Relationship between Mayfield nest-survival estimates and seasonal fecundity: A cautionary reply

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Source: The Auk, 122(3) : 1000-1001

Published By: American Ornithological Society

URL: https://doi.org/10.1642/0004-8038(2005)122[1000:RBMNEA]2.0.CO;2

Letters

The Auk 122(3):1000–1001, 2005

Relationship between Mayfield nest-survival estimates and seasonal fecundity: A cautionary reply.—Jones et al. (2005a) used data from an intensively studied population of Black-throated Blue Warblers (*Dendroica caerulescens*) to evaluate the correlation between empirical estimates of seasonal fecundity and estimates derived from a model developed by us (Farnsworth and Simons 2001). They reported that our model substantially underestimated seasonal fecundity. That conclusion was entirely in error. When used as described by Jones et al. (2005a), our model actually estimates substantially higher seasonal fecundity than that derived from empirical data. However, we do not recommend using our theoretical model in this manner to estimate seasonal fecundity or to assess population status. Here, we provide a brief discussion of modeling seasonal fecundity in multibrooded birds, with recommendations on using a modified version of our model for these purposes.

The model is a deterministic mathematical model that estimates seasonal fecundity on the basis of daily survival rates of nests and renesting behavior of breeding females (i.e. how quickly a female initiates a new nest after failed and successful attempts) within a limited breeding season. The model estimates the probability of fledging one or more broods. Jones et al. (2005a) apparently made one or more errors in interpretation or implementation when transcribing the mathematical description into an EXCEL spreadsheet. We reviewed our original published description and discovered a minor typographical error, which we redress here (see Appendix). However, that error alone could not have caused the surprisingly low values reported by Jones et al. (2005a).

Our model (Farnsworth and Simons 2001) was created to assess the constraints and trade-offs that shape the evolution of clutch size in multibrooded bird species. In that analysis, we examined how the allocation of eggs among multiple nesting attempts influenced seasonal fecundity under different conditions. Our theoretical investigation compared relative estimates of seasonal fecundity to find maxima. That analysis did not require an adjustment in brood sizes to account for partial losses before fledging. Such adjustments can easily be incorporated when estimating seasonal fecundity for actual breeding-bird populations (Farnsworth 1998). We recommend using our model to estimate the probability of fledging one brood and the probability of fledging two broods (and when necessary, the probability of fledging three and four broods) and multiplying those estimates by the average realized brood size (n_f = number of fledglings per successful nest). See the Appendix for mathematical substitutions to the model description in Farnsworth and Simons (2001).

We are not surprised that corrected estimates of seasonal fecundity from our model are higher than empirical estimates (Table 1 in Jones et al. 2005b). Our model assumes that each female continues to renest as long as sufficient time remains in the breeding season, up to a maximum number of nesting attempts. That renesting behavior may be unrealistic for many species, but our model can be adjusted easily to accommodate more conservative assumptions (see Appendix). By contrast, empirical estimates of seasonal fecundity are necessarily biased low. Even in the intensively studied population of Black-throated Blue Warblers at Hubbard Brook, observations are not perfect. For example, Jones et al. (2005a) described a banded male observed feeding a fledgling from an unobserved nest on their study site. Empirical studies will underestimate fecundity when some nests in the study area are not discovered or when females move into or out of the study area between nesting attempts. Some females that leave the study area during the breeding season may in fact breed elsewhere.

We commend Jones et al. (2005a) for attempting to compare seasonal fecundity estimates from a long-term empirical study with those derived from our modeling approach. We agree with those authors that accurate estimates of seasonal fecundity are vital for answering questions about population viability, source–sink dynamics, and conservation status. We also agree with Grzybowski and Pease (2005) that simple algorithms, assuming all females attempt a fixed number of nests, overestimate fecundity at high levels of nest survival and underestimate it at low levels of nest survival. However, we believe that our modeling approach overcomes that shortcoming by constraining the maximum number of nesting attempts in relation to the length of the breeding season. To make seasonal fecundity estimation more readily available to researchers, we have provided a copy of "Model 1" from Farnsworth and Simons (2001), including the modifications described here, at staff.xu.edu/~farnsworth/renest.xls.

