The Auk 118(4):973–982, 2001

HOW MANY BASKETS? CLUTCH SIZES THAT MAXIMIZE ANNUAL FECUNDITY OF MULTIPLE-BROODED BIRDS

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Abstract.—We developed deterministic models on the basis of nest survival rates and renesting behavior capable of predicting annual fecundity in birds. The models calculate probabilities of fledging from one to four nests within a discrete breeding season. We used those models to address theoretical issues related to clutch size. In general, birds require at least one day to lay an egg, and many species delay incubation until their entire clutch is laid. Because it takes longer to complete a larger clutch, and fewer such clutches can fit into a limited breeding season, there exists a clutch size for which annual fecundity is maximized. We asked, for a given amount of reproductive effort (i.e. a set number of eggs), does the age-old maxim "don't put all your eggs in one basket" apply? If so, in how many "baskets" should a nesting bird place its eggs? The answer depends on both likelihood of nest predation and length of the breeding season. Those results are consistent with the observed increase in clutch size with latitude (shorter breeding season length) and larger clutch sizes characteristic of cavity-nesting species (with higher nest survival rates). The models also predict that the size of replacement clutches should decrease as the breeding season progresses, and that intraseasonal decline in clutch size should be more pronounced when the breeding season is short. *Received 24 January 2000, accepted 24 April 2001.*

Ecologists have been fascinated by factors constraining avian clutch size for more than 50 years. Lack (1947, 1954) proposed that clutch size should reflect maximum number of young that adults can raise. Most discussions of optimal clutch size in birds have centered on productivity of a single clutch of eggs, but some have looked at the influence of clutch size on lifetime reproductive success (for a recent review, see Monaghan and Nager 1997). Another important measure of productivity is annual fecundity because many species attempt to nest more than once within a limited breeding season. In those species, length of the breeding season may be an important constraint on annual productivity leading to selection on clutch sizes that maximize annual fecundity.

Many birds lay one egg a day until their clutches are complete and then begin incubating. That means that larger clutches are exposed to predators for a longer period of time. For many species, predation usually results in loss of the entire clutch or brood (e.g. Wood Thrush, *Hylocichla mustelina;* Farnsworth 1998). Perrins (1977) related optimal clutch size directly to risk of predation. He proposed a mathematical model based on a constant daily survival rate of nests and the trade-off between clutch size and predation risk. He estimated fecundity (F) as,

$$F = ns^{n+L} \tag{1}$$

where n represents the clutch size, L is the number of days of incubation needed to hatch the eggs, and s is daily nest survival rate. We have changed Perrins' notation slightly to match notation used in our models. By taking the partial derivative with respect to n, Perrins related optimal clutch size to daily survival rate of nests:

$$n_{\text{opt}} = \frac{-1}{\ln(s)} \tag{2}$$

For example, with a daily nest survival rate of 0.95, the predicted optimal clutch size is 19.5 eggs.

The optimum predicted by Perrins' model would be reduced if daily nest survival rate were modeled to decrease with larger clutches. Skutch (1949) hypothesized that larger broods have higher predation rates due to increased activity at the nest. He reasoned that in altricial birds, more begging chicks and more frequent feeding trips by adults could attract attention of predators. There has been some empirical support for the mechanisms of that hypothesis (Mullin and Cooper 1998, Martin et al. 2000),

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but others have failed to find that (Roper and Goldstein 1997). Ricklefs (1977) developed an optimal clutch-size model for single nesting attempts that incorporated lower nest survival for larger clutch sizes. He concluded that even with higher predation rates on larger clutches, that alone was not likely to be a major factor determining evolution of clutch size.

Departing from traditional inquiries about clutch size at which fecundity of a single clutch is a maximum, some investigators have examined how clutch size may affect lifetime reproductive success. Lima (1987) developed a model in which an increase in clutch size was associated with an increase in predation risk to nesting females as well as to their dependent chicks, thus reducing her future reproductive potential. That model showed that under high nest-predation rates, smaller clutch sizes were more productive than larger clutch sizes. Murray (1979) used an interesting approach to evolution of clutch size by assuming that females are selected to produce the minimum clutch size necessary to replace themselves based on the Euler-Lotka equation. That model has predicted clutch sizes close to those observed for at least two species (Prairie Warbler [*Dendroica discolor*]; Murray and Nolan 1989, and Florida Scrub-Jay [*Aphelocoma coerulescens*]; Murray et al. 1989), but the model also requires the assumption that larger clutches incur a larger survival cost to the female, reducing her prospects for future breeding success.

