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Hatching asynchrony in birds: Multiple nesting attempts and the nest failure hypothesis

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ABSTRACT
Hatching asynchrony in birds, which occurs when incubation begins before egg laying is complete, has been a topic of study for many decades. The "nest failure hypothesis" posits that the distribution of the risk of nest predation across the nesting cycle (from egg laying to the fledging of young) determines the optimal degree of hatching asynchrony. If such risk is higher earlier in the nesting cycle, then much asynchrony (e.g., incubation on the first egg laid) is generally favored. Alternatively, if the risk of nest predation is concentrated later in the cycle, then greater synchrony (a late start to incubation) is favored. Adult mortality during incubation favors greater hatching synchrony. Existing models suggest that optimal hatching asynchrony should depend on the ratio of daily mortality risks prehatching and posthatching, or early and late in the nesting cycle. We show that these classic theoretical expectations depend critically on the assumption of a single nesting attempt per breeding season. Allowing for multiple nesting attempts per season leads to a large range of possible outcomes, often with large deviations from the expectations of single-attempt models. We show further that daily nest survival probabilities across the entire nesting cycle combine to influence optimal hatching asynchrony, not just a subset of values, or a ratio of values, as suggested by earlier theory. In addition, assumptions about the transitions in daily survival values between nesting stages (abrupt vs. gradual changes) are also important determinants of hatching asynchrony. Overall, however, a consideration of multiple nesting attempts does not alter the general expectation that high risk early in the nesting cycle favors hatching asynchrony, and that greater synchrony is favored by high risk later in the cycle or adult mortality during incubation.

Keywords: hatching asynchrony, multiple-nesting, nest failure hypothesis, nest survival

Eclosión asincrónica en aves: múltiples intentos de anidación y la hipótesis del fracaso del nido

RESUMEN
La eclosión asincrónica en las aves ocurre cuando la incubación comienza antes de que la puesta de los huevos haya terminado, y ha sido un tema de estudio por muchas décadas. La Hipótesis del Fracaso del Nido predice que la distribución del riesgo de depredación del nido a lo largo del ciclo de anidación (desde la puesta del huevo hasta el emplumamiento del polluelo) determina el grado óptimo de eclosión asincrónica. Si dicho riesgo es más alto a inicios del ciclo de anidación, entonces generalmente se favorece un alto grado de asincronía (e.g., incubación del primer huevo puesto). De modo alternativo, si el riesgo de depredación del nido se concentra al final del ciclo, entonces se favorece una mayor sincronización (un inicio tardío de la incubación). La mortalidad del adulto durante la incubación favorece una mayor sincronización en la eclosión. Los modelos existentes sugieren que la eclosión asincrónica óptima debería depender de la relación entre el riesgo diario de mortalidad antes y después de la eclosión, y a inicios y a fines del ciclo de anidación. En este trabajo mostramos que estas expectativas teóricas clásicas dependen de modo crítico del supuesto de un único intento de anidación por estación reproductiva. Si se consideran múltiples intentos de anidación por estación, esto lleva a un amplio rango de posibles resultados, usualmente con grandes desviaciones de las expectativas de los modelos de un único intento. Además, mostramos que la probabilidad de supervivencia diaria del nido a lo largo de todo el ciclo de anidación se combina para influir la eclosión asincrónica óptima, no solo un subconjunto de valores, o la relación de los valores, como sugiere la teoría existente. Adicionalmente, las suposiciones sobre las transiciones en los valores de supervivencia diaria entre las etapas de anidación (cambios abruptos vs. graduales) son también determinantes importantes de la eclosión asincrónica. En términos generales, sin embargo, la consideración de múltiples intentos de anidación no alterna la expectativa general de que un alto riesgo al inicio del ciclo de anidación favorece la eclosión asincrónica, y de que una mayor sincronización es favorecida por un alto riesgo a fines del ciclo o por la mortalidad de los adultos durante la incubación.

Palabras clave: anidación múltiple, eclosión asincrónica, hipótesis del fracaso del nido, supervivencia del nido

INTRODUCTION

Hatching asynchrony, which occurs when the incubation of eggs begins before the clutch is complete, is common in avian taxa (Clark and Wilson 1981, Ricklefs 1993, Stoleson and Beissinger 1995). Hatching asynchrony varies from complete asynchrony (incubation with the first egg), in which each chick hatches on a different day, to minimal asynchrony (incubation initiated on the penultimate egg), in which only the last chick hatches asynchronously (Lack 1954, Clark and Wilson 1981). The initiation of incubation on the penultimate egg is relatively common in passerines (Clark and Wilson 1981). Complete hatching synchrony occurs when incubation begins after the clutch is complete, which leads to uniformly aged nestlings. Complete synchrony is also fairly common in many avian families (Clark and Wilson 1981, Ricklefs 1993, Stoleson and Beissinger 1995). Incubation strategies and other complications can also influence the degree of hatching asynchrony (Stoleson and Beissinger 1995).

