

A MODEL TO PREDICT BREEDING-SEASON PRODUCTIVITY FOR MULTIBROODED SONGBIRDS

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ABSTRACT.—Breeding-season productivity (the per capita number of offspring surviving to the end of the breeding season) is seldom estimated for multibrooded songbirds because of cost and logistical constraints. However, this parameter is critical for predictions of population growth rates and comparisons of seasonal productivity across geographic or temporal scales. We constructed a dynamic, stochastic, individual-based model of breeding-season productivity using demographic data from Wood Thrushes (*Hylocichla mustelina*) in central Georgia from 1993 to 1996. The model predicts breeding-season productivity as a function of adult survival, juvenile survival, nesting success, season length, renesting interval, and juvenile-care intervals. The model predicted that seasonal fecundity (number of fledglings produced) was 3.04, but only 2.04 juveniles per female survived to the end of the breeding season. Sensitivity analyses showed that differences in renesting interval, nesting success, fledglings per successful nest, and adult and juvenile survival caused variation in breeding-season productivity. Contrary to commonly held notions, season length and fledgling-care interval length did not cause variation in breeding-season productivity. This modeling exercise emphasizes the need for demographic data for songbird species, and we encourage biologists to use similar models to evaluate productivity in songbird populations. Received 1 July 1999, accepted 8 February 1999.

BREEDING-SEASON PRODUCTIVITY, which we define as the per capita number of offspring surviving to the end of the breeding season, is an important life-history parameter that often is required for models of population growth (Pulliam 1996). However, most analyses of population viability rely on estimates of nesting success or seasonal fecundity as surrogate parameters for breeding-season productivity (e.g. Ricklefs and Bloom 1977, Holmes et al. 1992, Roth and Johnson 1993, Pease and Grzybowski 1995). Population modeling exercises have emphasized the need for demographic data for songbird species that might be used to predict breeding-season productivity (Thompson 1993, Donovan 1995a, Powell et al. 2000).

For songbirds that nest multiple times during a season, direct estimates of breeding-season productivity require estimates of season length, renesting-interval length, nesting suc-

cess, female survival, and juvenile survival, which are parameters that require constant monitoring of females and young during the breeding season. Pease and Grzybowski (1995) developed a model that used nesting success and lengths of the nesting season and renesting interval to estimate seasonal fecundity for a multibrooded species. However, their model probably overestimates seasonal fecundity because it does not incorporate female mortality during the breeding season. Pease and Grzybowski's (1995) model also does not incorporate juvenile mortality, which is necessary to predict breeding-season productivity.

For animal species with short bursts of reproductive effort, breeding-season productivity could be calculated as the product of (1) nesting success (probability of nest surviving until nestlings fledge), (2) mean number of offspring per successful nest, and (3) mean number of nesting attempts per female per year. However, multibrooded species produce juveniles over a period of several months. Juvenile survival during the breeding season is not 100% (An-

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ders et al. 1997, Powell et al. 2000). Also, juveniles produced early in the breeding season may have a lower chance of surviving to the end of the breeding season than juveniles produced late in the breeding season (Krementz et al. 1989). Some viability analyses for multi-brooded songbirds (Donovan et al. 1995b, Anders et al. 1997, Trine 1998) impose a "general" juvenile mortality rate on the numbers of juveniles produced during the year in an attempt to estimate productivity. This approach seems unwise at worst and imprecise at best, in light of the previous discussion.

Our objective was to construct a simulation model that would predict breeding-season productivity for a multibrooded songbird species. Beyond predicting a critical parameter value that we could not measure in the field, the model allows manipulations of demographic parameters, season length, and renesting-interval length that are not possible in empirical studies.

METHODS

We studied multibrooded Wood Thrushes (*Hylocichla mustelina*) at the Piedmont National Wildlife Refuge (PNWR) in central Georgia from 1993 to 1996. Radio-marked females began nesting in late April, and the last radio-marked fledglings left the nest in early August. Therefore, the 45-day battery life of our transmitters was shorter than the breeding season.

