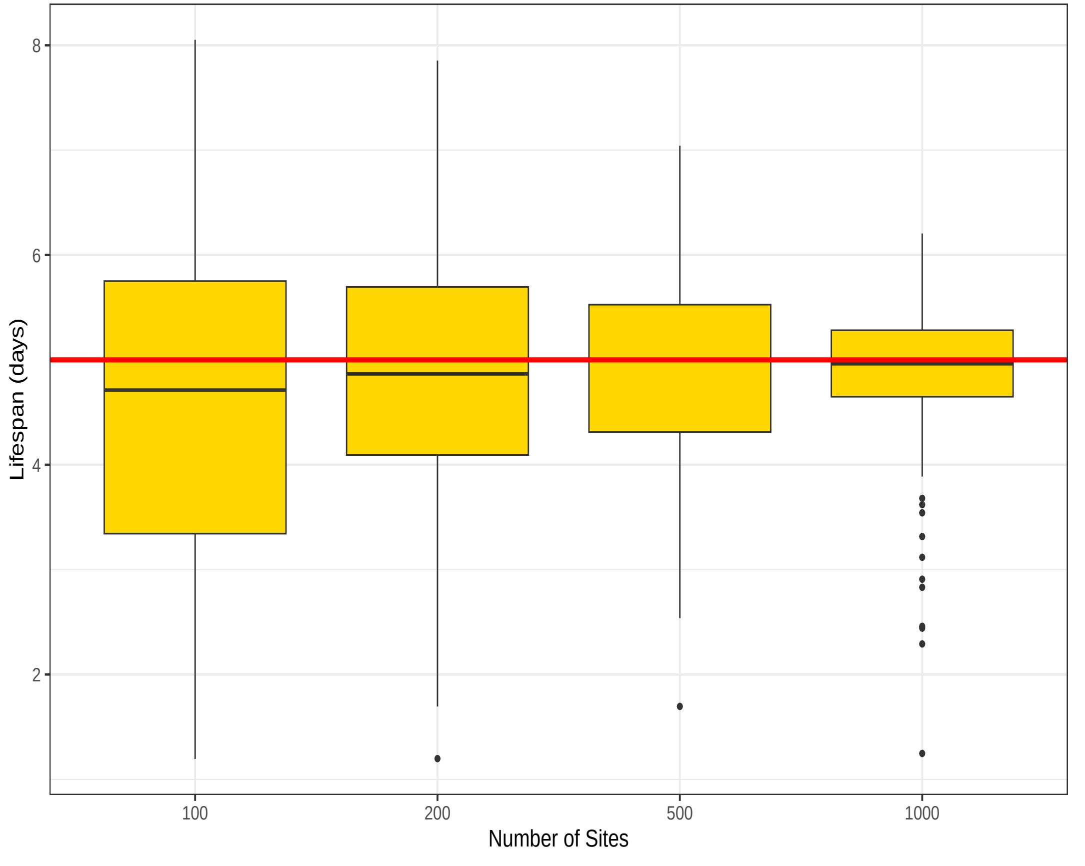

FIGURE 8 Derived lifespan estimates ($\hat{\Lambda}$) across 250 simulation runs when fitting the daily model with input $\phi_d = 0.8$ when varying the number of sites $S = \{100, 200, 500, 1000\}$. The relationship $\hat{\phi}_w = \hat{\phi}_d^7$ was used, as well as $\hat{\Lambda} = \frac{1}{1-\hat{\phi}_d}$. The red line indicates the expected lifespan of $\Lambda = 5$.

7. Place a linear trend through these indices and using the slope estimate calculate annual growth rate for each sampled dataset.
8. Report the 95% quantiles of the annual growth rate across the 250 iterations.

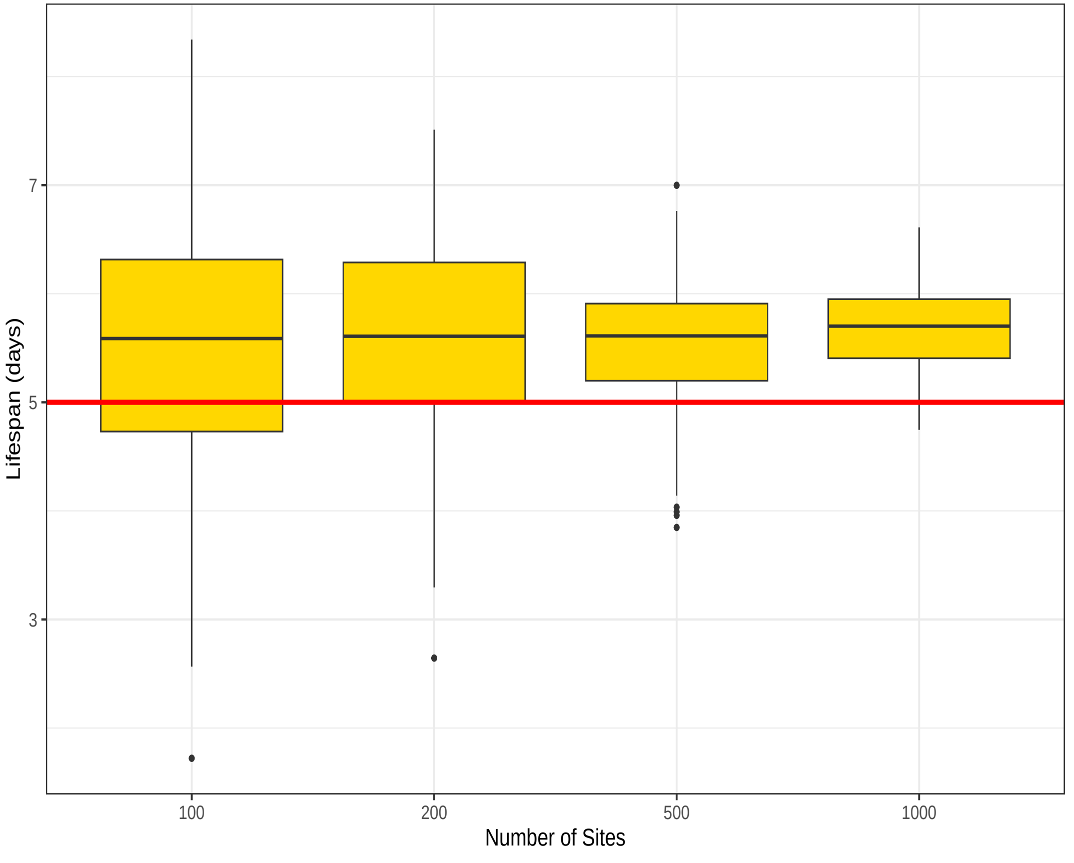

FIGURE 9 Derived lifespan ($\hat{\Lambda}$) estimates across 250 simulation runs when fitting the weekly model with input $\phi_d = 0.8$ when varying the number of sites. The relationship $\hat{\phi}_w = \hat{\phi}_d^7$ was used, as well as $\hat{\Lambda} = \frac{1}{1-\hat{\phi}_d}$. The red line indicates the expected lifespan of $\Lambda = 5$.