Extended molt phenology models improve inferences about molt duration and timing

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ABSTRACT

Molt is an essential life-history event in birds and many mammals, as maintenance of feathers and fur is critical for survival. Despite this molt remains an understudied life-history event. Non-standard statistical techniques are required to estimate the phenology of molt from observations of plumage or pelage state, and existing molt phenology models have strict sampling requirements that can be difficult to meet under real-world conditions. We present an extended modelling framework that can accommodate features of real-world molt datasets, such as re-encounters of individuals, misclassified molt states, and/or molt state-dependent sampling bias. We demonstrate that such features can lead to biased inferences when using existing molt phenology models, and show that our model extensions can improve inferences about molt phenology under a wide range of sampling conditions. We hope that our novel modelling framework removes barriers for modelling molt phenology data from real-world datasets and thereby further facilitates the uptake of appropriate statistical methods for such data. Although we focus on molt, the modelling framework is applicable to other phenological processes that can be recorded using either ordered categories or approximately linear progress scores.

Keywords: Bayesian inference, individual heterogeneity, mark–recapture, molt, pelage phenology, plumage

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LAY SUMMARY

• Molt is an essential but understudied life-history event in birds and many mammals.
• The analysis of molt data requires non-standard statistical techniques and existing molt phenology models have strict sampling requirements that can be difficult to meet.
• We present new statistical models for molt timing and duration.
• We demonstrate that these models improve inferences about molt duration and timing under a wide range of realistic sampling conditions.

Los modelos extendidos de fenología de la muda mejoran las inferencias sobre la duración y el momento de la muda

RESUMEN

La muda es un evento esencial en la historia de vida de las aves y de muchos mamíferos, ya que el mantenimiento de las plumas y del pelaje es crucial para la supervivencia. A pesar de esto, la muda sigue siendo un evento de la historia de vida poco estudiado. Se requieren técnicas estadísticas no convencionales para estimar la fenología de la muda a partir de observaciones del estado del plumaje o pelaje, y los modelos de fenología de la muda existentes tienen requisitos estrictos de muestreo que pueden ser difíciles de cumplir en condiciones del mundo real. Presentamos un marco de modelado extendido que puede adaptarse a las características de los sets de datos de la muda del mundo real, como reencuentros de individuos, estados de la muda mal clasificados y/o sesgo de muestreo dependiente del estado de la muda. Demostramos que tales características pueden llevar a inferencias sesgadas al usar modelos existentes de fenología de la muda, y presentamos cómo nuestras extensiones del modelo pueden mejorar las inferencias sobre la fenología de la muda en una amplia gama de condiciones de muestreo. Esperamos que nuestro nuevo marco de modelado elimine las barreras existentes para modelar los datos de fenología de la muda de los sets de datos del mundo real y, de esta manera, facilite aún más la adopción de métodos estadísticos apropiados para tales datos. Aunque nos centramos en la muda, el marco de modelado es aplicable a otros procesos fenológicos que pueden registrarse mediante categorías ordenadas o clasificaciones de progreso aproximadamente lineales.

Palabras clave: fenología del pelaje, heterogeneidad individual, inferencia bayesiana, marca-recaptura, muda, plumaje
INTRODUCTION

All birds and most mammals rely on feathers and fur, respectively, to deliver critical functions such as thermoregulation (Wolf and Walsberg 2000, Dawson et al. 2014), social signaling and crypsis (Caro 2005, McQueen et al. 2019), or flight (Matloff et al. 2020). Plumage and pelage are non-living keratinous structures subject to continuous wear and, therefore, must be replaced regularly through shedding and regrowth, a replacement process known as molt (Ling 1972, Newton 2009). Molt is an essential life-history event, which—unlike breeding—cannot be skipped, as the maintenance of pelage or plumage is necessary for survival (Ling 1970, Jenni and Winkler 2020). Birds and mammals have evolved a bewildering array of strategies to balance the molt process with demands imposed by breeding and migration (Beltran et al. 2018). Despite this, many aspects of the biology of molt, including environmental and behavioral drivers of its timing, extent and rate, remain poorly known (Bridge 2011, Marra et al. 2015), even though they may hold crucial clues to understanding animals’ responses to a changing environment (Tomotani et al. 2018, Zimova et al. 2020b, Kock et al. 2021, Hamner et al. 2022).

Phenology, the timing of seasonal biological phenomena, is a key aspect of plant and animal life. It defines the timing and duration of life-cycle events and thereby determines the ability of organisms to capture seasonally variable resources (Chuine and Régnière 2017). Phenological analyses often focus on the timing of particular life-history events, such as the dates of egg laying (Shutt et al. 2019) or parturition (Moyes et al. 2011). However, for many biological phenomena, including molt, exact dates of particular events are more difficult to observe than the state of the system itself. In most studies of free-living animal populations, the initiation, progression, and completion of molt cannot be observed fully in individuals. Rather, observations generally consist of snapshots of individuals that have old plumage or pelage, are in some stage of active molt, or have new plumage or pelage. Transition dates and the duration of molt in the population then have to be inferred from such data and this generally precludes the use of simple linear regression methods.

