



MODELING POPULATION GROWTH OF THE OVENBIRD (*SEIURUS AUROCAPILLA*) IN THE SOUTHERN APPALACHIANS

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ABSTRACT.—Studies of source–sink dynamics are often prompted by concerns about negative population trends. Estimates of population trajectories are usually based on assumptions about survival rates and empirical measures of fecundity. Most models ignore the influence of the rates of renesting and multiple brooding. We used the Ovenbird (*Seiurus aurocapilla*) as a model Neotropical migratory songbird species to investigate the relative effects of annual female survival and components of annual fecundity on population growth rates. We applied productivity data from a three-year field study and data from Hann (1937) to several models of annual fecundity to examine the sensitivity of lambda to variations in annual female survival and the likelihood of renesting and double-brooding. Our simulations illustrate the importance of incorporating estimates of annual survival and rates of additional breeding attempts in songbird population models because population growth rates are quite sensitive to variations in these parameters. Lambda is especially sensitive to survival estimates and changes with them at the same order of magnitude. Whenever feasible, female survival and probabilities of additional breeding attempts should be estimated by direct methods. The indirect methods used in our study (annual female survival estimated from the age ratio of breeding females, and rates of renesting and double-brooding determined from the timing of reproduction) probably underestimated these parameters. *Received 27 September 2005, accepted 21 December 2006.*

Key words: annual fecundity, annual survival, double-brooding, Ovenbird, population growth models, renesting, *Seiurus aurocapilla*.

Modelado del Crecimiento Poblacional de *Seiurus aurocapilla* en el Sur de los Apalaches

RESUMEN.—Frecuentemente, los estudios de la dinámica de fuentes y sumideros son motivados por preocupaciones relacionadas con tendencias poblacionales negativas. Las estimaciones de las trayectorias poblacionales usualmente están basadas en suposiciones acerca de las tasas de supervivencia y en mediciones empíricas de la fecundidad. La mayoría de los modelos ignoran la influencia de las tasas de renidificación y de las nidadas múltiples. Utilizamos a *Seiurus aurocapilla* como un modelo de una especie de ave canora migratoria Neotropical para investigar los efectos relativos de la supervivencia anual de las hembras y de componentes de la fecundidad anual sobre las tasas de crecimiento poblacional. Aplicamos datos de productividad de un estudio de campo de tres años y datos obtenidos de Hann (1937) a varios modelos de fecundidad anual para examinar la sensibilidad de lambda ante variaciones en la supervivencia anual de las hembras y en la probabilidad de renidificar y de tener nidadas dobles. Nuestras simulaciones ilustran la importancia de incorporar estimados de la supervivencia anual y de las tasas a las que tienen lugar intentos adicionales de reproducción en los modelos de poblaciones de aves canoras, pues las tasas de crecimiento poblacional son bastante

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sensibles a variaciones en esos parámetros. Lambda es especialmente sensible a los estimados de supervivencia, y cambia con éstos en el mismo orden de magnitud. Siempre que sea posible, la supervivencia de las hembras y las probabilidades de intentos de reproducción adicionales deben ser estimadas mediante métodos directos. Los métodos indirectos empleados en nuestro estudio (la supervivencia anual de las hembras fue estimada a partir del cociente de edades de las hembras reproductivas y las tasas de renidificación y de nidadas dobles a partir del momento de reproducción) probablemente subestimaron esos parámetros.

POPULATION DECLINES OBSERVED in Neotropical migratory landbirds in eastern North America are attributed primarily to habitat fragmentation, higher rates of predation, and brood parasitism (Wilcove 1985, Robbins et al. 1989, Terborgh 1992, Donovan et al. 1997, Askins 2000). These findings have stimulated many studies of bird reproductive success and source-sink dynamics in fragmented versus contiguous habitats (Villard et al. 1992, Faaborg et al. 1995, Manolis et al. 2000a, Flaspohler et al. 2001, Murphy 2001, Podolsky 2003). Of 356 studies of avian reproductive success published from 1984 to 1997 in nine major European and North American peer-reviewed journals, 54% did not distinguish between nest success and productivity, less than half considered renesting and second broods in multibrooded species, and only 10% properly estimated annual fecundity (Thompson et al. 2001). Recent studies have shown that renesting after a nest failure and double-brooding, often ignored by population-growth models, may account for $\leq 40\%$ of annual fecundity in birds (Murray 1991, 1992; Martin 1995; Schroeder 1997; Farnsworth and Simons 2001). Verhulst et al. (1997) developed a model predicting the trade-offs between successive reproductive attempts. Podolsky (2003) and Nagy and Holmes (2004, 2005) found that failing to account for the contribution of renesting and double-brooding in studies of avian demography can result in serious underestimates of annual fecundity, which could bias estimates of population growth rate, source-sink dynamics, and population viability.

