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Markov chain estimation of avian seasonal fecundity

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Abstract. Avian seasonal fecundity is of interest from evolutionary, ecological, and conservation perspectives. However, direct estimation of seasonal fecundity is difficult, especially with multi-brooded birds, and models representing the renesting and quitting processes are usually required. To explore the consequences of modeling decisions on inference about avian seasonal fecundity, we generalize previous Markov chain (MC) models of avian nest success to formulate two different MC models of avian seasonal fecundity that represent two different ways to model renesting decisions and breeding cessation. We parameterize both Markov chains (regular and absorbing) for two species (Eastern Meadowlark, *Sturnella magna*, and Dickcissel, *Spiza americana*) and compare the results using mean-square error of the estimated number of successful broods per breeding female. We also provide formulae for estimating the expected variation in female breeding success. The absorbing MC performed better for both species, although the regular MC performed almost as well when the duration of the breeding season was estimated by taking the 95th percentile of a negative binomial distribution fit to the observed durations among all females. In their simplest form the models contain very few parameters (four or five) and should also prove useful as a foundation for more complex models of avian seasonal fecundity and demography.

Key words: avian seasonal fecundity; Dickcissel; Eastern Meadowlark; Markov chain; multiple-brooded birds; nest success; *Spiza americana*; *Sturnella magna*.

INTRODUCTION

Avian seasonal fecundity can be estimated by following a cohort of females over the course of a full breeding season and dividing the number of offspring produced by the number of females that produced them (Murray 1991, Powell et al. 1999). However, cost and logistical constraints typically preclude direct estimation of fecundity, so modeling approaches that use field data, previously published data on the same or similar species, and careful assumptions, are often required (Pease and Grzybowski 1995, Powell et al. 1999, Mattson and Cooper 2007). For multi-brooded songbirds, the information required to parameterize such models includes nest survival rates, numbers of young produced per successful nest, and an estimate of the number of nesting attempts that a typical female will make during the course of a breeding season (Thompson et al. 2001).

Often, the number of nest attempts that a female will make is either poorly estimated or unknown and a biologically reasonable fixed number (or maximum) of total or successful nests is posited instead (Schmidt and Whelan 1999). Grzybowski and Pease (2005) showed that this may result in biased estimates of seasonal

fecundity and unrealistically long breeding seasons, and they advocated the use of a strict temporal limit (hereafter T) on the length of the nesting season to impose an implicit limit on the number of nests a female can attempt. However, the use of a single estimate of T for all females may introduce error in estimates of seasonal fecundity if there is large variation in quitting dates among females. Furthermore, available values for T are generally not measures of central tendency but often calculated as the difference between extreme dates, for example the earliest and latest dates on which nests were known to be active, or with eggs. DeCecco et al. (2000) pointed out that estimates of T derived from extreme dates may overestimate the length of a typical breeding season, which, in turn, could result in overestimation of annual reproductive success.

Because females must begin nesting in the same state (e.g., egg-laying), the empirical brood accumulation function will show an initial pulse at the age at which nests typically fledge (Fig. 1, solid line), after which some females will initiate second broods and others that failed in the first attempt will succeed in subsequent attempts. If it is assumed that, prior to T , all females will attempt to reneest after either failure or fledging, then the simulated accumulation function may show an even stronger stepwise pattern (Fig. 1, dashed line) because the model does not allow for the possibility that some females will choose not to reneest. Nest failure will