Several hypotheses have been proposed to explain hatching asynchrony in birds. One of the earliest and most widely known is the "brood reduction hypothesis" developed by Lack (1947, 1954) and expanded by others (e.g., Pijanowski 1992, Mock 1994). Here, incubation begins before the clutch is complete, creating clear age differences and a resulting dominance hierarchy within a brood. Typical clutch size reflects the number of chicks that could be raised in a good year; but in an unpredictably poor year, chicks low in the hierarchy will quickly perish, thus reducing brood size to that suitable under poor conditions. Another relatively well-examined hypothesis suggests that hatching asynchrony acts to reduce the peak feeding load on adults (Hussell 1972, 1985a, Mock and Schwagmeyer 1990). If nestlings hatch simultaneously, then the period of peak energy demand for each chick will occur at the same time. Accordingly, asynchronous hatching can spread out and thus lower the peak energy requirement of the whole brood (e.g., Bryant and Gardiner 1979, Siegel et al. 1999). Slagsvold and Wiebe (2007) suggested a similar "feeding constraint hypothesis," in which asynchronous hatching lessens constraints on the parent caused by interactions between prey size, energy demands, and foraging efficiency. Other major hypotheses focus on factors such as sibling rivalry, egg viability, and sexual conflict between parents (see Magrath 1990, Stoleson and Beissinger 1995).

The "nest failure hypothesis" for hatching asynchrony was first proposed by Clark and Wilson (1981) and has received considerable theoretical and empirical attention. This hypothesis holds that asynchronous hatching is generally a strategy to reduce total nest failure. Here, the degree of hatching synchrony is associated with the ratio of daily nest mortality in the posthatching (nestling) to prehatching (egg) periods. If the nestling stage is much more dangerous than the egg stage, then synchronous hatching is more productive than asynchronous hatching. Synchronous hatching effectively minimizes the time that the nest is exposed to the higher risk of predation during the nestling period. If nest survival does not vary much over the nesting cycle, then asynchronous hatching will maximize reproductive output; asynchrony leads to the earlier fledging of some young and thus minimizes overall nest failure (Murray 1994). Hussell (1985a) modified Clark and Wilson's (1981) model, concluding that hatching asynchrony is related to nest mortality early and late in the nesting cycle, specifically during the egg-laying and fledging periods. Relatively high mortality during the egg-laying period leads to asynchronous hatching, and high mortality in the nestling stage favors more synchronous hatching. Magrath (1988) extended Hussell's (1985a) model to examine danger to the incubating adult as a factor in hatching asynchrony. He argued that the length of the incubation period is extended by early incubation, which can induce a significant drop in parental survival if incubation is dangerous. Thus, danger during incubation favors synchronous hatching (i.e. delayed incubation), even when other factors would favor asynchrony. Murray (2006) expanded further on earlier theory, pointing out that a lower survival rate in late-hatched chicks (in asynchronous hatching) strongly favors greater hatching synchrony.

Here, we update and expand this body of work on the nest failure hypothesis. We focus much of our attention on multiple nesting attempts and their effects on expected patterns of hatching asynchrony. All existing theoretical treatments of the nest failure hypothesis assume a single nesting attempt per season (e.g., Clark and Wilson 1981, Hussell 1985a, Magrath 1988, Stoleson and Beissinger 2001, Murray 2006). Many birds, however, attempt 2 or more nests in a single season (Roper 2005, Schmidt and Whelan 2010). The possibility of multiple nesting attempts creates a risk dynamic different from that in a single nesting attempt; thus, incorporating multiple nesting attempts can markedly alter expectations about hatching asynchrony. We also consider the nature of transitions in daily nest survival across the stages of the nesting cycle. Current theoretical works assume abrupt transitions in daily nest survival across the nesting cycle. For example, daily nest survival changes abruptly from the incubation to the nestling stage once the first egg hatches (Clark and Wilson 1981). It is possible that nest survival could also change gradually as each egg hatches. Such gradual transitions in nest survival can greatly alter expectations derived from abrupt-transition models.
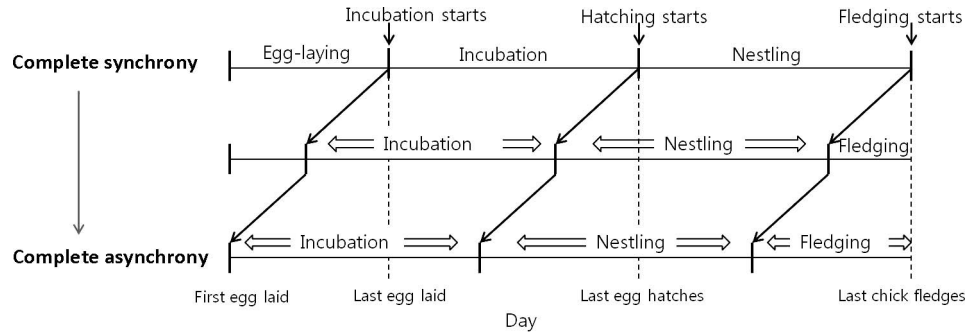
FIGURE 1. Schematic depiction of the 4 nest stages in Hussell's (1985a) model. In complete synchrony, incubation begins after clutch completion and all nestlings hatch and fledge at once (no fledging stage). In complete asynchrony, incubation begins with the first egg (no egg-laying stage) and all nestlings fledge gradually over a relatively long fledging period. For the intermediate case of partial synchrony, incubation begins after a shortened egg-laying period, and a correspondingly shortened fledging period occurs after the nestling period.