Nevertheless, we recognize that our model remains a gross oversimplification of the complex processes governing seasonal fecundity in real populations. Our model requires assumptions that may be unrealistic

for some populations. For example, the survival rate of nests may vary throughout the nesting cycle or nesting season. Similarly, the amount of time required to renest may vary throughout the nesting season. Temporal variations such as these are not incorporated in our current modeling framework. Those types of variability are more easily incorporated in alternative modeling strategies, such as individual-based simulations (see Farnsworth 1998).—George L. Farnsworth, *Department of Biology, Xavier University, Cincinnati, Ohio 45207, USA (e-mail: farnsworth@xavier.edu)*; and Theodore R. Simons, *USGS Cooperative Fish and Wildlife Research Unit, Department of Zoology, North Carolina State University, Raleigh, North Carolina 27695, USA*.

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Grzybowski, J. A., and C. M. Pease. 2005. Renesting determines seasonal fecundity in songbirds: What do we know? What should we assume? Auk 122: 280–291.

Jones, J., P. J. Doran, L. R. Nagy, and R. T. Holmes. 2005a. Relationship between Mayfield nest-survival estimates and seasonal fecundity: A cautionary note. Auk 122:306–312.

Jones, J., P. J. Doran, L. R. Nagy, and R. T. Holmes. 2005b. Mayfield nest-survival estimates and seasonal fecundity: Reply to Farnsworth and Simons. Auk 122:1001–1003.

Appendix

We correct an error in Farnsworth and Simons (2001). In that paper, equation 11 should be replaced with:

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

See Farnsworth and Simons (2001) for definitions of symbols.

The original formulation of the model had the assumption that all females renested as long as time remained in the breeding season (up to a maximum number of nesting attempts, m). The model can be amended easily to relax that assumption in populations where the probability of renesting is believed to be less than unity. To accomplish that, we introduce a parameter r, defined as the probability of renesting. Equation 3 in Farnsworth and Simons (2001) thus becomes:

$$P_i = s^{n+L}\sum_{j=i}^{m} r^{j-1}R_{i,j}$$

The original model also allowed a female to fledge as many broods as the maximum number of nesting attempts, m. That assumption may be violated in populations such as Black-throated Blue Warblers in New Hampshire, where females routinely engage in three nesting attempts but are not known to fledge three broods (J. Jones pers. comm.). A modification to the model to overcome that assumption is straightforward. Equation 4 in Farnsworth and Simons (2001) should be replaced with:

$$F = n_f\sum_{i=1}^{k} P_i$$

where k is the maximum number of broods per female per breeding season, and n_f is the realized brood size (number of fledglings per successful nest).

Received 1 April 2005, accepted 11 May 2005

The Auk 122(3):1001–1003, 2005

Mayfield nest-survival estimates and seasonal fecundity: Reply to Farnsworth and Simons.—Farnsworth and Simons (2005) questioned our use of their previously published fecundity model (Farnsworth and Simons 2001) in our assessment of the relationship between Mayfield nest-survival estimates and seasonal fecundity in the Black-throated Blue Warbler (*Dendroica caerulescens*) (Jones et al. 2005). Briefly, they disputed our finding that their model substantially underestimates seasonal fecundity and offered what they believe are the correct estimates based on the data we provided in our paper. After a detailed and amicable exchange with the model's senior author (Farnsworth), we discovered an error in how we had translated the model's description ("Model 1" in Farnsworth and Simons 2001) onto an EXCEL spreadsheet. This error, which was solely the responsibility of the senior author (J. Jones), undervalued the contribution of late-season successful nests to seasonal fecundity. Here, we examine the consequences of this mistake.

As part of this examination, we believed it would be useful to redo our original analyses on the basis of the corrected estimates of fecundity provided by the model's authors (Table 1). The corrected estimates exhibit a positive relationship with our observed fecundity values (major-axis model II: $F = 7.93$, df = 1 and 14, $P = 0.01$, $r^2 = 0.36$, observed = –0.26 + [0.63 × estimated]). However, the slope of this relationship is still significantly different from 1.0 ($t = 2.85$, $P < 0.02$). The model estimates average 75.6 ± 8.9% (mean ± SE) higher (range: 22.1% to 150.2%) than observed fecundity

TABLE 1. Estimates of seasonal fecundity (number of fledglings per female per year) for 16 years of data from a study population of Black-throated Blue Warblers at Hubbard Brook, New Hampshire. Sample sizes for empirical estimates and fledglings per successful nest are not necessarily the same within a given year.