As an additional complication, the observation of molt in the field can vary both in terms of which stages of the population can be sampled and how molt progress is recorded. For birds, two main types of recording systems exist for molt status (Dolnik and Gavrilov 1974, Ginn and Melville 1983): a simpler, qualitative type records molt status as a categorical variable (not started, in progress/active molt, completed), whereas a more quantitative type records the progression of individual feathers or feather tracts for birds in the active molt category. The latter is commonly scored in the field using a 6-point scale where 0 is an old unmolted feather and scores 1 to 5 represent stages of feather growth from the shedding of the old feather to a fully grown new feather (Ginn and Melville 1983). The sum of the primary feather scores for one wing (a scale of 0–45 or 50 for most passerine birds, which have 9–10 fully developed primary feathers) gives a quantitative measure of overall molt progression. Where feathers differ in size, raw molt scores do not necessarily increase linearly with time, which may be ameliorated by converting raw scores into the proportion of new primary feather mass grown (PFMG), using feather specific masses (Underhill and Joubert 1995, Bonnevie 2010b). In mammals, molt progress is typically described as the proportion of the molted body surface, often recorded under field conditions in a simplified manner as ordered categories that may or may not represent equal intervals of molt progress (Watson 1963, Beltran et al. 2019, Zimova et al. 2020a, Kock et al. 2021).

Underhill and Zucchini (1988) proposed a general modeling framework for both categorical and molt score data, applicable to species with a continuous molt strategy. Maximum likelihood inference for these models is implemented in the moult package for R (Erni et al. 2013). For categorical molt data, an approach based on the probit model was subsequently suggested by Rothery and Newton (2002), which can be implemented in general purpose linear model software. Both approaches for categorical molt data are special cases of ordinal regression models (Bürkner and Vuorre 2019), and are closely related to phenological models developed for specific applications across various ecological disciplines (Dennis et al. 1986, Candy 1991, Zimova et al. 2020b, Boersch-Supan 2021b), whereas the model for continuous score data has parallels to censored regression models such as the tobit model (Twisk and Rijmen 2009).

Underhill-Zucchini molt models assume that any variation in the molt duration can be modelled using covariates, that the times of molt onset follow a specified probability distribution, and, importantly, that individuals caught on each sampling occasion are a random sample of the modelled population. The latter implies that sampling probabilities need to be independent of molt stage and homogeneous for all individuals within each molt stage. This homogeneous sampling assumption is critical, as violations of it can lead to biased parameter estimates, as demonstrated by Bonnevie (2010a) and in the simulation studies below, and ultimately biased ecological conclusions.

However, the assumptions underlying the Underhill-Zucchini molt models, in particular with respect to random sampling across molt stages, can be difficult to meet with real-world molt data. This is a consequence of the complexities of molt itself as a biological process, as well as the vagaries of obtaining molt data in the field. In particular, uneven sampling across molt state is common in real-world molt data sets. This can have biological reasons, as individuals in peak molt are often restricted in their ability to move and may therefore have a different detectability than non-molting individuals. For example, molting birds may be more cryptic than non-molting birds (Newton 1966, Haukojoa 1971), whereas molting pinnipeds may be easier to observe at a haul-out than mobile non-molting individuals (Watts 1996). Alternatively, uneven sampling can result from the data collection process (e.g., when molt data arises from opportunistic ringing schemes with irregular sampling schedules). As a possible result of this, ad hoc statistical approaches have remained common in the analysis of molt data (Beltran et al. 2019, Kock et al. 2021, Mumme et al. 2021b). The lack of formal molt models which can simultaneously estimate the full phenological distribution of molt and accommodate imperfect real-world data limits the inferences that can be drawn about physiological, environmental, and behavioural drivers of the timing, extent and rate of molt and ultimately the drivers of animals’ annual cycles.

We present extensions to Underhill-Zucchini molt phenology models by using a Bayesian inference framework for parameter estimation that facilitates the analysis of real-world
molt data and improves inferences about molt duration and timing under a wide range of realistic sampling conditions. Although devised for avian primary feather molt, this modelling framework is applicable to all phenological processes that can be recorded using either ordered categories or approximately linear progress scores between well-defined start and end states.

METHODS

Molt Model Types

Five Underhill-Zucchini model types are distinguished depending on the molt data type (categorical or score) and the stages of molt that are sampled across the population (Underhill and Zucchini 1988, Underhill et al. 1990): The type 1 model is for purely categorical observations (molt not started, molt in progress/active molt, molt completed), whereas model types 2–5 require molt scores for all actively molting individuals. Type 1 (categorical) and type 2 models further require that pre-molt, molt, and post-molt individuals are all sampled. The type 3 model requires samples of active molt individuals only; whereas type 4 and 5 models were motivated by species that molt immediately before or after migration and are therefore not observable across all 3 molt categories (Table 1).