We estimated daily survival of females and juveniles from radio-marked birds using program SURVIV (White 1983), which uses likelihood-ratio tests (LRT) and Akaike Information Criteria (AIC) values to test between time-specific and constant-survival models. Survival estimates were obtained from 63 female and 38 juvenile Wood Thrushes (Powell et al. 1998). We used aerial telemetry to relocate birds that dispersed beyond the range of our hand-held telemetry equipment.

We also used program SURVIV (White 1983) to directly estimate nesting success using unequal monitoring intervals from 133 active nests and 1,624 exposure days. This method is similar to the Mayfield method (Mayfield 1975), but it does not require the assumptions of equal nest-visit intervals (Hensler and Nichols 1981, Bart and Robson 1982). We used AIC estimates from SURVIV to test between constant and time-specific nesting-success models. More details on telemetry methods, nest searching and monitoring, and parameter estimation are in Lang (1998), Powell (1998), and Powell et al. (1998). Although Lang (1998) and Powell (1998) reported constant

nesting success and individual survival estimates during the breeding season, the model could easily be adapted in situations that required time-specific estimates.

Model structure.—We constructed a dynamic, stochastic, individual-based model of Wood Thrush reproduction using SAS/IML (SAS Institute 1991) that incorporated female and fledgling dynamics. The model "followed" one Wood Thrush female and her offspring on a "random walk" through the breeding season (Fig. 1). We assumed that a mate was available for the female during the entire summer, so we did not model adult males. Our field observations indicated that the breeding season began on 24 April and that 15 July was the last day that nest construction could begin (82-day season). Each female that we radio-marked renested (after a failure or success) repeatedly before 15 July; therefore, we assumed the same for females in the model. We used five days as the time needed to build a nest (Roth et al. 1996). We defined a successful nest as a nest that produced at least one fledgling (i.e. a young that left the nest), and we used 18 days as the length of time that a female would care for fledglings before building another nest (Lang 1998). Fledglings were followed until 24 September, which is the median date of fall migration for Georgia (Beaton 1996, Roth et al. 1996).

Daily survival rates for females and juveniles (Lang 1998, Powell 1998), daily nesting success (Lang 1998, Powell 1998), and the number of fledglings per successful nest (Lang 1998, Powell 1998) were chosen randomly from proper distributions (see below) based on our field estimate of each demographic parameter and its variance (Table 1). Survival and nesting-success parameters were generated as beta random variables by specifying the parameter estimate and variance (from our field data) and solving for moment estimates of α and β , the beta parameters (Berger 1980:560). We then used SAS (1990:587–588) to generate the beta random variate (P) as a function of two gamma random deviates, with parameters α and β , respectively. The value of P generated was then used to generate the Bernoulli variable associated with the binary response (alive or dead, successful or unsuccessful).

We selected the number of fledglings per successful nest from a normal distribution and then rounded the random variable to the nearest integer to allow the model to follow individual offspring during the postfledging period. The demographic parameter estimates in Table 1 represent four years of pooled data, and the conditional variance associated with each parameter estimate does not reflect temporal variation in demographic parameters. We initially estimated true temporal variation by subtracting average estimated sampling variance from the variance among year-specific parameter estimates (Burnham et al. 1987:262, Link and Nichols 1994). However, this resulted in negative temporal variance estimates for