METHODS

Our depiction of the nesting cycle is based mainly on that of Hussell (1985a) and related models. Hussell identified 4 stages of the nesting cycle and corresponding values of daily nest survival: the egg-laying (P_0), incubation (P_1), nestling (P_2), and fledging (P_3) periods. The egg-laying period starts with the laying of the first egg and ends with the start of incubation (see Figure 1). The incubation period lasts from the onset of incubation to the first nestling hatched and will include further egg laying if incubation begins before the last egg. The nestling period runs from the first nestling hatched to the first nestling fledged. The fledging period is the time during which nestlings are fledging; this period occurs only when incubation begins before clutch completion. As developed by Hussell (1985a) for a single nesting attempt, the expected number of offspring fledged when incubation starts on the mth egg laid, $W(m)$, is

$$W(m) = P_0^{(m-1)t_1} P_1^{t_2} P_2^{t_3}\left(m + \sum_{i=1}^{N-m} P_3^{it_1}\right)$$

where N = clutch size ($m \leq N$), t_1 = laying interval (days between eggs), t_2 = incubation period (days) for a single egg, and t_3 = period (days) for a given chick to fledge (posthatching). As m decreases, the length of the egg-laying period is shortened and the equivalent number of days is effectively shifted to the fledging period (Figure 1). The length of the incubation and nestling stages does not change with m. Hussell (1985a) showed that (for a single nesting attempt) the only probabilities determining the optimal onset of incubation are P_0 and P_3. The probabilities P_1 and P_2 cancel out in the equations determining optimal asynchrony and, thus, play no role as determinants of asynchrony. We will refer to P_1 and P_2 as the "internal survival probabilities" because they cover the nesting stages occurring between (i.e. internal to) egg laying and fledging.

Clark and Wilson's (1981) original model assumed 2 nest stages: prehatching and posthatching. The prehatching period runs from the first egg laid to the first nestling hatched, and the posthatching period runs from the first nestling hatched to the last nestling fledged. Clark and Wilson's model is thus a special case of Hussell's (1985a) model in which nest survival rates are the same during (1) the incubation and egg-laying stages and (2) the nestling and fledging stages.

Magrath (1988) addressed the role of adult survival in hatching asynchrony and, for the parent, defined the nest stages differently from Hussell (1985a): egg laying (from first egg laid to onset of incubation), early incubation (from onset of incubation to last egg laid), incubation (from last egg laid to last egg hatched), and nestling stage (from end of hatching to last nestling fledged). Magrath's treatment of nest survival per se is the same as Hussell's (1985a; Figure 1). We follow Magrath's (1988) definition of the nest stages in our extension of his model.

Simulation Model

To address the influence of multiple nesting attempts on the nest failure hypothesis, we developed a stochastic simulation model (in Python 2.6) based on the day-to-day breeding process across a breeding season. A simulation model is the preferred approach here, given the unpredictable timing and many permutations of nest loss and renesting over a breeding season.

Our simulation model follows the basic structure of Hussell's (1985a) model, but a few additions are needed to cover the case of multiple nesting attempts, adult survival, and gradual transitions in nest survival across the nesting cycle. The multiple-nesting-attempts scenario allows a parent to make several nesting attempts within the breeding period, whereas single-nesting-attempt simulations allow only one (per existing theory). The breeding season in the multiple-nesting-attempts scenario lasts 90 days, which is

fairly typical for temperate species (Roper et al. 2010). With a baseline clutch size of 5 eggs and 34 days for a completely successful attempt (see below), 90 days allow for a maximum of 2 successful attempts. A greater number of unsuccessful attempts is possible. The exact length of the breeding season does not change the qualitative outcome of our simulations, provided that it allows for multiple nesting attempts. In the multiple-nesting scenario, the parent begins the next nesting attempt immediately after the previous attempt, if time permits. All simulated birds in the multiple-nesting scenario invest 3 days in nest building at the start of each attempt.

Nest contents survive with a daily survival rate for each nesting period as defined by Hussell (1985a). All eggs or nestlings share a common destiny. Thus, if nest predation occurs, all of the nest contents will be taken (also assumed in existing models). Parental survival is assumed to be 100% except for the simulation version of Magrath's (1988) model. For simplicity, we assume a single (female) parent representative of a fairly typical passerine.

A simulated breeding season begins with nest construction (3 days). Egg laying begins on the day after the end of nest construction. The clutch size of 5 eggs sets the maximum length of the egg-laying stage, with 1 egg laid day^{-1}. The nest survives each day of the egg-laying stage with probability P_0. Here and in all other similar cases, a random number is generated from a uniform distribution (0, 1). If the random number is less than P_0, then the nest survives that day. Each egg requires 12 days of incubation. The nest survives each day of the incubation stage (defined as in Figure 1) with probability P_1.