	Empirical estimates [a]	Correct model 1 estimates [b]	Fledglings per successful nest	Updated model 1 estimates [c]
1986	3.31	6.56	3.50	5.11
1987	3.55	7.15	2.88	4.34
1988	4.41	7.65	3.75	5.76
1989	3.44	5.29	3.53	4.17
1990	2.71	5.55	3.18	3.92
1991	3.53	7.74	3.40	5.86
1992	2.10	3.13	3.27	2.58
1993	2.35	4.73	3.20	3.21
1994	3.67	5.51	3.45	4.44
1995	2.24	4.43	3.14	3.03
1996	3.90	5.61	3.29	3.95
1997	3.29	4.86	3.67	3.92
1998	3.72	6.08	3.47	4.70
1999	3.91	5.20	3.37	3.81
2000	4.25	5.19	3.76	4.01
2001	2.09	5.23	2.75	3.14

[a] From Jones et al. (2005).
[b] Courtesy of George Farnsworth.
[c] Using online model (staff.xu.edu/~farnsworth/renest.xls).

values and are less representative at lower levels of observed fecundity (percentage of overestimate vs. observed fecundity; Pearson's $r = -0.55$, $P = 0.03$). Finally, the model estimates generate a value of $\lambda = 1.53$ (95% confidence interval [CI]: 1.43 to 1.64; see Jones et al. 2005 for population model details). For comparison, our observed fecundity values generated a value of $\lambda = 0.88$ (95% CI: 0.79 to 0.97). Whereas the direction of the differences between the model estimates and our observed seasonal fecundity differs greatly from our initial analyses, the overall conclusions of our original manuscript remain unchanged. Farnsworth and Simons's (2001) original model does not do a good job of predicting seasonal fecundity of a multibrooded species, and great care is needed in using nest-survival estimates (and models based on them) to assess population status or health.

In their letter, Farnsworth and Simons (2005) state that they did not intend for their original model to be used to estimate seasonal fecundity or to assess population status and offer three alterations to their original model to increase its use in a nontheoretical context: (1) relax the assumption that all females that can renest will do so if time permits, (2) restrict the number of successful broods to match empirical observations, and (3) use the number of fledglings per successful nest rather than clutch size to include the effects of partial predation. To test these recommendations, we reran our analyses using their updated model, now available online and easy to use. Although we assumed that all females that can renest would do so if there was enough time, we restricted the maximum number of broods (females never successfully raise more than two broods in a single season) and used the number of fledglings per successful nest rather than clutch size (Table 1). Grzybowski and Pease (2005:280) cautioned that "all estimates of seasonal fecundity in the literature derived by assuming a limited maximum number of nesting attempts or of successful broods are biased." However, we are confident that our modeling restrictions reflect realistic aspects of Black-throated Blue Warbler life history at Hubbard Brook.

The updated fecundity estimates (Table 1) exhibit a strong positive relationship with our observed values (major-axis model II: $F = 14.34$, df = 1 and 14, $P = 0.002$, $r^2 = 0.51$, observed = –0.14 + [0.83 × estimated]), and the slope of that relationship is not significantly different from 1 ($t = 0.74$, $P > 0.05$). The model estimates average 27.8 ± 5.0% higher (range: 5.7% to 66.0%) than observed fecundity values and still show a tendency to be less representative at lower levels of observed fecundity (percentage of overestimate vs. observed; Pearson's $r = -0.47$, $P = 0.06$). The updated model estimates generate a value of $\lambda = 1.23$ (95% CI: 1.14 to 1.32), which is significantly greater (no overlap in 95% CI) than the estimates based on our observations.