All of those studies have investigated influence of clutch size on either fecundity of a single nesting attempt or lifetime fecundity of a female. In this paper, our goal is to investigate the relationship between clutch size and a female's annual fecundity. We sought to begin by using a minimum number of assumptions. We describe here two mathematical models that are capable of incorporating the renesting behavior of multiple-brooded species. These models do not invoke mechanisms that have direct negative effects on larger clutches such as those employed by Ricklefs (1977), Lima (1987), and Murray (1979). This approach provides a new framework for testing ideas about clutch size. We use the models to find clutch size at which annual fecundity is a maximum. We examine how that optimal clutch size changes with changes in both the length of breeding season and survival rate of nests. Additionally, we investigate how intraseasonal variation in clutch size may affect annual fecundity.

Other models have been developed to estimate annual fecundity in multiple-brooded bird species (Ricklefs 1970, Pease and Grzybowski 1995), but those have not been applied to questions of optimal clutch size. Ricklefs (1970) developed a model that converted estimates of nest survival, season length, and renesting behavior into estimates of annual fecundity. It assumed a constant rate of nest initiation throughout the breeding season. That rate was set equal to rate of nest termination, keeping the number of active nests at equilibrium. In this model, survival rate of nests determined the proportion of successful nests and the average duration of a nesting attempt because higher predation rates increase proportion of nests that fail early in the nesting cycle. The resulting model calculated a constant number of fledglings produced per day for a large population (see also Ricklefs and Bloom 1977). Pease and Grzybowski (1995) developed an approach that incorporated pulses of nesting activity by allowing the number of active nests to fluctuate throughout the breeding season. Their model applied instantaneous rates of nest predation and brood parasitism in a continuous-time model adapted from Von Foerster equations. The model does not assume a constant rate of nest initiation throughout the breeding season. Our approach is based on a discrete-time probability model, roughly analogous to a special case of the model of Pease and Grzybowski (1995) with constant parameters and no parasitism. However, our model is capable of limiting number of eggs a female can lay per season; previous models have not included that potentially important constraint. Birds do not have unlimited resources (including a limited time remaining in the breeding season), and that limitation may have implications for evolution of clutch size.

MODEL DESCRIPTIONS

Our approach is based on the assumption that a nesting female will renest after her nest fails or she fledges a brood, provided there is enough time remaining in the breeding season to fledge another brood (for a list of parameters, see Table 1). The logical formulation of the model is as follows. A breeding female begins the season with an initial nesting attempt. She

TABLE 1. Parameters used to calculate annual fecundity in multiple-brooded bird species.

Parameter	Value(s)	Explanation
L	25 days	Length of nesting cycle from the time the last egg is laid to the time all chicks leave the nest
d	8 days	Number of days between failure of one nest and first egg of subsequent nest
D	14 days	Number of days from a successful nest to the first egg of subsequent nest
t	60, 90, 120 days	Length of breeding season
s	0.93, 0.95, 0.97	Daily nest survival rate
n	1 to 30 eggs	Clutch size
m	2, 3, 4	Maximum number of nesting attempts per season

lays one egg each day until her clutch is complete. The nest is subject to a constant probability of predation every day from the day the first egg is laid. If the first nest fails, and there is enough time remaining in the breeding season to complete another nest, the female will renest a set number of days later. Similarly, if the first nest successfully fledges young, and enough time remains in the season, the female will renest a set number of days later. The same rules apply any time a nest's fate is determined, with an additional restriction that females are limited to a fixed maximum number of nests per season. The restriction on the maximum number of nesting attempts was necessary to evaluate annual fecundity for different strategies of laying the same number of eggs with a uniform clutch size (e.g. three clutches of four eggs each vs. four clutches of three eggs each).