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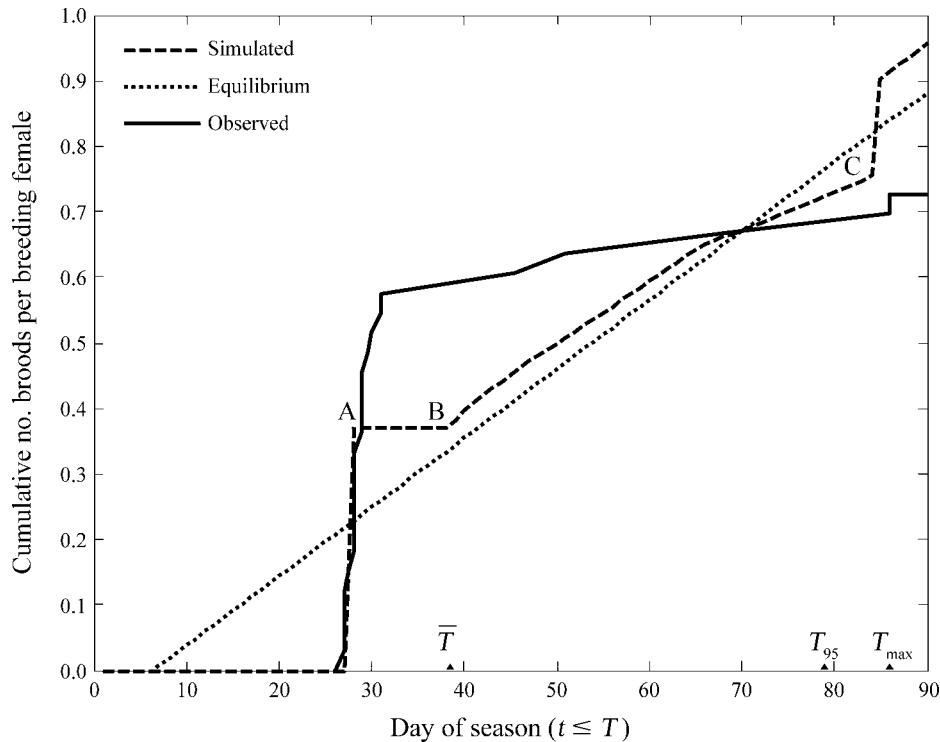


FIG. 1. Per-female accumulation of successful broods with season length under a regular Markov chain. The simulation plot (dashed line) exhibits qualitative jumps with each synchronized pulse of nest success. Labeled points indicate (A) pulse of first successful nests, followed by period of no growth until (B) females that failed in first attempt have had sufficient time to both initiate a new nest and succeed. Accumulation is then moderate until (C) the second pulse of nest success. Note that the sensitivity of the simulation model (the partial derivative of the dashed line with respect to time) of the number of successful broods produced will also depend strongly on the estimated value of breeding season length and ranges from close to zero (between points A and B) to near infinite (just prior to point A, just after point C). Each pulse of broods will be successively smaller until the accumulation function converges on the equilibrium value (dotted line, Eq. 5). This figure was generated using the regular MC (Eq. 4) with data from Eastern Meadowlark, *Sturnella magna* (Table 1). The solid line gives the observed brood accumulation function for Eastern Meadowlark. On the x -axis, variables are \bar{T} , mean breeding season length; T_{95} , 95th percentile of a negative binomial distribution fit to breeding season lengths; and T_{\max} , maximum breeding season length.

eventually result in an equilibrium probability distribution that a female is in any given state (egg-laying, incubation, brooding, post-failure, post-fledging) on any given day and the stepwise function will converge on a smooth, monotonically increasing function (Ricklefs 1970); see Fig. 1 (dotted line). However, the equilibrium is approached asymptotically and may not be representative of conditions at \hat{T} .

When seasonal fecundity is estimated using a mathematical model, we would also like to know how much confidence to place in the resulting estimate. Mattson and Cooper (2007) recently proposed an individual-based model of avian annual reproductive success that uses assumptions about the sampling distributions of input parameters to project variation in fecundity among females. Many previous modeling projects had also reported estimates of variation, whether in the form of confidence limits (DeCecco et al. 2000) or standard errors (Powell et al. 1999), and, although methods for obtaining these estimates of variation differ, the authors all seem to intend a similar interpretation to that of

Mattson and Cooper (2007), that their estimate of variation is a measure of the expected variation in projected seasonal fecundity among females. This differs from (and is likely to be much larger than) the sampling variance associated with any *given* estimate of expected seasonal fecundity, for which the estimated sampling variance conveys valuable information about the quality of the estimate and the associated field data used to generate it.

In this paper we describe a class of seasonal fecundity models based on Markov chain theory that is a natural extension of standard methods for estimating avian nest survival. In previous work we showed that common likelihood functions for estimating nest success (e.g., Johnson 1979) are special cases of a Markov chain, in which the states of fledging and failure are considered absorbing states (Etterson and Bennett 2005). Here we suggest that by changing the subject of the Markov chain to a breeding female, rather than a nest, and relaxing the assumption that fledging and failure are absorbing states, the nest survival models can be

TABLE 1. Numerical values (sampling variances) for all input parameters to both the absorbing and regular Markov chains.