The nestling stage begins after the first egg hatches, and it lasts for the 15 days necessary to raise and fledge the first-hatched chick(s). The nest survives each day of this stage with probability P_2. A final fledging stage follows the nestling stage if any degree of asynchronous hatching occurred. The length of this stage depends on m (the egg on which incubation begins) and becomes longer as m decreases (Figure 1). Nest survival during each day of this stage is P_3.

In the multiple-nesting scenario, additional nesting attempts (each with a new nest) may occur after a successful or unsuccessful nesting attempt. The parent will renest when the time remaining in the breeding season allows for another attempt. Otherwise, the current breeding season is over for that parent.

For a given set of conditions, we compared 5 different onsets of incubation, beginning with the first, second, third, fourth, and fifth eggs (or $m = 1–5$). One million simulated parental breeding seasons were run for each candidate value of m. The reproductive success of each simulated parent was calculated as the sum of the number of nestlings that fledged across a simulated breeding season. The optimal onset of incubation was determined

by the highest average number of nestlings fledged in the conditions under study. Fitness curves (evaluated across the candidate values of m) were occasionally fairly flat (2 adjacent options with similar fitnesses), but the large number of simulation runs always provided unambiguous assessments of the optimal onset of incubation and could duplicate precisely known theoretical results (see below).

Simulations focused on Clark and Wilson's (1981) model and Hussell's (1985a) model used daily nest survival values that covered a realistic range (see Ricklefs 1969) from 0.91 (low) to 0.99 (high). Very high survival values approaching 1.0 were also used to illustrate key points in Clark and Wilson's model. To illustrate important aspects of Hussell's model, values of P_0 and P_3 (daily survival during the egg-laying and fledging periods) were chosen such that the optimal initiation of incubation in the classical case ran from the first egg ($P_0 \approx P_3$) to the last egg ($P_0 \gg P_3$). Internal survival probabilities (P_1 and P_2) ranged from moderate (0.95) to high (0.99) values. Our qualitative results do not depend on the particular values chosen, but mainly on the relative magnitude of the values.

For the simulation version of Magrath's (1988) model, nest survival was determined as outlined above. However, the nest periods are defined differently for parental survival. Like Magrath (1988), we define the following periods and corresponding (single-female) parental daily probabilities of survival: egg-laying (P_{F0}), early incubation (P_{F1}), incubation (P_{F2}), and nestling (P_{F3}) periods (see above). We vary parental survival rates during early incubation (P_{F1}), while setting parental survival for all other periods at 0.999 (per Magrath 1988). The death of the parent results in the loss of all eggs or young from the ongoing nesting attempt. Following Magrath (1988), daily nest survival rates are fixed and equalized across the entire nest cycle (i.e. $P_0 = P_1 = P_2 = P_3$), and the length of both the incubation and nestling periods is 12 days.

RESULTS

We consider the effects of multiple nesting attempts on each of the basic theoretical treatments described above. Each is considered in chronological order. First, Clark and Wilson (1981) concluded that the ratio of mortality between posthatching and prehatching periods determines the optimal onset of incubation. This ratio is defined as (mortality after hatching) / (mortality before hatching), or as $(1 - P_A) / (1 - P_B)$, where P_A is the daily nest survival rate after the first egg hatches and P_B is the daily nest survival rate before any eggs hatch. Clark and Wilson (1981) stated the mortality ratio result without mathematical proof. Our simulations, however, verify this result for single nesting attempts (Table 1). In the single-nesting scenario, for a given mortality ratio, the optimal onset of incubation does not change even though the component mortalities vary over a

TABLE 1. Optimal onset of incubation (egg number, out of 5 eggs) in single-nesting-attempt and multiple-nesting-attempts scenarios under a given mortality ratio of posthatching to prehatching nest stages. The mortality ratio is $(1 - P_A) / (1 - P_B)$, as defined by Clark and Wilson (1981). Two examples are presented for each mortality ratio, the first covering realistic values and the second with very high values (but with the same ratio). The onset of incubation with egg 1 results in complete asynchrony; onset on egg 5 produces complete synchrony.

Mortality ratio	Daily nest survival rate		Onset of incubation (egg number)	
	Prehatching (P_B)	Posthatching (P_A)	Single attempt	Multiple attempts
1.0	0.990	0.990	1	1
	0.999	0.999	1	1
2.0	0.990	0.980	3	2
	0.999	0.998	3	2
3.0	0.990	0.970	4	2
	0.999	0.997	4	3
4.0	0.990	0.960	4	3
	0.999	0.996	4	4
5.0	0.990	0.950	5	3
	0.999	0.995	5	4
6.0	0.990	0.940	5	3
	0.999	0.994	5	4
7.0	0.990	0.930	5	3
	0.999	0.993	5	4
8.0	0.990	0.920	5	4
	0.999	0.992	5	4
9.0	0.990	0.910	5	4
	0.999	0.991	5	4

factor of 10 (Table 1). Fine-scale simulations (J. K. Lee and S. L. Lima personal observation) suggest that the ratio rule is not strictly true but is an excellent approximation (see also Hussell 1985b). Critical mortality ratios defining various optimal start-of-incubation options are essentially constant and independent of survival values (much more than indicated in Clark and Wilson's [1981] figure 1). Furthermore, it is possible to prove that strict ratio

dependence holds in defining the region in which completely synchronous hatching is optimal, which occurs when the mortality ratio exceeds the clutch size.