Model 1.—This model calculates the probability of successfully fledging one or more broods (P) and the resulting annual fecundity (F) when the clutch size (n) is constant throughout the season:

$$P_i = s^{n+L} \sum_{j=i}^{m} R_{i,j} \tag{3}$$

$$F = n \sum_{i=1}^{m} P_i \tag{4}$$

The term s^{n+L} is the probability of fledging a brood, and $R_{i,j}$ represents the probability that there will be enough time remaining in the season for the jth nest to fledge the ith brood. For example, $R_{1,3}$ is the probability the first two attempts fail with enough time remaining to complete a third nesting attempt. $R_{i,j}$ incorporates the ability to renest as well as the constraints of the limited breeding season (see Appendix for detailed calculations). The summation $\Sigma_{j=i}^{m} R_{i,j}$ is the sum of probabilities of all the independent ways to attempt the ith brood with a maximum of m nesting attempts. The annual fecundity is simply the product of clutch size (n) and the sum of P_i from 1 to m.

Because P_i represents the probability of fledging at least i nests, probability of failing to fledge any young is $1 - P_1$. The probability of fledging i and only i nests is $P_i - P_{i+1}$. Thus variance of seasonal fecundity is

$$\sigma_F{}^2 = \sum_{i=0}^{m} (P_i - P_{i+1})(in - F)^2 \tag{5}$$

Model 1 assumptions:

1. Clutch size is constant for all nests.
2. A female nests up to m times if there is time remaining in the breeding season.
3. Daily nest survival is constant and independent. Nest survival does not vary during the breeding season, for different nest stages, or for different nests.
4. All eggs hatch and all chicks fledge in successful nests.
5. There is no adult mortality during the breeding season.
6. The time it takes to initiate the subsequent nesting attempt does not vary.

Model 2.—We relaxed the assumption of constant clutch size to examine possible advantages of having different clutch sizes during the season. We allowed each of four possible nesting attempts to have a different clutch size (n_1 to n_4). All other assumptions above still apply to that model. With that approach, it is no longer useful to have the parameter m or to calculate P_i because clutch sizes will vary with different ways a female can fledge i broods. The new estimate of annual fecundity can be calculated directly as:

$$F = \sum_{i=1}^{4} \left(\sum_{j=i}^{4} n_j s^{n_j+L} R_{i,j} \right) \qquad (6)$$

The nesting cycle ($n_j + L$) now depends on clutch size of a particular nesting attempt because it takes one day to lay each egg of the jth clutch (n_j). The expected number of chicks fledged from the jth nesting attempt is the product of the clutch size (n_j) and probability the nest will survive for the length of the jth nesting cycle ($n_j + L$). The calculations of $R_{i,j}$ in model 2 incorporate an approximation for the probability of renesting (see Appendix for details).

METHODS

We evaluated the model for a variety of parameter values typical of natural populations. For all models tested, we used the same values for three parameters (Table 1). The value used for L (25 days) is realistic for a taxonomically diverse array of bird species, including precocial as well as altricial species. For precocial species, L can be defined as length of time from onset of incubation to hatching of the eggs (e.g. for Northern Bobwhite [*Colinus virginianus*], $L = 24$ days, and Mallard [*Anas platyrhynchos*], $L = 26$–29 days; Baicich and Harrison 1997). For altricial species, L represents addition of the incubation stage and the nestling stage (e.g. for Carolina Wren [*Thryothorus ludoviscianus*], and Wood Thrush, $L = 26$ days; Baicich and Harrison 1997). The values used for the renesting intervals ($d = 8$ and $D = 14$ days) are typical for species that renest quickly such as the Prairie Warbler and Black-capped Vireo (*Vireo atricapillus*; Pease and Grzybowski 1995). The values for breeding season length (t) and daily nest survival rate (s) were chosen to represent a range of possibilities in order to examine trends in optimal clutch size.

Model 1 with no limit on number of eggs.—We computed annual fecundity for a hypothetical, multiple-brooding species with a breeding season (t) of 90 days and a daily nest survival rate (s) of 0.95. We allowed breeding females to attempt a maximum of four nests, and we varied the clutch size from 5 to 20 eggs.

Model 1 with limited number of eggs.—To further examine trade-offs between clutch size and annual fecundity, we compared different nesting strategies: two large clutches, three medium clutches, or four small clutches. We asked: for a given level of reproductive investment, measured as the total number of eggs laid, which strategy yields highest annual fecundity? Resources available to a breeding female are limited, and it is reasonable to assume that those limits constrain number of eggs a female can lay (*sensu* Milonoff 1989). Using the same values for daily survival rate ($s = 0.95$), we examined expected fecundity for a female restricted to laying a maximum of 12 or 24 eggs with a breeding season length (t) of 60, 90, and 120 days. We used the same model parameters to examine effect of different nest survival rates on optimal clutch size. Using the moderate season length ($t = 90$ days), we examined annual fecundity for daily nest survival rates ($s = 0.93$, 0.95, and 0.97).