Definition	Symbol	Eastern Meadowlark	Dickcissel
Daily nest survival probability	s	0.965 (0.00001)	0.950 (0.001)
Probability of quitting after a successful nest	q_s	0.67(0.011)	0.94 (0.003)
Probability of quitting after a failed nest	q_f	0.42 (0.013)	0.71 (0.007)
Days from first egg to fledging	a	28 (0.22)	22 (0.08)
Days from fledging to first egg of next nest	w_s	28 (24.3)	24 (24)
Days from failure to first egg of next nest	w_f	10 (5.5)	7 (0.81)
Mean breeding season length	\bar{T}	45 (14.6)	27 (5.7)
Maximum breeding season length	T_{\max}	93 ()	69 ()
95th percentile of a negative binomial distribution fit to breeding season lengths	T_{95}	86 (319)	49 (123)

Notes: Sampling variance for the maximum observed breeding season length (T_{\max}) is unknown. Therefore we substituted the sampling variance associated with the cumulative percentile of the fitted negative binomial distribution used for T_{95} , but evaluated at T_{\max} .

adapted to models of seasonal fecundity. We use two distinct classes of Markov chains, absorbing and regular (Kemeny and Snell 1983), to represent contrasting extremes for modeling seasonal breeding. The absorbing Markov chain (MC) contains quitting parameters that control the cessation process, whereas the regular MC requires temporal limits as a stopping rule.

To keep our treatment as simple as possible we use the MC models to estimate the expected number of successful broods produced per breeding female, b . To estimate seasonal fecundity, an estimate of b must be combined with information about the expected number of offspring per successful brood and the probability that a female breeds. Such information can be incorporated into the models, but it would lengthen and complicate our treatment without giving additional insight into stopping rules. We illustrate with two examples using data on Eastern Meadowlark, *Sturnella magna* (Kershner et al. 2004) and Dickcissel, *Spiza americana* (Walk et al. 2004). For each species we compare the performance of the absorbing MC to that of the regular MC, where the true value of b is taken to be the observed number of successful nests divided by the number of females that produced them. Thus the work we describe has four primary objectives: (1) to demonstrate the utility of Markov chain theory for modeling and analysis of seasonal fecundity, (2) to provide a flexible and robust statistical basis for fecundity estimation that can be incorporated in more general models of avian productivity and demography, (3) to provide worked examples of Markov chain model applications to questions about avian seasonal fecundity, and (4) to compare the performance of alternative timing mechanisms for modeling avian seasonal fecundity.

METHODS

The simplest model that we will consider contains four parameters: s , a , q_s , and q_f (respectively, daily nest survival probability, time from first egg to fledging, and probability that a female quits breeding after a successful (subscript s) or failed (subscript f) nest; see Table 1). Together, these parameters govern a female's trajectory through four states during the course of a

breeding season: actively nesting, failed in her previous attempt, fledged her previous attempt, and finished breeding. The MC matrix (\mathbf{M}) fully specifies the dynamics of this model:

$$\mathbf{M} = \begin{bmatrix} 1 & 0 & 0 & 0 \\ q_s & 0 & 1 - q_s & 0 \\ 0 & s^a & 0 & 1 - s^a \\ q_f & 0 & 1 - q_f & 0 \end{bmatrix} \begin{matrix} \text{Finished} \\ \text{Fledged} \\ \text{Active} \\ \text{Failed.} \end{matrix} \quad (1)$$

Note that the text to the right of the matrix in Eq. 1 is not intended as mathematical symbols, but rather as labels for the rows. Similar labels could be applied to the columns with column 1 pertaining to the state of being "Finished," column 2 to "Fledged," and so on. The cells of the Markov chain in Eq. 1 give the probability of transition from the state represented by the row to the corresponding state represented by the column. For example, $\mathbf{M}_{21} = q_s$, which is the probability of transition from the state of having fledged a nest (row 2) to the state of being finished breeding (column 1). The state "Finished" is an absorbing state: once a female quits she remains there ($\mathbf{M}_{11} = 1$) and, given sufficient time, all females eventually quit.