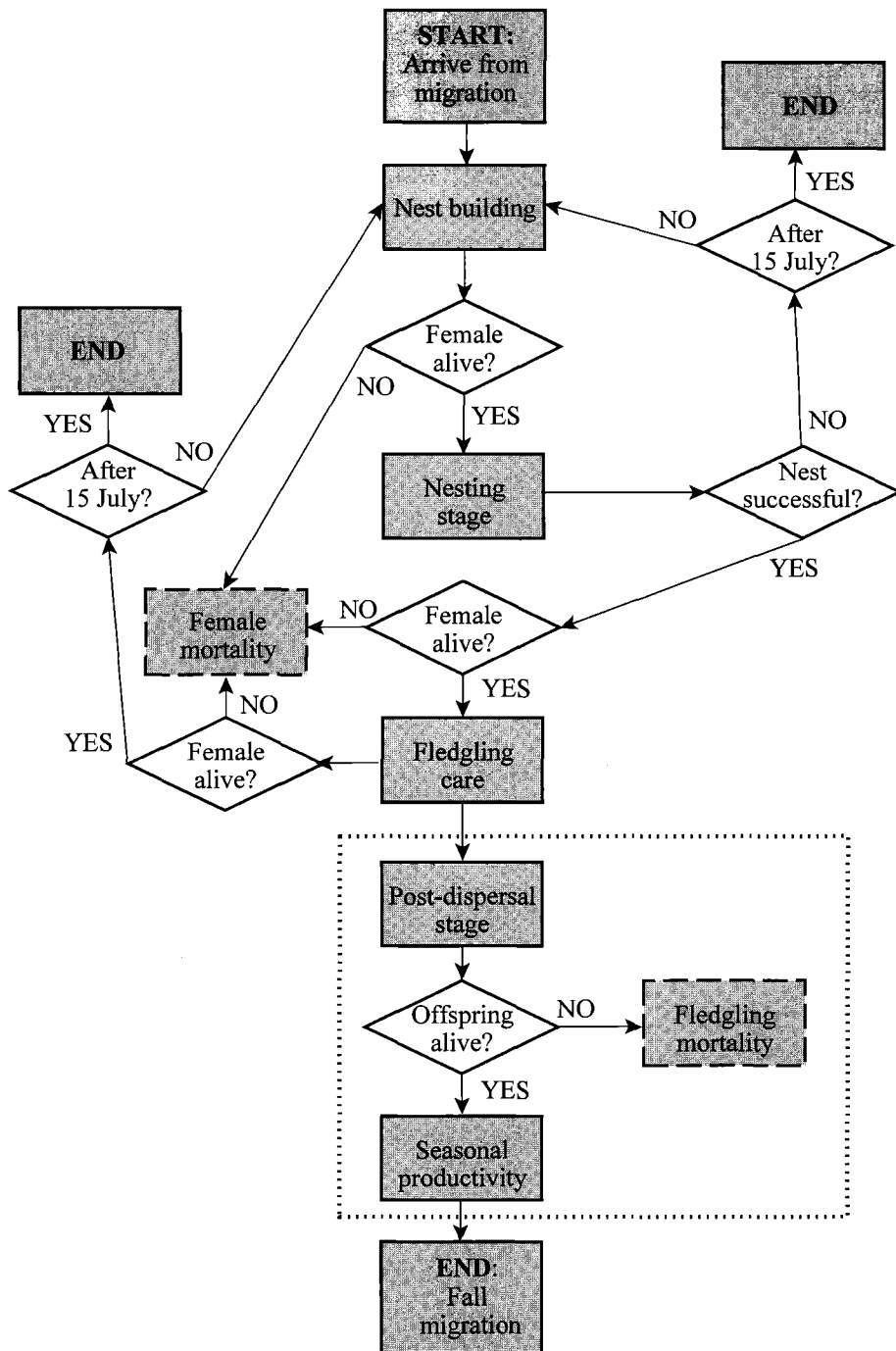


FIG. 1. Flow chart summary of our individual-based model of Wood Thrush reproduction. Demographic model parameters were stochastic and were based on field data collected at the Piedmont National Wildlife Refuge in central Georgia, 1993 to 1996. The model follows an adult female and her offspring (dotted box) to the end of the breeding season. Although this figure summarizes the breeding season in stages, daily demographic parameters were used in the model (see Table 1).