Basic Likelihood Functions for Different Data Types

Data likelihoods for Underhill-Zucchini models follow a modular structure. Following the notation of Underhill and Zucchini (1988), samples consist of pre-molt individuals (l), individuals in active molt (j), and post-molt individuals (k). Individuals in each category are observed on days \( t = t_1, \ldots, t_l \); \( u = u_1, \ldots, u_l; v = v_1, \ldots, v_k \), respectively. Molt scores for actively molting individuals, where available, are encoded as \( y = y_1, \ldots, y_j \).

For a given date \( t \), each molt state has a probability of occurrence

\[
P(t) = \Pr(Y(t) = 0) = 1 - F_T(t)
\]

\[
Q(t) = \Pr(0 < Y(t) < 1) = F_T(t) - F_T(t - \tau)
\]

\[
R(t) = \Pr(Y(t) = 1) = F_T(t - \tau)
\]

where \( F_T \) is the cumulative probability function of the molt initiation dates of individuals in the population, and \( \tau \) is the mean duration of molt in the population. Note that in the notation of Underhill and Zucchini (1988) \( t \) is doubly defined. It is both a generic variable of time in the model derivation, and when indexed, denotes the sample dates of pre-molt birds in the data likelihoods. Further, assuming a linear progression of the molt indices over time, the probability density of a particular molt score at time \( t \) is

\[
q(t,y) = f_T(t) \phi(t) = \frac{1}{\sqrt{2\pi \sigma^2}} e^{-\frac{(t - \mu)^2}{2\sigma^2}}, \quad 0 < y < 1
\]

In existing implementations, the unobserved molt start dates of individuals in the study population are assumed to follow a normal distribution with mean molt start date \( \mu \) and population standard deviation of molt start dates \( \sigma \), such that

\[
F_T(t) = \Phi \left( \frac{t - \mu}{\sigma} \right)
\]

where \( \Phi \) is the standard normal distribution function and

\[
f_T(t) = \phi(t) = \frac{1}{\sqrt{2\pi}} e^{-\frac{t^2}{2}}.
\]

It is further assumed that the likelihood has \( p \) parameters \( \theta = (\theta_1, \theta_2, \ldots, \theta_p) \). If there are no covariate data, then \( p = 3 \) and \( \theta = (\mu, \tau, \sigma) \). Otherwise, the effect of covariates on the molt parameters can be modelled using linear predictors on \( \mu \) and \( \tau \), and log-linear predictors on \( \sigma \) (Erni et al. 2013), that is,

\[
\mu = \mu_0 + X_u \beta_u
\]

\[
\tau = \tau_0 + X_T \beta_T
\]

\[
\sigma = \exp(\sigma_0 + X_\sigma \beta_\sigma)
\]

and consequently \( \theta = (\mu_0, \beta_u, \tau_0, \beta_T, \sigma_0, \beta_\sigma) \).

Full likelihood expressions for model types 1–5, which represent typical combinations of available molt records are given in Supplementary Material F. Molt parameters for model types 1–5 can be estimated using a maximum likelihood approach implemented in R package moult (Erni et al. 2013). We here also introduce a Bayesian estimation approach using fast Hamiltonian Monte Carlo samplers (Carpenter et al. 2017), which is implemented in R package moultmcmc (Boersch-Supan et al. 2023a). Further details of the software implementation and installation instructions are provided in Supplementary Material A. A joint likelihood for data of types 1 and 2 is straightforward to derive by combining the types 1 and 2 data likelihoods, as outlined by Underhill and Zucchini (1988), and this integrated type 12 model (T12; Supplementary Material F) is also implemented in moultmcmc.

Extensions to the Underhill-Zucchini framework

We propose extensions to the Underhill-Zucchini modelling framework to address 2 features of real-world molt data: the misclassification of non-molting individuals, and the presence of molt status-dependent sampling bias. These methods are implemented in the R package moultmcmc (Boersch-Supan et al. 2023a).