In column-stochastic form, which is equally valid, these models closely resemble matrix population models with which many readers will be more familiar (Caswell 2001, Erterson and Bennett 2005). However, an important consequence of the stochastic nature of Markov chains is that the rows (or columns, if column-stochastic) sum to unity. Therefore the dominant eigenvalue of a Markov chain is invariably 1. Other concepts from projection matrix theory are useful for the analysis of Markov chains. For example in a projection matrix the dominant right eigenvector gives the stable age (or stage) distribution (Caswell 2001), whereas in a regular Markov chain, the dominant eigenvector describes the equilibrium probability distribution among states that is asymptotically approached (Kemeny and Snell 1983). Here we have chosen the row-stochastic form to facilitate comparison with commonly available texts on basic Markov chain theory (especially Kemeny and Snell [1983], whose notation we follow closely). We estimated the expected number of broods

fledged per female (\hat{b}) according to Eq. 1 using the fundamental matrix \mathbf{N} (Appendix A; see Kemeny and Snell 1983):

$$\hat{b} = \mathbf{N}_{21} = \frac{\hat{s}^a}{\hat{q}_f + \hat{s}^a(\hat{q}_s - \hat{q}_f)}. \tag{2}$$

To estimate the sampling variance of \hat{b} ($\widehat{\text{var}}(\hat{b})$), we used the delta method (Seber 1982), assuming the sampling covariances among estimated model parameters (s, a, q_s, q_f) to be zero. To estimate the expected variation in number of broods produced among females (σ_b^2) we again used the fundamental matrix (see Appendix A) to obtain:

$$\hat{\sigma}_b^2 = \hat{b}^2 \left[\hat{q}_f \left(\frac{1 - \hat{s}^a}{\hat{s}^a} \right) + 1 - \hat{q}_s \right]. \tag{3}$$

Using five parameters ($s, a, w_s, w_f,$ and T ; see Table 1), we can construct a regular MC for a breeding cycle that also allows renesting and multiple brooding (w_s and w_f , respectively, are the expected number of days between successfully fledging a nest [subscript s] or quitting a failed nest [subscript f] and laying the first egg of a new attempt). Note that the parameter T (breeding season length) does not appear in the regular MC, which contains no absorbing states, and so no intrinsic stopping mechanism, but is used to determine when the process ends:

$$\mathbf{M} = \begin{bmatrix} 0 & \mathbf{0} & 0 & 0 & \mathbf{0} & 0 & \mathbf{0} & 0 & 1_1 \\ s_a & \mathbf{0} & 0 & 0 & \mathbf{0} & 1 - s_a & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \ddots & \mathbf{0} & \mathbf{0} & \mathbf{0} & \vdots & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ 0 & \mathbf{0} & s_1 & 0 & \mathbf{0} & 1 - s_1 & \mathbf{0} & 0 & 0 \\ 0 & \mathbf{0} & 0 & 1_{w_s} & \mathbf{0} & 0 & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \ddots & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \\ 0 & \mathbf{0} & 0 & 0 & \mathbf{0} & 1_{w_s - w_f} & \mathbf{0} & 0 & 0 \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \ddots & \mathbf{0} & \mathbf{0} \\ 0 & \mathbf{0} & 0 & 0 & \mathbf{0} & 0 & \mathbf{0} & 1_2 & 0 \end{bmatrix} \tag{4}$$

where $s \equiv s_1 = \dots = s_a, w_s > w_f$, and females begin the nesting season upon laying their first egg. As with the absorbing MC, the entries in Eq. 4 give the probability of transition from the state described by the row to the state described by the column, but with the added condition that each transition requires exactly one day. In Eq. 4, the ellipses (which represent blocks of the matrix that are not printed because they would take too much space) indicate an ordered progression that can be deduced from context. For example, the ellipses in $\mathbf{M}_{3,2}$ represent the daily age-specific nest survival probabilities, $s_{a-1}, s_{a-2}, s_{a-3}, \dots, s_2$. Other ellipses indicate vectors of ones. Bold zeros in the matrix represent portions of the matrix that, when expanded to the same dimension as the corresponding ellipses, are vectors or sub-matrices of zeros of the appropriate dimension.

Our regular MC (Eq. 4) is designed to perform similarly to Pease and Grzybowski's (1995) simple model, although there are important differences. First, we define the initiation of a nest attempt as the day on which the first egg is laid. Although this ignores prior events such as pair formation and nest construction, it conditions the initiation of the stochastic process on a specifically defined, observable event (the laying of the first egg). The beginning and end of pair formation and nest construction may not be as easily defined or observed for many species. This results in definitions of w_s and w_f to be the durations, in days, between the end of a previous nest and the day on which the first egg is laid in a subsequent nest (Table 1). Second, we use the symbol " T " to represent the length of the breeding season, whereas Pease and Grzybowski (1995) use " s_s " (but we have already reserved " s " for the nest survival rate; see Etterson and Bennett 2005). Third, our mean age parameters are restricted to integers. This is not necessary, but the generalization is complicated (in particular for a ; see Etterson and Bennett 2005) and would not change conclusions concerning stopping rules. To emphasize the daily time step used by Eq. 4 we have subscripted the nonzero entries to indicate the daily aging of nests.