TABLE 1. Parameter estimates (\pm SE) used in the breeding-season productivity model for Wood Thrushes. Data collected from 1993 to 1996 at Piedmont National Wildlife Refuge, Georgia.

Parameter	Estimate	Time period	Source
Daily female survival	0.9973 \pm 0.006	Breeding season	Powell et al. 2000
Daily juvenile survival	0.9966 \pm 0.001	Postfledging period ^a	Lang 1998, Powell et al. 2000
Daily nesting success	0.9482 \pm 0.006	Breeding season	Lang 1998, Powell 1998
Fledglings/successful nest	2.786 \pm 0.645	24 April to 15 July	Lang 1998, Powell 1998
Fledglings/successful nest	2.889 \pm 0.601	24 April to 31 May	This study
Fledglings/successful nest	2.800 \pm 0.644	1 to 30 June	This study
Fledglings/successful nest	2.333 \pm 0.577	1 to 15 July	This study

^a Includes postdispersal period.

our parameters. Therefore, we doubled the conditional (i.e. sampling) variance to ensure that our prediction of breeding-season productivity was not more precise than the underlying demographic parameter estimates (J. D. Nichols pers. comm.).

Stochastic demographic parameters, once selected, were held constant for one simulated breeding season of n days. Mortality of individuals and nests was simulated daily by choosing a uniformly distributed random number, x_i , $x:0 \leq x \leq 1$, for each simulated day i , where $i = 1, \dots, n$. If x_i was greater than the stochastic demographic parameter value (P), the nest failed or the individual died on day i (e.g. $P = 0.998$; $x_1 = 0.553$, $x_2 = 0.999$; individual survives on day 1 when $x_1 < P$ but dies on day 2 when $x_2 > P$). A different x_i was chosen for adult survival, each juvenile's survival, and nesting success. The SAS/IML program can be obtained from L. A. Powell.

Analysis.—The model outputs were (1) the number of nests initiated by the female during the year, (2) the number of successful nests for the female during the breeding season, and (3) the number of fledglings produced by the female that survived to the end of the breeding season. Because the model incorporated several stochastic components, we performed 200 simulations to obtain mean and variance estimates for the model outputs. By setting female and juvenile survival at 1.00 (no mortality), we could use the model to predict annual production (as defined by Ricklefs and Bloom 1977) and seasonal fecundity (as defined by Pease and Grzybowski 1995). We compared the model's predictions of seasonal fecundity and breeding-season productivity using a Z-test.

We used a sensitivity analysis to assess the contributions of the four demographic parameters to the model's performance. We compared the model's predictions within a range of possible demographic parameter values. To determine the effect of variance in demographic parameters, we compared breeding-season productivity predictions under three other variance levels: 0.5, 2, and 4 times the estimate used in the model. We also performed sensitivity analyses by varying the values used for season length, nest-building interval, and fledgling-care interval to test for biases that might result if our parameter values

were incorrect. To determine if a time-specific estimate of brood size (number of fledglings per successful nest) was appropriate, we compared the model's predictions under constant and time-specific brood-size estimates from our field data (Table 1). We compared the model's predicted number of nests initiated by females to field data in an attempt to verify the model's performance. To avoid a Type I error that might occur with a linear regression analysis using so many data points, we simply compared the model's predictions of seasonal fecundity and breeding-season productivity using a Z-test and 95% confidence intervals of the predictions along the sensitivity gradient.

RESULTS

The model predicted that female Wood Thrushes attempted an average of $3.96 \pm$ SE of 0.10 nests per breeding season. Females under constant and time-specific estimates of the number of fledglings per successful nest had similar chances of producing no successful nests. About half of the females had one successful nest during the breeding season, and less than one-third of them had two successful nests during the breeding season (Fig. 2). Breeding-season productivity of Wood Thrushes at the PNWR was 2.04 ± 0.12 offspring per female per year using a constant estimate of the number of fledglings per successful nest, and 2.10 ± 0.11 using a time-specific estimate. With no female or juvenile mortality, the model predicted that seasonal fecundity was 3.04 ± 0.14 offspring per female.