In the multiple-nesting-attempts scenario, mortality-ratio-dependent asynchrony no longer holds (Table 1). Here, absolute values of daily survival determine the onset of incubation. Furthermore, compared to the single-nesting scenario, multiple nesting favors greater asynchrony in hatching (lower optimal m). Note that the latter result reflects a special case of the multiple-nesting version of Hussell's (1985a) model, rather than a general effect of multiple nesting attempts.
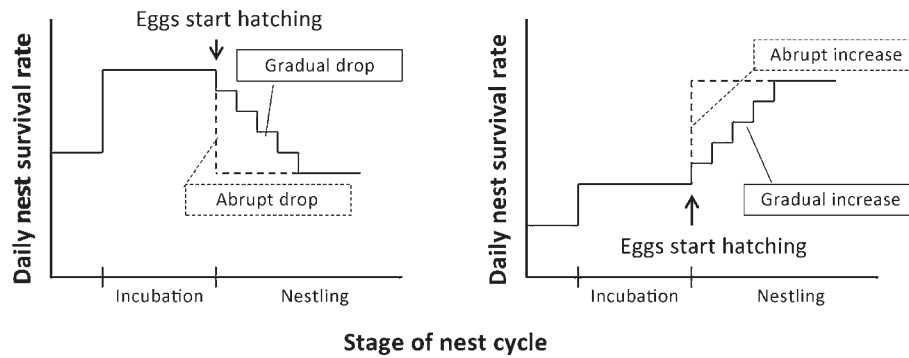
Hussell (1985a) modified Clark and Wilson's (1981) model by dividing the nesting cycle into egg-laying, incubation, nestling, and fledging stages (see above). Hussell's (1985a) model yielded results conceptually very similar to those of Clark and Wilson (1981), despite the differences in defining the nesting cycle. A key point here is Hussell's conclusion that the internal probabilities (P_1 and P_2, related to incubation and nestling stages) do not influence the onset of incubation.

Our single-nesting scenario corresponds to the situation envisioned in Hussell's (1985a) model (Table 2), in that internal daily nest survival rates do not affect the optimal onset of incubation in our simulations. Even with substantial drops in internal nest survival from 0.99 to 0.95, the optimal onset of incubation is unchanged for a given set of daily survival values for the egg-laying (P_0) and fledging (P_3) stages. The mortality ratio of the egg-laying to fledging stages is the key determinant for asynchronous hatching (results not shown), a result conceptually similar to that of Clark and Wilson (1981).

In the multiple-nesting scenario, however, internal nest survival rates are a major determinant of hatching asynchrony (Table 2). When internal daily nest survival rates are relatively high, synchronous hatching (later onset of incubation) is more favorable. Lower internal nest survival rates have the opposite effect, favoring greater asynchrony.

TABLE 2. Optimal onset of incubation (egg number, out of 5 eggs) in single-nesting-attempt and multiple-nesting-attempts scenarios. Shown are the daily probabilities of nest survival for the 4 nesting stages as defined by Hussell (1985a). In a given case, only the internal daily nest survival values (P_1 and P_2, during incubation and nestling stages) change, varying from high to moderately low in each case. Values of P_0 and P_3 were chosen such that optimal onset values ranged from 1 to 5 for a single attempt.

	Daily nest survival rate				Onset of incubation (egg number)	
	Egg-laying (P_0)	Incubation (P_1)	Nestling (P_2)	Fledging (P_3)	Single nesting attempt	Multiple nesting attempts
Case 1	0.94	0.99	0.99	0.93	1	4
		0.97	0.97		1	3
		0.95	0.95		1	2
Case 2	0.96	0.99	0.99	0.93	3	4
		0.97	0.97		3	3
		0.95	0.95		3	2
Case 3	0.99	0.99	0.99	0.94	5	5
		0.97	0.97		5	3
		0.95	0.95		5	2

FIGURE 2. Schematic description of abrupt and gradual transitions in nest survival (as defined in the text) across the period when eggs are hatching. A clutch size of 5 eggs is assumed, with incubation beginning on the first egg. The figure on the left corresponds to the case in which nest survival drops when eggs hatch; the opposite holds for the figure on the right.

The effect of multiple nesting attempts can be substantial. In case 1 (Table 2), multiple attempts alter Hussell's (1985a) model's expectation of complete asynchrony ($m = 1$) to much greater synchrony. Case 3 shows a similarly stark switch to asynchrony with declining internal probabilities of survival. Changes in daily survival during the incubation or nestling periods alone have similar effects (see below).