Model 2 with no limit on number of eggs.—We computed the optimal strategy for each of the nine combinations of season length and nest survival rate in the absence of any limitation on total number of eggs. We tested a broad range of combinations of clutch size for each of the four nesting attempts.

Model 2 with limited number of eggs.—In a similar manner, we compared expected annual fecundity from different strategies of laying a set number of eggs without the restricting assumption that all clutches are the same size.

RESULTS

Model 1 with no limit on number of eggs.—Under the assumptions of model 1 with no additional constraints, there exists a maximum expected annual fecundity of 5.13 chicks at a clutch size of 13 eggs (Fig. 1) when the season was 90 days long and survival rate was 0.95. Probability of fledging at least one nest was 0.375, and probability of fledging two nests was 0.020. Peak annual fecundity from single-brooding alone was 5.02 chicks, which occurred at a clutch size of 16 eggs. Both probability of fledging zero chicks (e.g. $1 - P_1 = 0.625$ for $n = 13$ and $1 - P_1 = 0.686$ for $n = 16$) and the variance (e.g. $\sigma^2 = 47.2$ for $n = 13$ and $\sigma^2 = 55.1$ for $n = 16$) was higher for larger clutches.

Model 1 with limited number of eggs.—When number of eggs was limited, smaller clutches were more productive than large clutches for both long breeding seasons (Fig. 2) and low survival rates (Fig. 3). With a seasonal limit of

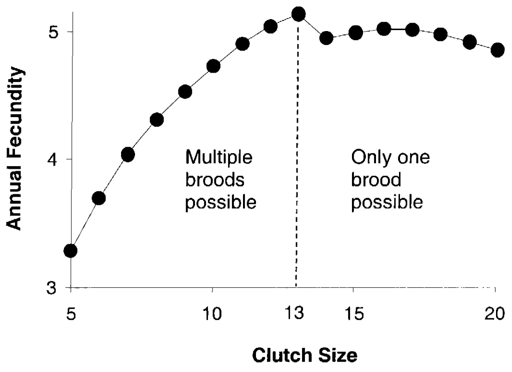

FIG. 1. Expected annual fecundity versus clutch size for a bird with season length (t) of 90 days, and daily nest survival (s) of 0.95. The dotted line represents the optimal clutch size. This occurs at the maximum clutch size for which double-brooding is possible (13 eggs).

12 eggs, a clutch size of 6 eggs (2 clutches) produced the maximum number of fledglings when the season length was 60 days long ($F_{n=6}$ = 2.05, $F_{n=4}$ = 1.73, $F_{n=3}$ = 1.40). A clutch size of 4 eggs (3 clutches) produced the maximum when the season was 90 days long ($F_{n=6}$ = 2.45, $F_{n=4}$ = 2.51, $F_{n=3}$ = 2.25). And a clutch size of 3 eggs (4 clutches) produced the most fledglings when the season was 120 days long ($F_{n=6}$ = 2.45, $F_{n=4}$ = 2.71, $F_{n=3}$ = 2.72). When the breeding season length was held constant at 90 days to investigate effect of survival rate, maximum expected fecundity was achieved with a clutch size of 4 eggs (3 clutches) at survival rates of 0.93 and 0.95. A clutch size of 6 eggs (2 clutches) was most productive with a nest survival rate of 0.97. A similar result was achieved when total number of eggs a female could lay was restricted to 24 eggs. With a short season, the best strategy was to lay two clutches of 12 eggs. A moderate breeding season favored three clutches of 8 eggs, and a long season favored four clutches of 6 eggs. When the season length was held at 90 days, the largest clutch size (n = 12, m = 2 clutches) was most productive at the highest survival rate (s = 0.97) and the smallest clutch size (n = 6 eggs, m = 4) was most productive at the lowest nest survival rate (s = 0.93).