Misclassification of non-molting individuals: The lumped molt model

In birds, active primary molt is generally unambiguously identifiable on a specimen, but the distinction between the two non-molting categories can be more challenging, both conceptually

| Model type | Pre-molt     | Molt         | Post-molt   |
|------------|--------------|--------------|-------------|
| 1          | Categorical0 | Categorical  | Categorical1|
| 2          | Categorical0 | Score (0,1)  | Categorical1|
| 3          | Not observed | Score (0,1)  | Not observed|
| 4          | Not observed | Score (0,1)  | Categorical1|
| 5          | Categorical0 | Score (0,1)  | Not observed|
| 12         | Categorical0 | Mix of categorical and score (0,1) | Categorical1 |

TABLE 1. Sampling situations and data types distinguished in the Underhill-Zucchini molt modelling framework.
and practically. The transition from old plumage to active primary molt, and the transition from active molt to new plumage are reasonably discrete, marked by the shedding of the first feather, and the completion of growth on the last, respectively. These transitions are conceptually straightforward, and the natural order of the categories across the molt process motivate the framing of these models as ordered categorical regression models. However, this conceptualisation ignores feather or fur wear between successive molt seasons (i.e., the gradual transition from new to old plumage or pelage following the completion of a molt cycle). This can make the assignment of non-molting individuals to pre-molt and post-molt categories ambiguous, both because wear can be difficult to assess, leading to misclassified data, and—when the molt season is long—individuals in worn and unworn stages can co-exist in the population (Craig et al. 2014), which is incongruous with the notion of linear time implied by the ordered categorical framework.

This classification problem can be sidestepped by distinguishing only two categories of individuals: molting and non-molting individuals. The probability of occurrence for the former is the same as in the standard model (i.e., Q(t), Equation (2) and/or q(t), Equation (4)). The probability of the latter then follows from Equations (1) to (3) as

\[ PR(t) = 1 - Q(t) = P(t) + R(t) \]  

(10)

Because the two non-molting categories are treated as indistinguishable, we refer to this model variant as the lumped model below, and denote it with the letter L in abbreviations (e.g., the lumped type 2 model [T2L]).

Repeated measures data: The recaptures model

A large amount of avian molt data is collected in conjunction with bird ringing (Ginn and Melville 1983, Rose et al. 2020), and as a result mark-recapture information may be available for the individuals for which molt status is recorded. Similarly, many demographic studies of mammals use marks and can therefore record repeat observations of individual's molt status (Zimova et al. 2022). Repeat observations can provide direct observations of the speed of molt in an individual (Underhill and Zucchini 1988; Underhill-Zucchini model estimates the distribution of molt start dates in a population. It is therefore conceptually straightforward to accommodate repeat measures of individuals by treating individual-level molt start dates as random intercepts that follow that very distribution.

We propose a recaptures model which allows for heterogeneity in start dates \( \mu_s \) but assumes a common molt duration \( \tau \). We focus here on models for continuous molt score data (types 2–5), as even small numbers of recaptures can provide a large amount of information.

Following Equation (7) an individual's start date \( \mu_s \) then becomes

\[ \mu_s = \mu_0 + \mu'_s + X_{s,\mu} \beta_{\mu} \]  

(11)

where \( X_{s,\mu} \) is a row vector containing the values of individual-specific predictors (in the same format as \( X_{s,\mu} \)), and \( \mu'_s \) is an individual-level random effect intercept

\[ \mu'_s \sim \text{Normal}(0, \sigma_s) \]  

(12)

where \( \sigma_s \) is the individual-specific standard deviation defined in Equation (9). When repeated molt score measurements of the same individual are available during active molt, we can exploit the linearity assumption and analogous to Equation (4) treat observed molt scores \( y_{ni} \) on dates \( t_{ni} \) as

\[ y_{ni} \sim \text{Normal}(\mu_n + \mu'_n + \gamma_{ni} \tau, \sigma_i) \]  

(13)

where \( i \) indexes the \( i \)th observation on individual \( n \), and \( \sigma_i \) captures any unmodelled variance in \( \tau \) as well as any measurement error in \( y \). While recaptures within the non-molting categories hold little additional information value, recaptures across molt categories can provide additional information (Wang 2020), and the corresponding likelihoods for non-molt observations are based on the relevant cumulative distribution functions (Equations (1) and (3); Twisk and Rijmen 2009). We refer to this model variant as the recaptures model below, and denote it with the letter R in abbreviations (e.g., the type 2 recaptures model [T2R]). The recaptures framework conceptually extends to the type 1 model for categorical molt data; however, exploratory simulations for this study demonstrated that the type 1 recaptures model typically requires a large number of recaptures per individual to be well identified (P.B.-S. personal observation). This is in agreement with the general finding that parameter estimation in the type 1 model typically requires larger sample sizes than estimation in model types using continuous molt scores (Boersch-Supan 2021a).

Simulation Studies

We use simulation studies, motivated by real-world data, to demonstrate when violations of the standard molt models lead to biased inferences, and to demonstrate that our extensions of the Underhill-Zucchini modelling framework are useful to improve inferences in these conditions. We use relative bias compared to the simulated parameter values, and coefficient of variation (CV) of the posterior estimate as measures of accuracy and precision, respectively. As the molt start date (day of year) is a circular variable, its absolute value and hence relative measures can be arbitrarily scaled. We therefore calculated bias and precision for this parameter relative to the reference value for the molt duration to obtain an ecologically meaningful measure.