We next focus on the transition between the incubation and nestling stages (as defined in Figure 1). All models to date have assumed abrupt transitions in daily nest survival across various stages of the nesting cycle. However, as outlined above, nest survival during this transition between incubation and hatching could depend on the number of nestlings hatched. We incorporated such a gradual change in nest survival into our simulation as a "stepped linear" transition in nest survival across the hatching period: daily nest survival rate $= P_2 - (P_2 - P_1) \cdot H/C$. As noted above, P_1 is the daily nest survival rate during the incubation period and P_2 is the daily survival rate during the nestling period; H is the number of nestlings hatched so far, and C is the clutch size. This equation produces the patterns illustrated in Figure 2.

Table 3 compares the effects of abrupt vs. gradual transitions in nest survival (from P_1 to P_2) as eggs hatch

TABLE 3. Optimal onset of incubation (egg number, out of 5 eggs) with abrupt and gradual transitions in daily nest survival (see Figure 2) during the transition from incubation to the nestling stage (as indicated by the arrows). Results are shown for the single-nesting-attempt and multiple-nesting-attempts scenarios. In a given case, only the internal daily nest survival values are varied (daily survival during incubation P_1 and nestling P_2 stages). Case-specific values of P_0 and P_3 are those from Table 2. For each case, examples of transitions from P_1 to P_2 cover both moderate (change of 0.02) and major (change of 0.04) gradual changes from high to low and vice versa.

| | | | | | | Onset of incubation (egg number) | | | |
| | | Daily nest survival rate | | | | Abrupt transition | | Gradual transition | |
	Egg-laying (P_0)	Incubation (P_1)		Nestling (P_2)	Fledging (P_3)	Single	Multiple	Single	Multiple
Case 1	0.94	0.99	→	0.97	0.93	1	3	1	3
		0.99	→	0.95		1	3	1	1
		0.97	→	0.99		1	3	1	4
		0.97	→	0.95		1	2	1	2
		0.95	→	0.99		1	2	2	4
		0.95	→	0.97		1	2	1	2
Case 2	0.96	0.99	→	0.97	0.93	3	4	2	3
		0.99	→	0.95		3	3	2	2
		0.97	→	0.99		3	3	3	4
		0.97	→	0.95		3	3	2	2
		0.95	→	0.99		3	3	5	5
		0.95	→	0.97		3	2	3	3
Case 3	0.99	0.99	→	0.97	0.94	5	4	4	4
		0.99	→	0.95		5	3	3	2
		0.97	→	0.99		5	4	5	5
		0.97	→	0.95		5	2	4	2
		0.95	→	0.99		5	3	5	5
		0.95	→	0.97		5	3	5	3

TABLE 4. Optimal onset of incubation (egg number, out of 5 eggs) as a function of parental survival during the early incubation period (P_{F1}) in single-nesting-attempt and multiple-nesting-attempts scenarios. Daily parental survival rates during all other periods are fixed at 0.999 ($P_{F0} = P_{F2} = P_{F3} = 0.999$). All daily nest survival values apply to all nesting stages (i.e. $P_0 = P_1 = P_2 = P_3$; all values are per Magrath 1988: table 2).

| | Daily nest survival rate | | | | | | | |
| | 0.96 | | 0.97 | | 0.98 | | 0.99 | |
P_{F1}	Single	Multiple	Single	Multiple	Single	Multiple	Single	Multiple
0.990	2	4	2	5	3	5	5	5
0.992	1	3	2	4	2	5	4	5
0.994	1	3	1	3	2	4	3	5
0.996	1	2	1	2	1	3	2	4
0.998	1	1	1	1	1	1	1	2
0.999	1	1	1	1	1	1	1	1

under single- and multiple-nesting scenarios. In the single-attempt scenario with abrupt transitions, changes in internal survival probabilities (P_1 and P_2) do not change the optimal onset of incubation, even with substantial changes in absolute values. This result follows from the Hussell's (1985a) standard model and Table 2. In the multiple-attempts scenario with abrupt transitions, changes in the internal probabilities do cause shifts in the optimal onset of incubation (see Table 2). Gradual transitions in daily nest survival from P_1 to P_2 often change these "abrupt" expectations substantially. Consider first a comparison between the abrupt- and gradual-transition cases of the single-attempt scenario (Table 3). Here, with gradual transitions, internal probabilities do influence the optimal onset of incubation in the single-attempt scenario. A general trend here is related to whether there is a gradual increase or decrease in daily nest survival in the transition between the internal survival probabilities. A gradual increase tends to favor an increase in synchrony, whereas a gradual decrease tends to favor greater asynchrony. A comparison within the multiple-attempts scenario between abrupt and gradual transitions in internal probabilities suggests that the latter (gradual transitions) accentuated the trends seen in the former (Table 3). Here, with gradual transitions, deviations from the standard Hussell results (single nesting attempt with abrupt transitions) can be substantial. The variable effects of gradual vs. abrupt transitions from P_1 to P_2 can be explained via their effects on unhatched eggs. For example, with asynchronous hatching and an abrupt drop in nest survival (from P_1 to P_2), the drop is applied to the entire nest once the first egg hatches, including the unhatched eggs. Thus, the entire nest suffers from the sudden drop. With gradual transitions in nest survival, later-hatched eggs have the advantage of not experiencing a drastic drop in survival when the eggs start to hatch. This subtle effect favors asynchronous hatching with a gradual drop in internal survival rates. In the case where nest survival increases

from incubation to the nestling period, a gradual increase applies a relatively lower survival rate to unhatched eggs compared to an abrupt increase; thus, synchronous hatching becomes more favorable.