Consequently, even though the recommendations of Farnsworth and Simons (2005) greatly improve the predictive ability of their fecundity model (presumably, lowering the renesting probability would

further improve the estimates), the results still might lead to incorrect assessments of population health (i.e. a growing rather than barely stable population). One way in which the updated Farnsworth and Simons model might be improved further is to incorporate variation (by age or calendar day) in nest-survival rates (Shaffer 2004). In conclusion, we believe that an important result of this exchange and Farnsworth and Simons's updated model is their contribution to the growing recognition (see also Gzrybowski and Pease 2005) that researchers can no longer rely on simple measures (e.g. percentage of nest success or nest survival) or simple assumptions in the absence of detailed field data (e.g. all females attempt a fixed number of nests) when attempting to evaluate population status.—Jason Jones, *Department of Biology, Vassar College, Poughkeepsie, New York 12604, USA (e-mail: jajones@vassar.edu)*; Patrick J. Doran, *Wildlands Project, P.O. Box 455, Richmond, Vermont 05477, USA*; Laura R. Nagy, *Environmental Protection Agency, 200 SW 35th Street, Corvallis, Oregon 97333, USA*; and Richard T. Holmes, *Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755, USA.*

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Received 12 April 2005, accepted 15 May 2005

The Auk 122(3):1003–1004, 2005

A possible connection between crop milk and the maximum size attainable by flightless pigeons.—The Dodo (*Raphus cucullatus*) of Mauritius and the Solitaire (*Pezophaps solitaria*) of Rodrigues were approximately the same maximum size (~22.5 kg; Livezey 1993). Worthy (2001) recently estimated the weight of the extinct, flightless pigeon *(Natunaornis gigura)* of Fiji as "slightly smaller" than the Dodo's, which suggests that there might be some innate feature of these birds that limits the size they can attain. This limitation may have been the ability of the adults to produce sufficient crop milk to carry the young through the crucial early stages of their growth.

Like other columbids, Dodos and Solitaires presumably fed their young crop milk. Through the course of evolution from a relatively small, flying bird to a far larger, flightless one, the food requirements for a growing young (a cubic function) must have increased relatively more rapidly than the area of the lining of the crop (a square function). Besides reducing clutch size to the minimum of one, which the Dodo and Solitaire had done, the size of the crop itself can be enlarged, which is shown by the large bulge in the region of that organ in the detailed contemporary paintings of Dodos, or by increasing the area of the lining that produces the "milk" by means of folds or other inward projections of it. The Dodo's very large crop probably had a dual function: (1) adding space for food storage, so the Dodo could take a maximum amount of a large fruit; and (2) producing crop milk. The case of the Solitaire was quite different. Leguat's (1708) figure of the female—the only picture of a Solitaire by a contemporary who knew those birds well—does not show any indication of a very large crop or a partial separation of the stomach and the crop as in the Dodo. The picture shows instead two feather-covered "risings," one over each side of the crop. Those "risings" may have contained parts of the crop in which the lining was folded or otherwise increased in area. If that is true, they may have been the precursors of glands—in which case, Leguat's likening them to the beautiful bosom of a woman was more appropriate than he imagined. Leguat stated that those "risings" were found only in the female; because of the unusually great degree of sexual dimorphism in this species (Livezey 1993), Leguat was probably correct. If these (potential) glands of the female provided enough crop milk to bring the young beyond the stage during which crop milk was needed, it may have made possible a division of labor, whereby the male supplied food to his mate and to himself during that period. That may have been accomplished by the male's making tours of the pair's territory (or even beyond it), collecting food items in his crop, bringing them back to the female at the nest, and regurgitating them before her, a method that may have been used by both parents to feed the young after the crop-milk stage.

The Passenger Pigeon (*Ectopistes migratoria*) of North America, and presumably the Nicobar Pigeon (*Caloenas nicobarica)* of islands in the Indo-Australasian region, also laid clutches of one egg and moved in large flocks to areas of abundant food to breed. It was therefore vital for the young to be fledged and able to move with the flocks when the food supply was exhausted. Presumably, the crop milk from both parents accelerated the growth to that

point. On the other hand, the single clutch of some of the large pigeons, including the largest, crowned pigeons (*Goura*), is consistent with the crop-milk hypothesis.

Although we are not likely ever to prove or disprove a connection between crop milk and size in these pigeons, examination of the linings of crops of a variety of living pigeons for projections that might increase their surface area may offer clues as to how such areas evolved or which pigeons were ancestral to the Solitaire.—Robert W. Storer, *Museum of Zoology, University of Michigan, 1109 Geddes Avenue, Ann Arbor, Michigan 48109, USA. E-mail: rwstorer@umich.edu*

Acknowledgments

I thank both reviewers for their excellent suggestions.

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Received 23 April 2005, accepted 15 May 2005