As with the absorbing MC, the quantities of interest are obtained from the fundamental matrix, \mathbf{Z} :

$$E(b)_T = \hat{b} \rightarrow z_{a+1,1} + \alpha_1(T - 1) \tag{5}$$

and

$$\sigma_b^2 \rightarrow T\alpha_1(2z_{1,1} - 1 - \alpha_1) \tag{6}$$

where α is the dominant right eigenvector of \mathbf{M} (the limiting vector to which all rows of \mathbf{M} converge when \mathbf{M} is raised to a sufficiently large power), and z_{ij} is the entry in row i , column j of \mathbf{Z} (Appendix A; see Kemeny and Snell 1983). As with the absorbing MC, the sampling variance of \hat{b} may be obtained using the delta method (Seber 1982). The arrows in Eqs. 5 and 6 indicate that these formulae are asymptotically valid. If fecundity is still coming in pulses (i.e., plateaus in the brood accumulation function; Fig. 1) then equilibrium has not been reached. Factors that contribute to a quicker approach to equilibrium include low daily nest survival rate, s , and a large ratio of $a:w_s$.

Example data

Input parameters for our sample comparisons come from radio-tracked populations of Eastern Meadowlark and Dickcissel at Prairie Ridge State Natural Area, Illinois, USA. Kershner et al. (2004: Table 1) reported renesting data from 51 nest attempts by 33 radio-tagged Eastern Meadowlarks, summarizing the outcome of each nest attempt followed by the subsequent decision by surviving females to renest, cease breeding, or emigrate from the study area. Similarly, Walk et al. (2004: Fig. 1) reported renesting data from 46 nest

TABLE 2. Observed data and model results for Eastern Meadowlark (*Sturnella magna*) using two Markov chain (MC) formulations; b is the expected number of successful broods per breeding female.

Data or model	\hat{b}	Var(\hat{b})	Bias(\hat{b})	MSE(\hat{b})	$\hat{\sigma}_b^2$
Observed	0.73	0.025			0.39
Absorbing MC	0.72	0.016	-0.005	0.02	0.55
Regular MC					
\bar{T}	0.34	0.003	-0.38	0.15	0.11
T_{\max}	0.86	0.280	0.13	0.30	0.24
T_{95}	0.78	0.042	0.06	0.04	0.22

Notes: Where cells are blank, no entries are possible. See Table 1 for definition of breeding season length parameters, T .

attempts by 37 radio-tagged Dickcissels (see Plate 1). For both studies we assumed that all females that emigrated ceased breeding (Kershner et al. 2004, Walk et al. 2004). Some females were also censored at decision points due to radio-tag failure.

We estimated q_s and q_f as the simple proportions of known decisions to cease breeding after success or failure, respectively, assuming all females that emigrated also quit breeding (Appendix B). Daily survival was estimated using the Mayfield (1975) estimator. Estimates of w_s and w_f were taken directly from field-monitoring data. The date of the end of a nest attempt was interpolated using a weighted (by daily survival) average over each day during the monitoring interval in which the nest attempt ended. The date of the first egg in the next nest was estimated by backdating the known age of the nest. Finally, the length of breeding season for each female was estimated as the difference between the last active date of her last nest (interpolated as above) and the date when she laid the first egg of her first nest. The resulting estimates, with sampling variances, are reported in Table 1.

Comparison of absorbing and regular Markov chains

To compare the predictions of the two models that differed in reneating and stopping rules (q_s and q_f) vs. (w_s , w_f , T) we compared the model predictions Eqs. 2 and 5 to the observed mean number of successful broods produced for each species. Having noted that the regular MC is likely to be sensitive to errors in estimating breeding season length (Fig. 1), we estimated T in three ways. First, we estimated the simple mean of T over all females (\bar{T}). Second, we took the maximum observed value (T_{\max}). Third, we fit a negative binomial distribution to the observed values and took the 95th percentile as the maximum breeding season length (T_{95}). We compared relative model performance using estimated mean squared error (MSE), where $\text{MSE}(\hat{b}) = E(\hat{b} - b)^2 = \text{var}(\hat{b}) + \text{bias}(\hat{b})^2$ (Williams et al. 2002:45), and $\text{bias}(\hat{b}) = E(\hat{b}) - b$. All computing was done using MATLAB 7.4 (MathWorks 2007). We also estimated the expected variance in number of broods produced per female (σ_b^2) using Eqs. 3 and 6 and compare this to the observed variance.