Misclassification of non-molting individuals

This simulation study is motivated by a dataset presented by Erni et al. (2013), which features molt records of Southern Masked Weavers (Ploceus velatus) from the Western Cape region of South Africa. In this dataset birds in apparent new and apparent old plumage are recorded throughout the year, even though observations of active molt are reasonably well constrained to a six-month period. This results in biologically implausible inferences from the type 2 molt model, leading Erni et al. (2013) to recommend the use of the type 3 model, even though this model can suffer from weak identifiability, especially when the population standard deviation of the start date is large relative to the molt duration (Underhill and Zucchini 1988; Supplementary Material Figure 3).

We recreate this dataset by simulating molt records based on molt parameters for Southern Masked Weavers (start date = 14 January, duration = 75 days, start date SD = 29 days; Oschadleus 2005), and randomly misclassifying a pre-defined proportion of non-molt records (i.e., a subset...
of “old” records is changed to “new” and vice versa). Each simulation was based on 156 randomly drawn sampling dates throughout the calendar year, with 7 capture events per sampling day, yielding 1,092 molt records per simulation. Sampling of the virtual population was without replacement, so each molt record originated from a unique virtual individual. We repeated this procedure for a total of 8 misclassification rates between 0 and 20%, and for 100 replicate simulations of the unmodified molt data. Molt parameters were then estimated from the simulated data using the T1, T1L, T2, T2L, and T3 models, and the obtained parameter estimates and their estimated precision were compared.

**Parameter estimation in the presence of molt-status dependent sampling bias**

Not accounting for uneven sampling can lead to biased inferences about molt parameters (Bonnevie 2010a). We demonstrate that information in recaptures of actively molting individuals can be exploited to overcome these biases, using 3 simulated data sets.

**Constant molt-dependent sampling bias**

The first set of simulations assumes that molting individuals have a lower capture probability than non-molting individuals, regardless of molt progress. We simulate a virtual population (molt start date = on year day 150, molt duration = 65 days, start date SD = 10 days) sampled on 104 days with 5 capture events per sampling day for a total of 520 molt records. Sampling of individuals was conducted with replacement and recapture rates of individuals were allowed to vary by varying the size of the virtual super-population between 50 and 1,000 individuals. To ensure an even spread of simulation scenarios across the simulation parameter space we used a Latin square approach (Carnell 2022) to create 100 sets of simulations where capture probabilities of molting individuals ranged between 0.1 and 1.0 relative to non-molting individuals, and recapture rates of individuals across the population ranged between 0 and 20%.

These parameters mean that within each resulting data set, there are on average between 2.1 and 10.4 observations per recaptured individual within a season. Molt parameters were then estimated from the simulated data using the T1, T1R, T2, and T2R models and compared to the corresponding simulation parameters. To visualize bias in the estimated molt parameters across the simulation parameter space we fitted generalized additive models of the general form relative bias in molt parameter ~ model type + te(recapture rate, relative capture probability, by = model type) where te() denotes a tensor product smooth with four degrees of freedom per dimension (Wood 2017). General additive model (GAM) predictions that were significantly different from zero were then plotted against the simulation parameters.

**Non-constant molt-dependent sampling bias**

In reality, sampling biases are likely to be more complex, as the impact of molt on individuals’ behavioral capabilities and/or detectabilities vary during the progress of active molt. For example, wing raggedness in birds (i.e., the size of the gap in the wing created by shed and incompletely regrown feathers; Bensch and Grahn 1993) is largest at intermediate molt progress, which implies that birds with intermediate molt scores are the least able to fly and hence potentially least likely to be captured. Such a bias towards records of birds in the early and late stages of molt is not uncommon in real-world molt datasets, and our second set of simulations emulates the sampling bias found in a citizen science dataset of molt scores from Eurasian Siskins (Spinus spinus; Insley et al. personal communication). The virtual population for this set of simulations (start date = year day 197, duration = 78 days, start date SD = 9) was sampled on 25 occasions between year day 150 and year day 300 with 30 capture events per occasion. Capture probabilities of simulated individuals were a function of their molt status (Supplementary Material Figure 1). This reflects the targeted sampling approach of the emulated real-world data set. Recapture rates were allowed to vary using the same Latin square approach as above, but we additionally explored the sensitivity of molt models to individual heterogeneity in the molt duration τ, by allowing individual-specific molt durations τi drawn from a Normal distribution with a coefficient of variation in the molt duration στ/τ between 0% and 10%. We used a total of 200 simulation scenarios with recapture rates of individuals across the population between 1% and 100% and an average of 2.0–13.4 observations per recaptured individual. Molt parameters were then estimated from the simulated data using the T3, T3R, T5, and TSR models and compared to the corresponding simulation parameters. Bias in the estimated molt parameters was interpolated across simulation scenarios using GAMs and visualized as described above.