Sensitivity analyses showed that differences in length of the breeding season did not cause variation in breeding-season productivity (62-day vs. 92-day season; $Z = 1.05$, $P = 0.29$), and the constant and time-specific models of the number of fledglings per successful nest usually were not different (Fig. 3). Increasing the

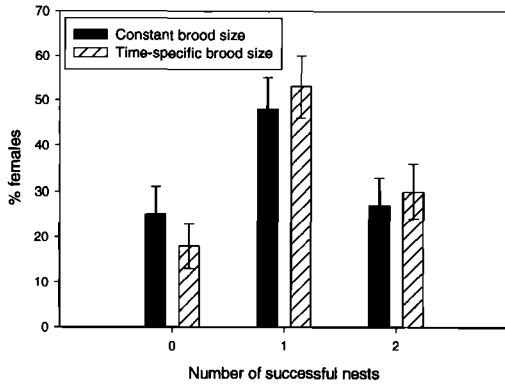


FIG. 2. Predicted proportion of female Wood Thrushes ($n = 200$ replications) producing zero, one, and two successful nests based on constant and time-specific estimates of the number of fledglings per successful nest. Whiskers denote 95% confidence intervals.

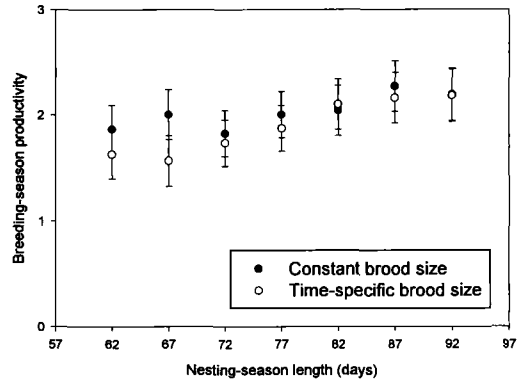


FIG. 3. Effect of nesting-season length on breeding-season productivity as predicted by the model ($n = 200$ replications). Breeding-season length used in other simulations was 82 days. Whiskers denote 95% confidence intervals.

nest-building interval caused breeding-season productivity to drop from 2.09 ± 0.11 offspring per female (3-day interval) to 1.74 ± 0.11 (9-day interval) offspring per female ($Z = 2.20, P = 0.03$). Parental-care intervals did not cause breeding-season productivity to vary significantly (13-day interval; breeding-season productivity = 1.97 ± 0.12 ; 28-day interval; breeding-season productivity = 1.87 ± 0.11 ; $Z = 0.56, P = 0.57$).

The model predicted that breeding-season productivity was approximately zero if juvenile and female daily survival rates fell below 0.975 (100-day survival rate of 0.08). Breeding-season productivity rose sharply within a narrow range of daily female and juvenile survival rates, and 100% juvenile survival resulted in higher breeding-season productivity than 100% female survival (Fig. 4). High nesting success resulted in higher breeding-season productivity than high adult and juvenile survival rates, and declines in nesting success resulted in an almost linear decline in breeding-season productivity within the range of perturbed values (Fig. 4). The number of fledglings per successful nest dramatically affected breeding-season productivity estimates; values of 1, 2, 3, and 4 fledglings per successful nest resulted in 0.76, 1.57, 2.31, and 3.28 fledglings surviving to the end of the breeding season, respectively. The model was not sensitive to the variance in female survival ($Z = 0.41, P = 0.68$) or juvenile survival ($Z = 1.46, P = 0.14$), but

increases in variance in nesting success, from one-half the variance estimate to four times the variance estimate, increased breeding-season productivity from 2.01 ± 0.11 to 2.36 ± 0.13 ($Z = 2.05, P = 0.04$).