RESULTS

Of the 33 surviving females followed by Kershner et al. (2004), 12 fledged no broods, 18 fledged one brood, and three fledged two broods, resulting in 0.73 ± 0.16 successful broods per female, mean \pm SE (Table 2). Two-thirds of female Eastern Meadowlarks quit breeding after successfully fledging a brood, but less than one-half quit after a failed brood (Table 1). The absorbing MC accurately predicted b , but substantially underestimated sampling variance and overestimated the expected variance among females (σ_b^2 ; Table 2). The regular MC (Eq. 4) performed dismally when \bar{T} was used as a measure of breeding season length, grossly underestimating b , $\text{var}(b)$, and σ_b^2 (Table 2). With T_{\max} as the breeding season limit, the regular MC substantially overestimated b and $\text{var}(b)$, but underestimated σ_b^2 (Table 2). Finally, with T_{95} as the breeding season limit, the regular MC moderately overestimated b and $\text{var}(b)$, but underestimated σ_b^2 (Table 2).

Of the 37 female Dickcissels followed by Walk et al. (2004), 20 fledged no broods, 16 fledged one brood, and one fledged two broods, resulting in a mean of 0.49 ± 0.12 successful broods per female (Table 3). Most female Dickcissels quit breeding after successfully fledging a nest and more than two-thirds quit after a failed nest (Table 1). The absorbing MC substantially underestimated b , $\text{var}(b)$ and σ_b^2 (Table 1). As previously described, the regular MC performed poorly when \bar{T} was used as a measure of breeding season length, underestimating all three quantities of interest. With T_{\max} as the breeding season limit, the regular MC grossly overestimated b and $\text{var}(b)$, but underestimated σ_b^2 (Table 3). Finally, with T_{95} as the breeding season limit, the regular MC moderately overestimated b and $\text{var}(b)$, but underestimated σ_b^2 (Table 2).

As measured by mean squared error (MSE), the absorbing MC performed better for both species, but was followed closely by the regular MC with T_{95} as the breeding season limit (Tables 2 and 3). The remaining two regular MC models were not competitive (Tables 2 and 3). The absorbing MC underestimated sampling variance ($\text{var}(b)$), whereas the regular MC with T_{95} overestimated sampling variance for both species. All models underestimated σ_b^2 , with the exception of the

TABLE 3. Observed and model results for Dickcissel (*Spiza americana*) using both Markov chain formulations.

Data or model	\hat{b}	Var(\hat{b})	Bias(\hat{b})	MSE(\hat{b})	$\hat{\sigma}_b^2$
Observed	0.49	0.015			0.31
Absorbing MC	0.41	0.008	-0.08	0.01	0.26
Regular MC					
\bar{T}	0.25	0.003	-0.23	0.06	0.09
T_{\max}	0.79	1.054	0.30	1.14	0.23
T_{95}	0.53	0.027	0.05	0.03	0.16

Notes: Where cells are blank, no entries are possible. Variables are as defined in Tables 1 and 2.



PLATE 1. (Upper) A female Dickcissel, banded and fitted with a radio transmitter. The antenna can be seen extending above the bird's back and tail. (Lower) A Dickcissel nest, with four Dickcissel eggs and a single Brown-headed Cowbird egg. Brood parasitism by cowbirds occurred in $\sim 1\%$ of the Dickcissel nests studied. Photo credits: Jeff Walk.

absorbing MC applied to Eastern Meadowlark (Tables 2 and 3).

DISCUSSION

Meadowlark and Dickcissel models

Strict adherence to MSE as an index of model performance suggests that the absorbing MC performs better than the regular MC for both species, although we know of no guidelines that would allow one to conclude just how much better a given model performs based on a given difference in MSE. More importantly, our analyses reveal strengths and weaknesses of each approach for modeling avian seasonal fecundity. The absorbing MC appeared to be slightly more accurate, but this was due in part to its tendency to underestimate sampling variance, which led to a smaller value for

MSE. The performance of the regular MC with T_{95} as stopping rule was almost as good in both cases. However, the choice of the 95th percentile of a negative binomial distribution for breeding season lengths lacks biological justification and may not always perform well. As illustrated in Fig. 1, there is potential for large error when imposing a temporal limit on a stochastic process that has not yet reached equilibrium. To reinforce this point, the percentiles of the same fitted negative binomial distributions from which T_{95} was obtained can be evaluated at T_{\max} . For Eastern Meadowlark, this percentile is 0.969, a difference of only 0.019, which resulted in an overestimation of 0.13 in \hat{b} .