**Mixed record types for active molt**

A third kind of sampling bias can arise when active molt is recorded in multiple ways. This case is motivated by the British and Irish Ringing Scheme (Raillie et al. 1999) which allows recording of active molt using the 6-point feather score scale as well as the simpler categorical markers. As a result, active molt records may consist of a mixture of categorical and score data, and excluding either data type to fit the type 1 or 2 model can affect the quantity of active molt records relative to non-molt records (as the latter can be converted from one scoring system to the other without loss of information). The third set of simulations therefore is based on datasets simulated as molt scores of which a pre-defined proportion of active molt score records are degraded to categorical molt records. Molt observations were simulated as for the misclassified records case, and simulated data sets were degraded by recoding between 0 and 100% of molt scores to categorical molt codes. Molt parameters were then estimated from the simulated data using the T1, T2, T3, and T12 models. We also fitted the type 2 model to data rebalanced by subsampling. For this we followed the approach proposed by Bonnevie (2010a), and randomly discarded non-molt records until the proportion of non-molt to active molt records matched the proportion of days inside and outside the expected molt period across the sampling period, based on established molt durations for the relevant target species. We denote parameter estimates from this approach T2S (type 2 subsampled). The obtained parameter estimates and their estimated precision were compared across all fitted models.

**Real-World Data Example: American Redstart Molt**

Having established the performance of the extended molt models using simulations, we briefly demonstrate that these models are also suitable for real-world datasets. For this
Bayesian inference for molt phenology models

Bayesian inference for molt phenology models

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purpose, we used primary molt data from American Redstart
(Setophaga ruticilla; Mumme et al. 2021a). These data were
collected during summer and fall banding operations, 1986–
2000, in southwestern Pennsylvania, USA. Details about the
data collection are given by Mumme et al. (2021b), who
noted that these data did not fulfill the assumptions underlying
standard Underhill-Zucchini models. The data consist of 428
sets of primary molt scores from 344 individuals, of which 42
individuals were captured at least twice within a single year.
The bulk of the molt scores are from individuals in active
molt; therefore, we used T3 and T3R models to analyze fea-
ther mass-corrected molt scores (Bonnevie 2010b) and com-
pared parameter estimates between the standard T3 model
and the recaptures T3R model. A worked example providing
R code for this analysis is included in the Supplementary
Material.

RESULTS

Bayesian estimation of molt parameters for standard molt
models provided comparable results to the existing max-
imum likelihood method by Erni et al. (2013) (Supplementary
Material B). The comparative performance of standard and
extended molt models under different sampling and recording
scenarios is detailed below.

Misclassification of Non-molting Individuals

Simulation results showed that estimates of the start date
standard deviation \( \sigma \) using the T1 and T2 models were biased
upwards when even a small proportion of non-molting
individuals was misclassified. Estimates of duration \( \tau \) were
initially less strongly affected, showing a small negative bias
under model T1 and negligible bias under model T2 for mis-
classification rates < 10%. However, beyond a misclassifi-
cation rate of 10% estimates from both models were positively
biased. Estimates of the start date \( \mu \) were increasingly nega-
tively biased with increasing misclassification rates. Estimates
of all parameters obtained from both lumped model types
T1L and T2L, and the T3 model (which ignores no-molt
records) were unbiased (Figure 1A). Lumped models (T1L,
T2L) offered slightly poorer precision than their unlumped
equivalents in the absence of misclassification, but their pre-
cision was otherwise unaffected by the degree of misclassifi-
cation, and in all cases their precision was better than that of
the corresponding T3 model (Figure 1B).

Constant Molt Dependent Sampling Bias

Simulation results showed that estimates of all parameters
from the T1 and T2 models were affected when the sampling
probability of molting individuals dropped below 50–75%
relative to non-molting individuals (Figure 2). The type 2
recapture model (T2R) was able to overcome this bias, but
the stronger the sampling bias, the more individuals with re-
captures during active molt were needed to obtain unbiased
parameter estimates. Parameter estimates were generally un-
biased whenever active-molt recaptures from 10 or more indi-
viduals were available. Gains from using the type 1 recaptures
model (T1R) were negligible for recapture rates comparable
to typical mark-recapture datasets obtained from physical

FIGURE 1. (A) Even a small proportion of misclassified non-molting individuals can bias parameter estimates from the standard types 1 and 2 models. The type 3, and lumped type 2 models offer unbiased estimates in the presence of misclassification. (B) Among the unbiased models, the lumped type 2 model provides more precise estimates compared to the standard type 3 model, which only takes actively molting individuals into account. Points show mean estimates for 100 simulation runs.
capture methods, although the T1R model outperformed the standard T1 model at high individual recapture rates (Supplementary Material D).