We were relatively confident that we observed all nesting attempts of eight females in 1995 and 1996, because we radio marked them in early May and remarked them during the breeding season (Powell 1998). The average number of nesting attempts from this small sample was 3.13 ± 0.37 (95% CI 2.40 to 3.86) and ranged from two (both successful) to five

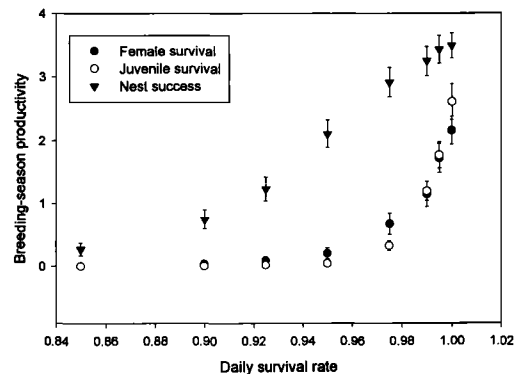


FIG. 4. Predictions of breeding-season productivity under varying survival rates (0.85, 0.90, 0.925, 0.95, 0.975, 0.99, 0.995, and 1.00). All parameters, with the exception of the parameter of interest, were stochastic, and whiskers denote 95% confidence intervals ($n = 200$ replications).

(all failures) during the breeding season. The 95% CI for our small sample overlapped the model's prediction of 3.96 nesting attempts (95% CI 3.77 to 4.15).

DISCUSSION

The highly mobile nature of multibrooded songbirds, including movements between nests and natal dispersal, has prevented biologists from accurately estimating breeding-season productivity. The costs and logistics of directly measuring songbird breeding-season productivity are very large (Pease and Grzybowski 1995), and most studies have provided only a few pieces of the demographic puzzle. Our modeling exercise shows the benefits of using a simulation model to predict a parameter that is critical to our understanding of songbird population dynamics. The model's prediction of breeding-season productivity was approximately two-thirds the prediction of breeding-season fecundity (i.e. the number of young fledged). The average loss of one offspring per female per year from female and juvenile mortality is significant, and such a bias would affect the predictions of population-viability analyses. Our results suggest that productivity is overestimated if survival of females and juveniles during the breeding season is not considered.

Seasonal fecundity fails to be a useful parameter for comparisons between time periods or study areas if adult or juvenile survival vary over time or among different habitats. Ricklefs and Bloom (1977) acknowledged that differential survival of females between study areas could bias yearly production estimates, but they assumed equal survival among their study areas. For some isolated populations, end-of-season mist netting may result in useful indices of productivity (J. Bart pers. comm.). Constant-effort mist netting across large spatial scales has also been used to compare changes in productivity indices over time (DeSante et al. 1996). However, most songbird populations probably exhibit high natal dispersal (Anders et al. 1998, Lang 1998, Vega Rivera et al. 1998), and mist-netting data may not provide an accurate index of breeding-season productivity if dispersal movements vary in distance and direction among years.

The model predicted that approximately half

of the Wood Thrush females have one successful nest per year, whereas about 20% of the females are unsuccessful in all nesting attempts (Fig. 2). Roth et al. (1996) reported that 22% of color-banded female Wood Thrushes were unsuccessful in Delaware. These predictions and observations suggest that a sizeable proportion of the population does not produce young each year. Roth et al. (1996) also suggested that age and environmental breeding conditions may contribute to individual female variation in productivity. We did not determine the age of adults, and our model did not account for these factors.