The relatively large variance in number of successful broods (σ_b^2) predicted for Eastern Meadowlarks by the absorbing MC results from a few females experiencing

exceptionally long breeding seasons. The absorbing MC of Eq. 1 does not keep track of time. This becomes obvious when you consider that the events described by the matrix entries do not, in general, require an equivalent period of time to occur. Thus a successful nest requires a days, whereas an unsuccessful nest requires something less than a days, and a quitting event is dimensionless. Therefore, in Eq. 1 there is no temporal limit beyond which a female will no longer initiate new nests. As the season progresses, the probability that a female has already quit breeding approaches unity, but only asymptotically. This is a more sophisticated set of stopping rules than those against which Grzybowski and Pease (2005) argued, but the model still exhibits at least some of the dynamics (i.e., a nonzero probability of an unrealistically long breeding season) that prompted their criticism.

However, our analyses suggest that temporal limit methods (represented by the three parameterizations of the regular MC) also have weaknesses. In particular, for both species, the regular MC considerably overestimated b (Tables 2 and 3) when the natural limit (maximum breeding season length, T_{\max}) was applied. Pease and Grzybowski (1995) provide recommendations for handling this by truncating the initial and terminal tails of the breeding pool. Ricklefs and Bloom (1977) provided an equation for estimating breeding season length using information about the number of nests initiated per month, which also has the advantage of allowing estimation of T when individual females are not marked. Otis et al. (1993) provided likelihood equations for estimating the duration of life history events that may prove useful for estimating breeding season lengths when female breeding histories are incomplete, which might occur if females are added to (or censored from) the sample continuously throughout the season.

For both species, some nest attempts could have been missed due to censoring resulting from several causes. Kershner et al. (2004) reported that 11 of 33 females were censored at some point in the season due to radiotag failure. However, the 22 uncensored females only managed to produce two successful nests (after their initial attempt), suggesting that the remaining censored females probably produced about one additional successful nest between them. To explore the importance of this censoring we added another successful attempt, respectively, to a female that had previously raised no broods and to a female that had successfully fledged one brood. We found that, although the numbers changed slightly, the overall patterns that we reported above remained robust. In both studies some failed nests may have been missed if they failed quickly, which would result in bias in our estimated quitting probabilities. The short monitoring interval employed in these studies suggests that there are not likely to have been many such nests, if any (Kershner et al. 2004, Walk et al. 2004). Fretwell (1986) suggested that female Dickcissels may disperse long distances between successful nest attempts.

If true, this could invalidate our assumption that emigrating females quit breeding, resulting in biased quitting probabilities and underestimation of the actual number of broods fledged per female. However, the Fretwell (1986) hypothesis has yet to be substantiated.

Phenology of temperate-breeding, multi-brooded birds

Regardless of bias, variance, and MSE, the choice of a particular modeling approach should also depend on which method best captures the timing of initiation, reinitiation, and cessation of breeding. The two modeling strategies that we have described, using a regular vs. an absorbing MC, will likely differ in performance depending on the degree of seasonality and synchrony exhibited by the population of interest. For birds that both initiate and cease breeding synchronously, the regular MC may perform better than the absorbing MC. However, many lines of research, reviewed briefly below, suggest that timing of breeding events and factors that influence it vary considerably among species and among populations within species.

For north-temperate breeding birds, seasonal breeding is correlated with the summer period of reliable high-quality food, which has long been presumed the ultimate cause for the timing of the initiation of avian breeding in the spring (Immelmann 1973). However, within this general pattern, there is considerable variation in exact timing, with some birds breeding highly synchronously (Ims 1990a). Many diverse hypotheses, ranging from sexual selection to predator swamping, have found support in empirical studies (reviewed by Ims 1990a, b). In contrast, Iwasa and Levine (1995) proposed a general model for optimal timing of life history events, for which they used avian breeding as a concrete example. Their model suggested that seasonal breeding should vary in the degree of synchrony depending only on the relative spatial scales of disturbance processes vs. population regulation. Similarly, Richter (1999) used ideal free models to show that reproductive synchrony should increase with the amount of direct density-dependent mortality of offspring.