Non-Constant Molt Dependent Sampling Bias

Using simulated data with a similar sampling bias to a real-world dataset we further demonstrate that inferences from the recaptures model were much less biased than inferences from the standard model, and that bias decreased with an increasing proportion of individuals with repeated observations during active molt (Figure 3). Parameter estimates for were generally unbiased whenever active-molt recaptures from 5 or more individuals were available for the T3R model, and 10 or more individuals for the T5R model. We also show that unmodelled individual heterogeneity in the molt duration \( \tau \) exacerbated biases and that the proportion of individuals with recaptures required to obtain unbiased parameter estimates approximately doubled when the unmodelled variation in the molt duration increased from 0 to 10%.

Mixed Record Types for Active Molt

Discarding molt records with incomplete active molt scores can lead to similar parameter biases in the T2 model as biased sampling of molting individuals. Simulation results showed that the re-balancing through subsampling allows unbiased estimates from the T2 model (Figure 4A), but the precision of those estimates suffers because subsampling reduces the sample size available to the model (Figure 4B). Using all available data by including categorical molt records allows unbiased inferences with a precision that is at least as good, if not better than the corresponding T1 model (Figure 4).

Real-World Data Example: American Redstart Molt

As noted by Mumme et al. (2021b), the American Redstart data do not fulfill the assumption of homogeneous capture probabilities, as individuals at intermediate molt progress are underrepresented in the data (Figure 5A). As a consequence a naive T3 fit to the data yields biologically non-sensical parameter estimates, with an estimated molt duration of 14.3 days.

![Figure 2](image-url)
Bayesian inference for molt phenology models

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(95% confidence interval [CI]: 10.8–20.4), and a molt start date on July 15 (year day 196; 95% CI: 193–199), well after most observed birds have commenced molt, and a population standard deviation of the start date of 6.99 days (6.30–8.22; Figure 5B, C). As a consequence, the estimated 95% molt interval (i.e., the time interval in which 95% of the population are expected to be in active molt, defined as the polygon bounded by the mean molt trajectory ± $1.96 \times$ Start date SD; orange shaded area in Figure 5C) only encapsulates a fraction of the observed molt records. In contrast, the T3R recaptures model estimates a molt duration of 39.3 days (37.3–41.1), a mean start date on July 3 (year day 184; 95% CI: 183–185), and a population standard deviation of the start date of 10.8 days (9.98–11.8; Figure 5B, C). The corresponding 95% molt interval (blue shaded area in Figure 5C) encapsulates the majority of observations, suggesting a much more appropriate model fit. The T3R estimates also show good agreement with the estimates for molt duration and midpoint of primary molt reported by Mumme et al. (2021b) (Table 2).

DISCUSSION

Understanding the mechanisms underlying the timing and duration of molt and its position in the annual cycle is crucial to understanding birds’ and mammals’ responses to a changing environment (Watson 1963, Hällfors et al. 2020, Hanmer et al. 2022). Our work contributes to this goal by expanding existing molt models, in particular by adding the option of exploiting information contained in mark–recapture data. This allows a relaxation of assumptions about random sampling of molting individuals which are inherent in existing molt models, but are often difficult to meet under field conditions. We demonstrate that violations of the assumptions of standard molt models can lead to biased inferences about molt phenology. The extended models we present here are more robust to non-random sampling of individuals, and thus allow better inferences about molt phenology from imperfect, real-world datasets.

Our extended molt models are particularly useful when repeated sampling of individuals is possible, which has
important consequences for the design of molt phenology studies. As avian molt observations are often collected in conjunction with ringing, the identification of recaptured individuals is in principle possible, and although within-season recaptures are generally rare in avian molt datasets (Ginn and Melville 1983; Rose et al. 2020, Mumme et al. 2021b), we demonstrate both through simulation and with a real-world dataset that even a small number of recaptured individuals can drastically improve the accuracy and precision of molt parameter estimates. In the case of the real-world American Redstart example, our molt parameter estimates from the extended Underhill-Zucchini are similar to the estimates derived by Mumme et al. (2021b) using information from the recaptures alone for the molt duration, and an ad-hoc approach to estimate the molt start date (Table 2). However, unlike the ad-hoc approach, our extended Underhill-Zucchini model estimates the molt start date, its population standard deviation, and the molt duration simultaneously and therefore consistently estimates the correlated uncertainties in these 3 parameters. Robustly estimating the 3 parameters is important when trying to understand population-level changes in the phenology of molt, as changes in the full phenological distribution of molt at the population-level can arise from both individual-level and population level effects that may have different mechanistic drivers and/or consequences for intra- and interspecific ecological interactions (Hällfors et al. 2020, Hanmer et al. 2022, Macphie et al. 2023). Additional applications of both the lumped and recaptures molt models to real-world data are presented in Boersch-Supan et al. (2023b), who demonstrate that these models can address uncertainty about the assignment of non-molting birds, and that even small proportions of recaptures (~1% of ~4,300 captured individuals) can sufficiently constrain molt models to improve parameter precision and mitigate against parameter biases caused by uneven sampling. Further empirical research is required to better understand how much recapture data is required to overcome molt-status dependent sampling biases. A key requirement for robust inferences about molt durations and start dates using the recaptures models is to estimate both the duration parameter and the population standard deviation of the start date well. Our simulations demonstrated that this can be the case with within-molt recaptures from as few as 5–10 individuals; however, larger sample sizes are required when unmodelled individual heterogeneity in the molt duration is present. Additionally, while our modelling approach addresses heterogeneity in capture probabilities with respect to molt status, it relies—as many mark–recapture methods—on the assumption that (re)captured individuals are representative of the sampled population as a whole (Nichols et al. 1984, Cubaynes et al. 2010, Abadi et al. 2013). This assumption (i.e., that all individuals of a certain molt status are equally catchable) may not always hold, and it is therefore important to assess whether the sample of recaptured individuals differs in any potentially relevant characteristics from the sample of not recaptured individuals.