Although model building in population ecology always involves trade-offs among generality, realism, and precision (Levins 1966), limited demographic data often impose a number of simplifying assumptions on source-sink models of forest passerines. These include assumptions about model parameters that are often difficult to estimate in the field, such as dispersal (Nichols et al. 1981), the number of breeding

attempts (Pease and Grzybowski 1995, Powell et al. 1999, Grzybowski and Pease 2005), the relationship between clutch size and annual fecundity (Flaspohler et al. 2001; Farnsworth and Simons 2001, 2005), and annual survival rates of females (Temple and Cary 1988, Faaborg et al. 1998, Burke and Nol 2000, Simons et al. 2000).

We examined the importance of annual female survival and rates of renesting and double-brooding in models of songbird population growth. We used the Ovenbird (*Seiurus aurocapilla*) because it is a common model for songbird source-sink relationships. The Ovenbird is generally considered a single-brooded species (Van Horn and Donovan 1994), though there is a single report of three cases of double-brooding (Zach and Falls 1976). In contrast to most published studies of Ovenbird demographics (Gibbs and Faaborg 1990, Donovan et al. 1995b, King et al. 1996, Burke and Nol 1998, Porneluzi and Faaborg 1999, Flaspohler et al. 2001, Manolis et al. 2002, Mattsson and Niemi 2006), our research was conducted near the southern extent of the species' range, where a longer breeding season may provide greater opportunities for double-brooding. Our objectives were to develop alternative models of Ovenbird annual fecundity in Great Smoky Mountains National Park based on our field estimates of nesting success and brood size, and both observed and published estimates of female survival, and rates of renesting and double-brooding. We also wanted to assess how assumptions about these parameters influence estimated population growth rates.

METHODS

MODELING APPROACH

Study area.—Great Smoky Mountains National Park, established in 1934, is located along the North Carolina-Tennessee border. Our seven

study sites, cumulatively covering >700 ha, were located between Gatlinburg, Tennessee (N35°42'52", W83°30'41"), and Waterville, North Carolina (N35°47'02", W83°06'44"), within the Gatlinburg, Mount Le Conte, Jones Cove, Mount Guyote, Hartford, Waterville, Cove Creek Gap, and Luft Knob U.S. Geological Survey quadrangles. The sites support large continuous tracts of mixed deciduous forest 75–100 years old, at elevations of 400–1,100 m.

Annual fecundity and population growth rate.—We define annual fecundity (F) as the number of juvenile females produced annually per breeding female (Ricklefs 1973). In the simplest case, assuming 100% pairing success of females, equal fledgling sex ratio, and monocyclic reproduction with no renesting after a nest failure, annual fecundity can be computed from empirical estimates of the average fledged brood size (B) and nesting success (p_s) sensu Mayfield (1975) as: $F = \frac{1}{2} B p_s$. Hypothetically, females could also undertake several consecutive breeding attempts by renesting after previously failed nests and double-brooding after successful nests. We developed models of Ovenbird annual fecundity to explore how variations in four demographic parameters, annual survival of adult (P_A) and juvenile (P_J) females and rates of renesting (p_r) and double-brooding (p_d), influence predictions about population growth rates. Pulliam (1988) defined the finite rate of population growth (lambda) as $\lambda = P_A + P_J F = 1$ for a population at equilibrium, and $\lambda > 1$ for a source population. Published Ovenbird population models include a variety of assumptions about renesting and double-brooding. Perneluzi and Faaborg (1999) assumed monocyclic reproduction with no renesting, Donovan

et al. (1995b) and Burke and Nol (2000) assumed one renesting after failure, and Flaspohler et al. (2001) considered a 5–10% possibility of double-brooding. Hann's (1937) benchmark three-year study of a marked Ovenbird population reported up to five unsuccessful consecutive breeding attempts, but no reliable evidence of double-brooding. We re-examined Hann's data and found clear evidence of no more than three renesting attempts following an unsuccessful first nest (Table 1). Thus, estimates of lambda will vary according to assumptions about p_r and p_d . Below, we consider six basic scenarios grouped in two alternative models.