Magrath (1988) argued that the parental survival rate during incubation is a major determinant of hatching asynchrony. As hatching asynchrony increases (m decreases), the period from the onset of incubation to laying of the last egg is extended, thus lowering parental survival rate if incubation is dangerous. Such an effect favors greater synchrony in hatching, which minimizes overall incubation time. We examined this idea under single-nesting-attempt and multiple-nesting-attempts scenarios.

Table 4 shows the optimal onset of incubation for different combinations of daily parental survival during the early incubation period (P_{F1}) and daily nest survival (per the values used by Magrath [1988]). Note that we used a fixed daily nest survival across the entire nesting cycle ($P_0 = P_1 = P_2 = P_3$), a situation that favors completely asynchronous hatching (Clark and Wilson 1981, Hussell 1985a). The results of our single-nesting-attempt simulations are identical to those calculated by Magrath (1988). In the single-attempt scenario, for all values of daily nest survival, greater synchrony in hatching becomes more favored as parental survival during incubation decreases. The effect of a drop in parental survival (P_{F1}) becomes more substantial as overall nest survival increases. Complete synchrony ($m = 5$) can be favored despite the fact that fixed daily nest survival probabilities greatly favor complete asynchrony. As mentioned above, greater synchrony in hatching limits parental exposure to danger during early incubation. With multiple nesting attempts, lower daily parental survival during incubation favors even greater and more widespread hatching synchrony (Table 4). This effect is especially apparent under relatively high nest survival. Since the death of the parent eliminates opportunities for future reproduction, the effect of parental survival rate is much stronger in the multiple-nesting scenario than in the single-nesting scenario.

DISCUSSION

The study of hatching asynchrony in birds has a long history, which can be traced most prominently to the early work on adaptive brood reduction by Lack (1947, 1954) but, in fact, had its origins in much earlier work (see Magrath 1990). Many other hypotheses for hatching asynchrony have been forwarded, such as reducing peak work load on parents (Hussell 1972, Mock and Schwagmeyer 1990, Wiebe et al. 1998) or reducing the probability of nest failure (reviewed by Magrath 1990). No single hypothesis has emerged as a general explanation of hatching asynchrony (Magrath 1990, Ricklefs 1993, Stoleson and Beissinger 1995, Stenning 1996), and it seems likely that several of the hypotheses suggested thus far are valid in a subset of avian taxa or systems.

We focused our attention on the nest failure hypothesis for hatching asynchrony (Clark and Wilson 1981). The basic idea here is that, all else being equal, incubating eggs as early as possible (with the first egg) will minimize the risk of complete nest failure, since this strategy leads to the earliest possible fledging of at least some young. Clark and Wilson (1981) showed that early-onset incubation will maximize overall reproductive output if the risk of nest failure is higher earlier in the nesting cycle, whereas increasing degrees of hatching synchrony are favored as that risk shifts to the later portions of the cycle. Hussell (1985a) extended this result to a multistage view of the nesting cycle, and others have incorporated adult mortality during incubation (Magrath 1988) and other factors (Murray 2006) into the basic hatching asynchrony models.

All of these earlier insights into the nest failure hypothesis were developed in the context of a single nesting attempt. However, not only are multiple nesting attempts per breeding season common across avian taxa, but the ability to nest multiple times is likely a key strategy for dealing with high levels of nest predation (see Lima 2009). Our analysis shows that incorporating an ability to renest into the nest failure hypothesis can greatly alter both quantitative and qualitative expectations of hatching asynchrony. One of those expectations concerns the ratio result of Clark and Wilson (1981), in which the optimal degree of hatching asynchrony depends on the ratio of daily nest mortalities early and late in the nesting cycle. Our simulation model incorporating multiple nesting attempts suggests that optimal hatching asynchrony depends on the actual survival (or mortality) values rather than a simple ratio. Hussell's (1985a) result, in which daily nest survival during incubation and nestling stages (the "internal probabilities") does not influence optimal hatching asynchrony, also does not hold under a multiple-nesting-attempts scenario. These internal probabilities can have a major effect on expected patterns of hatching asynchrony, shifting the optimal onset of incubation to early or late eggs, depending on the circumstances. Furthermore, the nature of the transitions (gradual vs. abrupt) between internal probabilities can also have a surprisingly large impact on expected hatching asynchrony, with a tendency to work against expectations derived from an assumption of abrupt transitions across the nesting cycle.