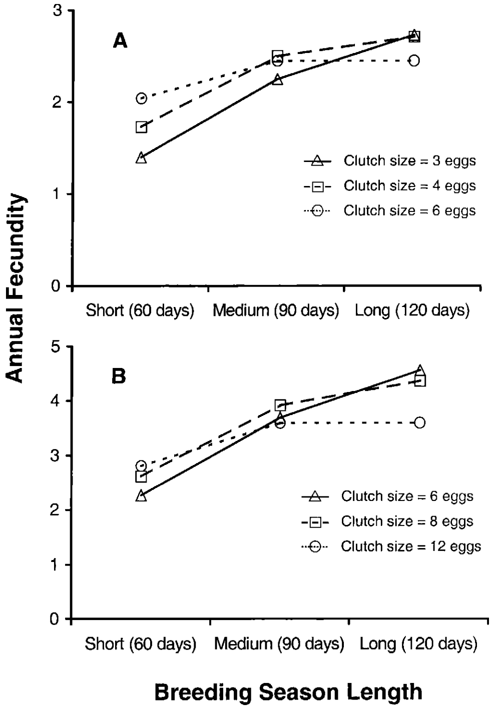

FIG. 2. Annual fecundity versus season length for different ways to lay a maximum of (A) 12 eggs and (B) 24 eggs. Daily nest survival was constant (s = 0.95). Triangles represent a maximum of m = 4 clutches, squares m = 3 clutches, and circles m = 2 clutches. Annual fecundity is higher for smaller clutch sizes as the length of the breeding season increases.

Model 2 with no limit on number of eggs.—Larger clutches were more productive when nest survival rates were high, and more uniform clutch sizes were more productive when breeding seasons were long (Table 2).

Model 2 with limited number of eggs.—When total number of eggs laid was restricted to either 12 or 24, the same trend in optimal clutch size was apparent (Table 2). Longer seasons and higher levels of nest predation favored more nesting attempts with fewer eggs in each clutch. When breeding season was short and levels of nest predation were low, the most productive strategy had large initial clutches and small replacement clutches with no eggs reserved for the third or fourth nesting attempt. In general, longer seasons favored clutches of more uniform size. The two scenarios with the longest season and lowest survival had maximum productivity when clutch sizes were uniform ($n_1 = n_2 = n_3 = n_4$).

TABLE 2. Nesting strategies that maximize annual fecundity. Total number of eggs laid per year was unlimited or restricted to either 12 or 24 eggs. For each combination of season length and daily nest survival rate, we report the most productive combination of clutch sizes (n_1–n_4). Optimal clutches were smaller and more uniform throughout the season with longer seasons and lower nest survival.

Daily nest survival	60 days season				90 day season				120 day season			
	n_1	n_2	n_3	n_4	n_1	n_2	n_3	n_4	n_1	n_2	n_3	n_4
Unlimited number of eggs per season												
0.93	14	10	6	3	13	13	11	9	14	13	13	12
0.95	19	11	6	3	19	17	13	9	18	18	16	13
0.97	33	12	7	3	33	22	15	10	28	28	17	15
Number of eggs limited to 12 per season												
0.93	6	5	1	0	4	4	3	1	3	3	3	3
0.95	8	4	0	0	5	5	2	0	4	3	3	2
0.97	11	1	0	0	6	6	0	0	4	4	4	0
Number of eggs limited to 24 per season												
0.93	11	9	4	0	7	7	6	4	6	6	6	6
0.95	14	8	2	0	9	9	5	1	7	7	6	4
0.97	18	6	0	0	12	11	1	0	9	6	6	0

DISCUSSION

We developed models to predict clutch sizes that maximize annual fecundity of birds capable of renesting within a limited breeding season. The advantage of that approach is that the measure of annual fecundity is more ecologically relevant than fecundity of a single brood for such bird species. Other investigations of optimal clutch size have invoked compensatory mechanisms that have direct negative effects on fitness value of larger clutches, either by increasing predation rates on larger clutches (e.g. Ricklefs 1977) or by reducing future reproductive potential of adults (e.g. Lima 1987, Murray 1979). Although we do not dispute those potential mechanisms may be important for many species, it is important to understand how the optimal clutch size varies without those mechanisms. Our approach should serve as a new framework in which to test those and related ideas.