Single-renesting–double-brooding model.—A modification of Pulliam's (1988) model to incorporate renesting and double-brooding can be expressed as

$$\begin{aligned} \lambda &= P_A + P_J \frac{1}{2} [p_s B + p_s (1 - p_s) p_r B + p_s p_d p_s B + p_s p_d p_s (1 - p_s) p_r B] \\ &= P_A + P_J \frac{1}{2} B p_s [1 + p_r - p_s p_r + p_s p_d + p_s p_d (1 - p_s) p_r] \end{aligned} \tag{1}$$

This single-renesting–double-brooding (SRDB) model (Fig. 1A) assumes that there are successful (p_s) and unsuccessful ($1 - p_s$) first nests. Whereas some successful females ($p_s [1 - p_d]$) will stop reproducing, some ($p_s p_d$) will double-brood, and some of those ($p_s^2 p_d$) will succeed. Females that are unsuccessful on their first nesting attempt will renest with a probability p_r . Females that renested successfully, $p_s (1 - p_s) p_r$, will double-brood with a probability p_d and will produce $p_s^2 (1 - p_s) p_r p_d B$ offspring. All double-brooding females will stop breeding after their second nesting attempt, whether they are successful or not. Other model assumptions are a closed population (no dispersal and no recruitment);

TABLE 1. Multiple renesting after the previous nest failure and renesting rates (p_r) of Ovenbirds in Hann's (1937) study of color-banded individuals.^a

	Number of nests			
	First brood	Renesting 1	Renesting 2	Renesting 3
All nests	34	18	8	2
Failed nests	22	12	6	2
p_r^b		$p_{r1} = 0.82$	$p_{r2} = 0.66$	$p_{r3} = 0.33$

^a See pages 210, 219–221, and 224–226 in Hann (1937). In our reanalysis, we excluded empty nests found after desertion and one fledgling fed by a male of unknown status. All cases of five consecutive breeding attempts in Hann's (1937) study were based on nests that were found deserted. However, two renesting attempts after an unsuccessful first brood were well documented. Only two females made a fourth nesting attempt, and both failed before their nests were completed.

^b We estimated each p_r as the ratio of observed renesting attempts to failed nests. We then used these values to parameterize the multiple renesting model (Fig. 1; Tables 4 and 5). In no case was successful reproduction followed by a nesting attempt.