Qualitatively, however, the idea (as expressed by Clark and Wilson 1981, Hussell 1985a, and others) that higher risk early in the nesting cycle favors greater hatching asynchrony, whereas higher risk later in the cycle favors synchrony, is likely to hold in most cases. A simple mortality ratio approach (as in Clark and Wilson 1981) may also provide an approximation of optimal hatching asynchrony under the assumption of multiple nesting attempts. However, as shown by Magrath (1988), a greater risk of predation on an adult during incubation can negate or reverse expectations based on gross patterns of nest survival. In particular, such risk to the adult favors increased hatching synchrony. Our extension of Magrath's (1988) model shows that its basic outcome is greatly enhanced under the assumption of multiple nesting attempts.

Unlike other hypotheses focused on hatching asynchrony, work on the nest failure hypothesis has a long history of mathematical modeling, and the simplicity of the resulting predictions has prompted several quantitative tests of theory. Clark and Wilson (1981) applied their mortality ratio rule to a large comparative dataset and found a greater degree of synchrony than expected on the basis of their ratio rule (see also Slagsvold 1986). Our multiple-nesting version of their model actually does suggest greater synchrony (Table 1), but this is not a general expectation with a more finely divided nesting season (e.g., Table 2). Other detailed, species-specific tests have been done with great skill and attention to details. For example, Stoleson and Beissinger (2001) found that hatching asynchrony is favored because the egg-laying stage is very risky, and early incubation can hide and protect eggs from destruction. Another quantitative test examined hatching asynchrony in Great-tailed Grackles (*Quiscalus mexicanus*) to compare hatching asynchrony in the context of sex-specific energy requirements (Teather and Weatherhead 1988). Our theoretical results, however, complicate the interpretation of these quantitative tests, which were couched in terms of the original single-nesting-attempt models. An assumption of multiple nesting attempts would likely alter the quantitative predictions being tested in some empirical studies. Along these lines, we see no simple rules of thumb for estimating how hatching asynchrony, in the context of the nest failure hypothesis, would be expected to play out. A wide-ranging survey of the nest survival literature (cf.

Clark and Wilson 1981, phylogenetically updated) coupled with our theoretical approach could provide several new insights into hatching asynchrony.

A potentially important issue is how one represents changes in daily nest survival over a nesting cycle. The early approach of Clark and Wilson (1981) divided the nesting cycle into 2 periods, before and after hatching. Hussell (1985a) and others (Magrath 1998, Murray 2006) divided the cycle into 4 distinct components, corresponding to key events across the nesting cycle. We adopted Hussell's characterization to make a more direct comparison to past work. The assumption of 4 separate periods better captures some of the complexity in hatching asynchrony as a function of changing nest survival. Perhaps more problematic is the issue of abrupt vs. gradual transitions in daily survival probabilities across the nesting cycle. Past theory assumed abrupt transitions in daily survival, and our results suggest that this assumption is a critical aspect of those models. Gradual transitions in daily survival across the nesting stages can lead to markedly different expectations regarding hatching asynchrony. These sorts of gradual changes, which blur the distinction between traditional nesting stages, could correspond to a gradual increase in nest visitation or chick noise production posthatching, or a gradual decrease in parental brooding as chicks mature.

A modeling approach could be devised to incorporate continuous variation in nest survival over time, irrespective of nesting stages. Alternatives to the classic Mayfield (1961) method of estimating daily nest survival (e.g., Shaffer 2004) can be used to characterize such continuous changes in daily nest survival (e.g., Murray 1994, Grant et al. 2005). For our purposes, however, a stage-specific approach is conceptually much more straightforward that one based on continuous variation in survival. Nevertheless, an approach based on continuous variation could, in principle, be addressed using simulations similar to ours. We expect that the shape of such continuous survival curves will be an important aspect of optimal hatching asynchrony. However, basic hatching-asynchrony expectations regarding late vs. early risk (see above) should hold when such an approach is used.

Our models provide an important update and extension of the body of theory regarding the nest failure hypothesis, but aspects of avian breeding biology not included in our model could also influence hatching asynchrony. One such factor is the fate of nonfledged young once fledging begins under highly asynchronous hatching. As suggested by Murray (2006), a strong decline in the survival of late-fledged young (under asynchronous hatching) will likely favor much more synchrony than suggested by standard models. Alternatively, a drop in the viability of uncubated eggs over time (Arnold et al. 1987, Stoleson and Beissinger 1999) may favor greater asynchrony (or

immediate incubation) than suggested by current models (see Murray 2006). Evidence to date suggests that egg viability is a greater problem in the tropics than in temperate areas (Ardia et al. 2006, Wang and Beissinger 2011, Wang et al. 2011) but could prove important during the warmest portion of the temperate breeding season (Cooper et al. 2006). More generally, hatching asynchrony causes potential complications and conflicts (between feeding young and continued incubation) that must be resolved in some way for it to be favored by selection.

In summary, the nest failure hypothesis is based on the idea that the onset of incubation will have an important effect on the overall likelihood of a successful nest. Our results support this basic idea but suggest that the possibility of multiple nesting attempts per season will substantially change expectations compared to models based on a single nesting attempt. Further work along these lines will provide additional insights into this long-standing problem in avian life histories.

ACKNOWLEDGMENTS

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