Applying a model with uniform clutch size (model 1) to a hypothetical multiple-brooded bird species, we found that the selective pressures of nest predation and season length alone can produce clutch sizes typical of many species of precocial birds. When the only constraint on the production of eggs was a limit of four nesting attempts per season, the predicted optimal clutch size was 13 eggs (Fig. 1). In that case, even though probability of successfully fledging two broods was only 2%, it was enough to increase the expected annual fecundity above that produced by larger clutches. A 90 day season was not long enough to allow double-brooding for clutches >13 eggs. Annual fecundity from clutches of 16 eggs ($F = 5.02$, $\sigma^2 = 55.1$) was close to that for 13 eggs ($F = 5.13$, $\sigma^2 = 47.2$), but larger clutches had a higher probability of complete reproductive failure (fledge zero young for the whole season) and higher variance. In that case, the most productive strategy was also the safer strategy. It may be beneficial for a female to employ a bet-hedging strategy by laying eggs in several small clutches, increasing the probability that at least one of the nests will fledge young.

That model also produced interesting results when we limited number of eggs a female could lay annually. The age-old maxim, "don't place all your eggs in one basket," presents the question: in how many "baskets" should a female place all her eggs? For a nesting bird, the answer appears to depend on both the length of the nesting season and survival rate of nests. Shorter seasons (Fig. 2) and higher nest survival rates (Fig. 3) favor a nesting strategy of fewer, larger clutches. Although absolute fecundity estimates are sensitive to values of the parameters used, the predicted trends are not. With a breeding season of 120 days, a clutch size of three eggs is only slightly more productive than a clutch size of four eggs (Fig. 2A). However, for even longer breeding seasons, the fe-

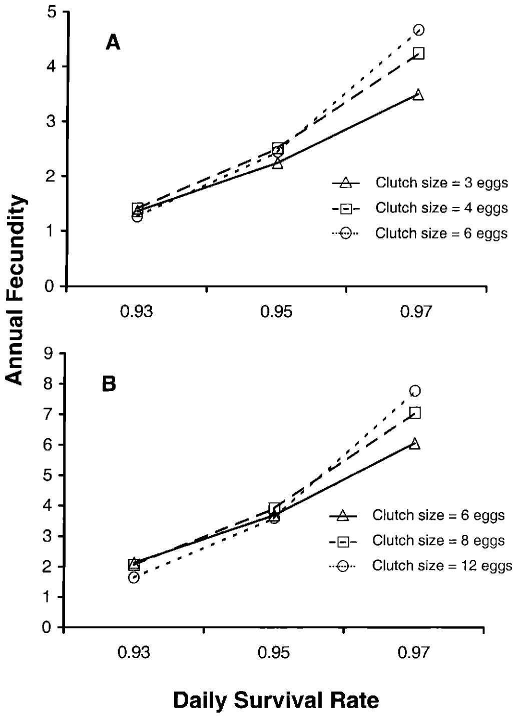

FIG. 3. Annual fecundity versus daily nest survival for different ways to lay a maximum of (A) 12 eggs and (B) 24 eggs. Season length (t = 90 days), nesting cycle (L = 25 days), and renesting intervals (d = 8 and D = 14 days) were held constant. Triangles represent a maximum of $m = 4$ clutches, squares $m = 3$ clutches, and circles $m = 2$ clutches. Annual fecundity is higher for larger clutch sizes as the daily survival of nests increases.

cundity of a strategy employing three-egg clutches outpaces that for four-egg clutches. Thus the trend is clear: longer breeding seasons favor more attempts of smaller clutches.

That result may help to explain two well-documented trends in clutch size. Clutch size generally increases with latitude, and species that nest in cavities have larger clutches than open-cup nesters (Lack 1947, Klomp 1970). Lack suggested the increase in clutch size with latitude reflected increasing breeding season day length and, hence, more foraging time for birds nesting farther north. However, that explanation failed to account for a similar increase in clutch sizes of nocturnal owls. Another theory to explain the trend was offered by Ashmole (1963), who proposed that clutch size was determined by differences in the breeding and nonbreeding season productivity of the environment. A harsh nonbreeding season allows the few survivors access to a rich food supply during the breeding season. That seasonal abundance allows birds to lay large clutches and raise large broods (Ricklefs 1980). The seasonality hypothesis accounted for latitudinal trends but failed to explain differences between cavity and open-cup nesters. Martin (1993) proposed that the large clutch sizes observed for cavity nesting species was not due to higher nest-survival rates, but was instead due to the need for nonexcavating species to maximize their fecundity from limited nest sites. In general, nonexcavating species have larger clutches than those species that excavate their own cavities. Our models predict both trends in clutch size as a function of breeding season length and nest survival rate. Larger clutches are favored as breeding season length decreases (as with increasing latitude, Fig. 2) and as nest survival rates increase (as for cavity nests, Fig. 3).