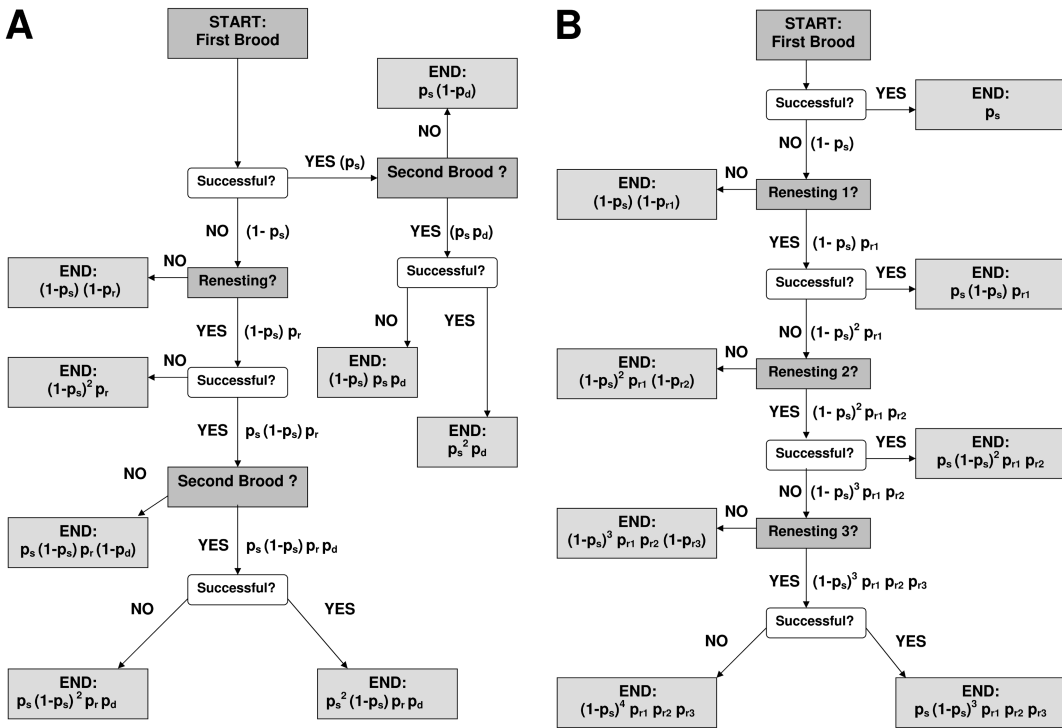


FIG. 1. Flow-chart summary of Ovenbird annual-fecundity models. (A) Single-renesting–double-brooding model is described by equation (1) and is based on our field data from Great Smoky Mountains National Park, 1999–2001. It assumes homogeneity of nesting success (p_s), *sensu* Mayfield (1975). The model is limited by one renesting attempt after nest failure (p_r). Successful first broods and successful renestings after the failed first broods are followed by a second breeding with a probability p_d . (B) Multiple renesting model is based on parameter estimates from this study and renesting rates reported by Hann (1937). Renesting probabilities for each consecutive renesting attempt are p_{r1} , p_{r2} , and p_{r3} . The model does not permit double-brooding, and all successful birds stop reproducing.

equal sex ratios; independence of P_A of p_s , p_r and p_{dij} ; and homogeneity of fledged brood sizes among consecutive breeding attempts. We examined five scenarios of this model based on setting renesting and double-brooding probabilities to 1 or 0, or by using values estimated from our field study and from Hann (1937): (a) $p_r = 0$, $p_d = 0$, (b) $p_r = 1$, $p_d = 0$, (c) $p_r = \{\text{estimated value}\}$, $p_d = 0$, (d) $p_r = 1$, $p_d = \{\text{estimated value}\}$, and (e) $p_r = \{\text{estimated value}\}$, $p_d = \{\text{estimated value}\}$.

Multiple renesting (MR) model.—This model is based on renesting probabilities reported by Hann (1937) (Table 1) and no double-brooding. We could not test (chi-square) the probabilities of renesting after the first (p_{r1}), second (p_{r2}), and third failures (p_{r3}) for homogeneity because of small sample sizes and, therefore, assumed $p_{r1} \neq p_{r2} \neq p_{r3}$. Model assumptions (Fig. 1B) differ from the SRDB

model in allowing up to four nesting attempts but only one successful reproduction per season:

$$\lambda = P_A + P_1 \frac{1}{2} B p_s [1 + (1 - p_s) p_{r1} + (1 - p_s)^2 p_{r1} p_{r2} + (1 - p_s)^3 p_{r1} p_{r2} p_{r3}] \quad (2)$$

We compared estimates of lambda for all model scenarios to examine the sensitivity of lambda to changes in annual female survival and variations in the rates of renesting and double-brooding.

ESTIMATING MODEL PARAMETERS

Annual reproductive success.—We searched study sites for nests from mid-April until the end of July following the guidelines of Martin and Geupel (1993). We rotated observers among sites

to minimize observer-related bias (Rodewald 2004). Nests were monitored every three days until the end of incubation, every other day until day 6 of the nestling stage, and then daily until nests were no longer active. We considered nests successful only if signs of successful fledging (flattened nest edge covered with feces and fledgling activity in the vicinity of nests) were observed (Manolis et al. 2000b). We estimated reproductive success by using daily survival rates (s_d) and nesting success (p_s) (Mayfield 1961, 1975) and estimating an average successful brood size (B). As recommended by Hensler and Nichols (1981), calculation of s_d and p_s was based on a minimum of 20 active nests with eggs or nestlings (nest-construction days excluded). Standard errors of s_d and test-statistics (z) for evaluating s_d variability among years, sites, and consecutive breeding attempts were calculated as in Johnson (1979). A confidence interval for p_s was approximated as a range of values between our high and low estimates. We used chi-square tests to evaluate variations of apparent nest predation (expressed as ratios of depredated nests to all nests) among years, consecutive breeding attempts, and sites (Donovan et al. 1995b, Porneluzi and Faaborg 1999, Burke and Nol 2000). Average clutch size, hatched brood size, and fledged brood size were tested for temporal and spatial heterogeneity using analysis of variance (ANOVA, general linear model; MINITAB, version 14.1; Minitab, State College, Pennsylvania).