Roth et al. (1996), Trine (1998), and Weinberg and Roth (1998) estimated seasonal fecundity of Wood Thrushes in Delaware, southern Illinois, and Delaware as 2.6, 0.5 to 1.5, and 3.62 fledglings per female, respectively. Donovan et al. (1995b) estimated seasonal fecundity of Wood Thrushes in fragmented and contiguous areas of Missouri and Minnesota/Wisconsin as 0.85 to 1.95 and 1.12 to 2.40 fledglings per female, respectively. With the exception of Weinberg and Roth (1998), these values are lower than our model's predictions of seasonal fecundity (with no effects of adult or juvenile mortality). None of the above studies used radio telemetry, so some nesting attempts may have been missed, which would negatively bias the seasonal fecundity estimate. All of the above studies reported medium to high levels of nest parasitism, with the exception of Weinberg and Roth (1998). Wood Thrush nests were parasitized at very low rates (<0.5%) at PNWR (Lang 1998), which probably accounts for our higher seasonal fecundity estimate. Female and juvenile mortality are probably less variable than parasitism rates among areas. Therefore, the effect of female and juvenile mortality on breeding-season productivity in other geographic locations may be similar to the effect at PNWR. Our model predicts that Wood Thrushes at PNWR lost an average of 1.0 fledglings due to female and juvenile mortality. A similar loss from yearly production in southern Illinois and Missouri would bring yearly production estimates to nearly zero, which reemphasizes the need to account for reductions in fledgling productivity due to mortality.

Our model does not distinguish between sources of nesting failure from predation or parasitism. For species or areas with high par-

asitism rates, Pease and Grzybowski's (1995) model may be integral to understanding the relative contribution of predation and parasitism to seasonal fecundity. Parasitism often reduces brood size without causing nesting failure (Pease and Grzybowski 1995), and our model suggests that such reductions in brood size could reduce breeding-season productivity more than increased rates of predation (Fig. 4). Similarly, biologists often focus on improving nesting success to increase breeding-season productivity, but our results indicate that small increases in adult and juvenile daily survival can also have a large positive effect on breeding-season productivity. Therefore, habitat managers should consider the effects of habitat manipulations on songbird predation.

The sensitivity analyses may also provide information of interest to evolutionary biologists. For example, it is commonly believed that females can improve their fitness by reneating quickly, either by limiting the length of care of juveniles or transferring care responsibilities to their mates (Jackson et al. 1989). The fledgling-care interval we observed may be longer than in other portions of the Wood Thrushes' breeding range (R. R. Roth pers. comm.). Our results suggest that because successful nests are infrequent (Fig. 2), lengthening the time spent caring for fledglings before reneating (within the interval of 13 to 28 days that we tested) does not affect breeding-season productivity. Likewise, Ricklefs and Bloom (1977) predicted that longer breeding seasons in the tropics should result in higher productivity. In our model, increasing season length from 62 to 92 days caused only slight increases in breeding-season productivity (Fig. 3). Shortening the nest-building interval resulted in increased breeding-season productivity, as predicted by Jackson et al. (1989). Therefore, on average, females that are able to remain in their territory and build nests quickly should contribute more offspring to the population. We are not suggesting that our predictions are necessarily true, but rather that they be considered as viable, potentially testable alternative hypotheses.

Validation of the model's predictions is problematic, because the outputs are difficult to measure in the field using radio transmitters with short battery life. If telemetry data were available for all juveniles produced by a subset of females, our model could be validated by

comparing the actual number of juveniles alive at the end of the year with the predictions of our model, parameterized with data from another subset of females. In the only model-validation process that we could perform, the confidence intervals for nesting attempts per female from field observations and model predictions overlapped, suggesting no differences between our model and the real world. However, the large error associated with the field sample could have resulted in a wide range of model predictions being validated.

The predictions of nesting attempts at PNWR may seem high to some biologists, and our data from the southern edge of the Wood Thrushes' range may be unique. However, our model can be applied to any data set for comparative purposes. Future research efforts should be undertaken to provide validation for this model or to explore the effects of longer nest-building intervals and season lengths on breeding-season productivity. Furthermore, we encourage biologists to incorporate models similar to ours in evaluations of population viability. This modeling exercise emphasizes the need for demographic research that simultaneously estimates survival and nesting parameters. Although these types of projects are logistically challenging, they are essential for satisfactory viability analyses.

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