For practitioners collecting and analyzing real world molt data sets, we strongly suggest that (1) individual feather scores of all encountered molting and non-molting birds are recorded; (2) that encountered birds are marked and that a sampling design that aims to maximise the probability of recapturing a proportion of marked individuals within the active molt period is used; and (3) that any fitted model is visually checked (e.g., by plotting the 95% molt interval against the observations using the molt_plot function in the moultmcmc package). The molt interval represents the time interval in which 95% of the population are expected to be in active molt, and it is defined as the polygon bounded by the mean molt trajectory ± 1.96 × Start date SD (Figure 5C). This interval should encapsulate a large proportion of the observed molt records (albeit not necessarily 95% of the observations, as this interval is not strictly equivalent to the prediction interval of a linear regression model). For more formal comparisons, expected daily frequencies of molt observations under the model can be computed and compared with the observed frequencies following the approach outlined by Underhill and Zucchini (1988).

Less invasive re-encounter methods, such as camera trapping, may be limited to providing less information-rich categorical molt data, but at the same time such methods can provide sufficiently high recapture rates to identify individual-level molt parameters where individuals are identifiable. Such data are currently more common in mammalian systems (Zimova et al. 2020a), but may become increasingly available for birds (O’Brien and Kinnaird 2008, Pyle 2022).

Although our study focusses on molt, the modelling framework we present is applicable to a wide range of ontogenetic and/or seasonal life-cycle transitions across many animal and plant taxa, as long as they can be recorded using either ordered categories or approximately linear progress scores between well-defined start and end states (Gosner 1960, Lancashire et al. 1991, Redfern 2010). As a consequence of this linearity assumption our models therefore do not currently address
more complex life-cycle transitions, such as—in the avian molt context—arrested molt, suspended molt, partial molt or Staffelmauser. However, our modelling framework is in principle further extendable to address these more complex phenomena, e.g., analogous to phenology models applied to invertebrate life-cycles (Candy 1991), albeit at the expense of estimating additional parameters. Our implementation of the recaptures models further assumes that all heterogeneity in molt duration is captured by relevant covariates (i.e., we do not allow for the separate estimation of the population variation in the molt duration and individual variation in the molt duration, and/or measurement errors in the molt scores of recaptured individuals—these quantities are confounded in the $\sigma_\tau$ parameter). Models to separately estimate these quantities can be derived in principle (Wang 2020), but robust parameter estimation, particularly in the presence of measurement error, requires much higher numbers of within-season recaptures per individual (ideally $\gg 3$) than we believe are achievable for most molt studies in wild bird populations, given that it is exceedingly rare that more than two within-season recaptures per individual are recorded in real-world molt data sets (Ginn and Melville 1983, Rose et al. 2020, Mumme et al. 2021b, Boersch-Supan et al. 2023b). Improved inferences about molt and other life-cycle events do not only allow for a better understanding of phenological cycles per se, but also processes linked to them, such as disease dynamics (Benedict et al. 2023), as well as informing the timing of conservation and management actions (Brom et al. 2023). We hope that our model extensions and their implementation in the R package moultmcmc (Boersch-Supan et al. 2023a) will continue to lower the hurdle of applying phenological models to empirical data describing molt and other life-cycle events.

**Supplementary material**

Supplementary material is available at Ornithology online.

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**Ethical statement**

This research was conducted in compliance with the British Trust for Ornithology’s Code of Good Scientific Practice.

**Conflict of interest statement**

The authors declare no competing interests.
Author contributions

P.H.B.S. and R.A.R. conceived the study; P.H.B.S. led model development, analysis, and writing with input from all authors; H.J.H. contributed to model testing; all authors contributed critically to the manuscript and gave final approval for publication.

Data availability

Data and code for the simulation and case studies are available at Boersch-Supan et al. (2024).

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