Perhaps the most interesting result of our model is that although smaller clutch sizes will never achieve the maximum fecundity possible with larger clutches, the constraints of season length and nest survival can make smaller clutches more productive on average than larger clutches. For example, in Figure 2B, with a season length of 120 days, there is enough time to raise two broods of 12 eggs (solid circles) but not enough time to raise three broods of 6 eggs (solid triangles). Thus, the maximum fecundity is 24 chicks with the larger clutch size, but the maximum fecundity is only 12 chicks with the smaller clutch size. It appears the probability of completing two attempts of 12 eggs is too low to compensate for the chance of fledging zero chicks. Even when a female is capable of laying 24 eggs, she is better off trying to raise only 12 chicks (6 at a time), and saving the other 12 eggs for renesting after nests fail. In fact, the model predicts that ~23% of the time, females with a clutch size of 6 eggs will not lay the maximum of 24 eggs per season.

We also found interesting patterns when we allowed clutch size to vary during the breeding season (model 2). Milonoff (1989, 1991) examined effect of different sizes of replacement clutches on annual fecundity, and showed that higher predation rates favor smaller initial clutches for precocial birds capable of renesting once or twice. When the first nest is more likely to fail, a female should save more resources for renesting. Our results agree with the predictions of Milonoff's renesting hypothesis and extend the approach to examine effects of a limited breeding season and multiple-brooding. Allowing clutch size to vary during the breeding season produced a trend toward smaller and more uniform clutches as breeding season length and nest predation rates increased (Table 2). Shorter breeding seasons, lower nest predation rates, or both favored fewer nesting attempts, larger initial clutches, and smaller replacement clutches. Slagsvold (1982) described a similar pattern with empirical data. He found that species with short breeding seasons and low nest-predation rates in Switzerland typically exhibited seasonal declines in clutch size.

We acknowledge that factors other than season length and nest survival rates can influence avian clutch size (see reviews by Monaghan and Nager 1997, Klomp 1970). In addition to the ideas involving direct costs associated with large clutches, such as those proposed by Skutch (1949), Lima (1987), and Murray (1979), other constraints on optimal clutch size are likely. For example, field studies have demonstrated effects of supplemental feeding and maternal effects on clutch size (e.g. Arsece and Smith 1988, Schluter and Gustafsson 1993, Nager et al. 1997). Renesting intervals are probably not independent of clutch size as we assumed in our models. In Great Tits (*Parus major*), renesting intervals increased when clutches were artificially enlarged, presumably reflecting higher costs of raising larger broods (Slagsvold 1984, Tinbergen 1987). Similarly, longer renesting intervals may reflect the additional time it takes females to accumulate reserves for larger replacement clutches (*sensu* Loman 1982). Other factors, such as molt, may also influence amount of time available for breeding. Tropical species may extend the breeding season by overlapping molting and breeding, allowing many nesting attempts with small clutches (Foster 1974). Although incorporation of those factors may make models more realistic, we do not believe that our simplifying assumptions alter the fundamental relationship between clutch size, length of the breeding season, and nest survival rates. Examining dynamics of more complex models should provide valuable insights into the factors constraining annual fecundity in birds.

ACKNOWLEDGMENTS

We thank Jeffrey Brawn, Steve Ellner, James Gilliam, Martha Groom, Kate Lessells, Jeremy Lichstein, Juan Manuel "Pajaro" Morales, Ian Newton, Sumita Prasad, Robert Ricklefs, Vanessa Sorensen, and anonymous reviewers for their thoughtful comments on earlier versions of this manuscript.