In many temperate breeding birds, initiation of breeding activity occurs as a proximate response to increasing day length, which also triggers the eventual onset of gonadal regression and a photorefractory period during which birds no longer respond to even very long days (Hahn et al. 2004). However, the degree to which photorefractoriness is absolute varies even among closely related species (MacDougall-Shackleton et al. 2006) and many temperate land birds have been documented breeding outside of their typical spring–summer season (Koenig and Stahl 2007). The basic mechanisms for cessation of breeding also vary with migratory strategy, with tropical residents and tropical–temperate migrants exhibiting less photoperiodic entrainment compared to temperate residents (Sharp 1996).

James and Shugart (1974) used principal components analysis to describe a complex multivariate relationship

between climate and the timing of breeding in American Robins (*Turdus migratorius*) that varies across the species' range. [Stutchbury and Robertson \(1987\)](#) showed that for Tree Swallows (*Tachycineta bicolor*) egg-laying dates showed much less variation than territory settlement dates, and they concluded that female swallows benefit from synchronous breeding. In contrast, [Yasukawa and Searcy \(1981\)](#) found that nest initiation dates for Red-winged Blackbird (*Agelaius phoeniceus*) females sharing the same mate were overdispersed in time; they concluded that females benefit from asynchronous nesting, which allows the male to contribute more to individual nest attempts. Other studies have further shown that food availability ([Hau 2001](#), [Hahn et al. 2005](#), [Nagy and Holmes 2005](#)) and weather patterns ([Hau 2001](#), [Deviche and Small 2005](#)) influence initiation and/or cessation of breeding. Taken together, the theoretical models, mechanistic models, and empirical data, all point to considerable variation in the timing of breeding events within and among species, suggesting that a multiplicity of modeling approaches will be required across the range of avian seasonal breeding strategies.

Future model developments

A major advantage of the Markov chain models we have described is their simplicity. When the absorbing MC results (Eq. 2) are coupled with the Mayfield (1975) method for estimating nest survival, an estimate of seasonal fecundity can be obtained using only a hand calculator. Similarly, the regular MC results (Eq. 5) can be obtained using simple spreadsheet software. This should make these basic methods available to a very wide audience. However, the MC models that we have presented also admit many potential generalizations and we will briefly describe several.

With sufficient data, the best approach to model annual reproductive success may be a mixture of the two types of models. For demonstration, we have assumed homogeneity in model parameters, regardless of which approach is used. In reality, many of these model parameters are likely to vary with time, especially nest survival rates (e.g., [Dinsmore et al. 2002](#), [Etterson et al. 2007](#)) and quitting probabilities. Thus, for example, we could borrow from the compelling strength of the argument presented by [Grzybowski and Pease \(2005\)](#) to force the quitting probabilities to approach unity as the season progresses, resulting in both flexible modeling of breeding decisions and an implicit limit on the length of the breeding season.

Because the MC models are stochastic matrices, they form the kernel for a maximum likelihood estimator for seasonal fecundity based on sequential field observations of nesting females (i.e., without intermediate parameter estimation steps). However, a major hurdle that will need to be overcome is the incorporation of a joint likelihood for observation error describing a female's observable states conditional on her actual breeding state, for example, to account for the

possibility of missing intermediate nest attempts. [Etterson and Stanley \(2008\)](#) used this approach on Markov chain nest survival models to show how ancillary evidence could be formally incorporated into likelihood functions for cause-specific nest failure. The joint likelihood could be constructed as a hidden Markov chain ([MacDonald and Zucchini 1997](#)) or, more generally, as a hidden process model ([Newman et al. 2006](#)). A further generalization would be to incorporate the MC models as "building blocks" within state-space models of avian abundance (e.g., [Buckland et al. 2004, 2007](#)). However, the design and fitting of such models requires considerable training, specialized software, and is often only possible within a Bayesian framework ([Buckland et al. 2004, 2007](#)). We have deliberately chosen to keep this foundational manuscript simple in hopes that it will therefore be accessible to the widest possible audience.

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APPENDIX A

Obtaining mean and variance formulae from fundamental matrices (*Ecological Archives* A019-027-A1).

APPENDIX B

Estimation of q_s and q_f , controlling for censored nests (*Ecological Archives* A019-027-A2).