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Associate Editor: J. Brawn

APPENDIX. We define $T_{i,j}$ as the maximum number of days remaining in the breeding season when j nests have been attempted and i nests have succeeded. Thus,

$$T_{i,j} = t - (j - i)d - (i - 1)D - ic. \qquad (7)$$

The probability of attempting the jth nest, which, if successful, would fledge the ith brood, can then be calculated as:

$$R_{i,j} = \begin{cases} s^{(i-1)c}(1 - s)^{j-i}G_{i,j}, & T_{i,j} \geq 0 \\ 0, & \text{elsewhere,} \end{cases} \qquad (8)$$

where c is the length of the breeding cycle ($c = n + L$). $R_{i,j}$ sums the probabilities of all the possible ways to succeed $i - 1$ times and fail $j - i$ times, with enough time remaining in the breeding season to complete another nest. If $T_{i,j}$ is <0, then $R_{i,j} = 0$ because the breeding season is too short to accommodate i complete nesting cycles and the renesting delays associated with fledging $i - 1$ broods and failing $j - i$ times. If $T_{i,j} \geq 0$, $G_{i,j}$ accounts for all the possible independent ways to renest within the limited season. When a female has not failed in any nesting attempt ($j = i$, $i = 1$ to 4),

$$G_{i,j} = 1 \qquad (9)$$

All females with enough time left in the season will renest with a probability of one. When a female fails once during the breeding season ($j = i + 1$, $i = 1$ to 3),

$$G_{i,j} = i \sum_{x=0}^{\min[T_{i,j}, c-1]} s^x \qquad (10)$$

Because one of the nests failed, the female lost x days during which that nest remained active. The summation term in Equation (10) accounts for those lost days. Number of days that can be lost is limited by either the length of the breeding season ($T_{i,j}$) or by number of days in the breeding cycle ($c - 1$). If the failed nest were to have survived c days, it would have fledged. When a female fails twice during the breeding season ($j = i + 2$, $i = 1$ to 2),

$$G_{i,j} = (2i - 1)\left[\sum_{x=0}^{\min[T_{i,j}, c-1]} (x + 1)s^x + \sum_{y=c}^{\min[T_{i,j}, 2c-2]} (2c - y)s^y\right] \qquad (11)$$

The x and y terms in Equation (11) represent number of days lost during the previous two failed nests. Now that number of lost days are divided between two nesting attempts, the upper limit (other than the length of the breeding season) is $2c - 2$ because neither of the two nests could have remained active longer than c days. The first summation term accounts for all the ways these lost days may be divided into the two failed attempts up to $c - 1$ days. The second summation term is necessary to correct for the fact that once the total number of lost days is greater than c, there are fewer ways to divide these days between two nesting attempts. Finally, when a female has failed three times during the breeding season ($j = 4$, $i = 1$),

$$
\begin{aligned}
G_{1,4} = {} & \sum_{x=0}^{\min(T_{1,4},c-1)} \frac{x^2 + 3x + 2}{2} s^x \\
& + \sum_{y=c}^{\min(T_{1,4},2c-2)} \\
& \times \left(\frac{y^2 + 3y + 2}{2} \right. \\
& \qquad \left. - 3\frac{(y - c)^2 + 3(y - c) + 2}{2} \right) s^y \\
& + \sum_{z=2c-1}^{\min(T_{1,4},3c-3)} \\
& \times \frac{(3c - z - 3)^2 + 3(3c - z - 3) + 2}{2} s^z
\end{aligned}
\tag{12}
$$

The terms x, y, and z are the total number of days lost during the three unsuccessful nesting attempts before attempting the fourth nest. The logic for Equation (12) is the same as that for Equations (10) and (11). The details are more complicated because the number of lost days must now be divided among three failed nesting attempts.

Model 2. To allow for variable clutch sizes within a season, we defined a new parameter, c_j, as the average length of the nesting cycle for the first j nesting attempts. When the values for c_j are used in the model, they are rounded to the nearest integer because the minimum time-step is a whole day. We substituted the new parameter c_j for c in Equation (7) such that:

$$
\begin{aligned}
T_{i,j} = {} & t - (j - i)d - (i - 1)D - (i - 1)c_{j-l} \\
& - (n_j + L)
\end{aligned}
\tag{13}
$$

All the c terms in Equations (8–12) are simply replaced by c_{j-1}. This is because the limitation due to the length of the season ($T_{i,j}$) must include the length of the jth nesting cycle ($n_j + L$), but the calculation of the re-nesting limits ($R_{i,j}$ and $G_{i,j}$) is only restricted by the nesting cycle of the previous ($j - 1$) nesting attempts, here modeled as the average of those nest cycles (c_{j-1}).