Annual survival of adult and juvenile females.—Although it is possible to estimate the adult survival of songbirds by recapturing marked birds, direct estimates of annual juvenile songbird survival are virtually nonexistent because of high postnatal dispersal (Greenwood and Harvey 1982, Holmes et al. 1996, Faaborg et al. 1998). Band returns for juvenile Ovenbirds are <1.5% at best (Hann 1937). Many studies of Ovenbird population viability have relied on a few published estimates of annual adult female survival (Flaspohler et al. 2001) and on an indirect estimate of juvenile female survival ($P_J = 0.31 = \frac{1}{2} P_A$) by Ricklefs (1973) and Temple and Cary (1988), derived from the data on adult songbird mortality and female productivity (Donovan et al. 1995a, b; Brawn and Robinson 1996; Burke and Nol 2000). We used an alternative method based on ratios of after-second-year (ASY) to second-year (SY) birds (Ricklefs 1973, 1997; May and Robinson 1985; Farnsworth

1998; Porneluzi and Faaborg 1999; Simons et al. 2000): $P_A = ASY \div (ASY + SY)$. Because previous studies reported a sex-related heterogeneity in Ovenbird survival (Wander 1985, Bayne and Hobson 2002), we used only females for P_A estimates. We captured females on nests using a butterfly net, aged birds by the shape of the third rectrix (Donovan and Stanley 1995), and assumed $P_J = \frac{1}{2} P_A$.

Multiple breeding attempts.—For modeling purposes, we used an indirect approach based on assumptions about the timing of reproduction, the duration of successful breeding attempts, and the length of the breeding season (Pease and Grzybowski 1995, Farnsworth 1998, Powell et al. 1999, Simons et al. 2000, Grzybowski and Pease 2005). We used the observed pattern of nest initiation and fledging in our populations to estimate p_r and p_d in our alternative models of annual fecundity. We used our three years of field data to estimate breeding-season length (average time between the earliest nest initiation and the latest fledging) and the duration of a nesting cycle from nest initiation until fledging. We estimated the number of potential successful reproductions per season as (breeding-season length) \div (nesting cycle + interval between two consecutive cycles). Female Ovenbirds arrive on breeding grounds over an average interval of seven days, and nest initiation takes place over seven days (Van Horn and Donovan 1994). Assuming a conservative estimate of nesting synchrony, we considered nests initiated within the first three weeks of the breeding season first broods. Nests initiated within the next three weeks were assumed to represent renesting, and nests started from week 7 on were attributed to second broods (Podolsky 2003). Assuming an independence of nests in our study and constant nest-searching effort, we estimated $p_r =$ renesting attempts \div [first broods \times (1 - p_s)] and $p_d =$ second broods \div (successful first broods + successful renesting attempts).

RESULTS

Chronology of reproduction.—From 1999 to 2001, we monitored 110 Ovenbird nests in Great Smoky Mountains National Park. On average, among three years, the earliest nest was initiated on 14 April and the latest on 20 June, with fledging on 18 July. Therefore, the breeding season of the Ovenbird lasted 96 days. We observed only minor annual variations in the timing of

reproduction. Ovenbirds started their nests, on average, two days earlier in 2001 and two days later in 2000 than in 1999. For first broods, the average nesting cycle lasted 31 days. The nesting cycle of renesting and double-brooding birds was one day shorter (Table 2). Observations of renesting intervals at four nests ranged from two to six days. Assuming a conservative renesting interval of seven days, the duration of the breeding season at our study sites would allow for, at most, two successful broods in a season: $96 \div 38 = 2.5$. For modeling purposes, we used observed patterns of nest initiation to differentiate among consecutive reproductive attempts (Fig. 2). First nests were initiated on 29 April ± 0.5 days (range: 14 April–4 May; $n = 62$) and fledged on 29 May ± 0.8 days (range: 15 May–2 June). We assumed renesting peaked on 14 May ± 1.1 days ($n = 28$) with a peak of fledging on 11 June ± 2.3 days. Second broods were assumed to start on 3 June ± 1.7 days ($n = 20$) and fledge on 2 July ± 2.9 days.

Annual reproductive success.—On average, Ovenbirds laid 4.49 ± 0.07 eggs per nest (range: 3–6; $n = 89$) and raised 3.79 ± 0.19 fledglings (range: 1–6; $n = 43$) per successful brood (Table 2). There was no significant site effect on clutch size, brood size, or number of young fledged. Clutch size varied significantly among years, and both clutch and hatched brood sizes declined significantly over the breeding season (Table 3). However, we found no spatial or temporal

heterogeneity in fledged brood sizes and therefore used the same brood size (B) in all models. Of 62 failed nests, 10 were abandoned (5 before egg laying and 5 during egg laying and incubation), 29 were depredated during incubation, and 23 were depredated during the nestling period. We found no evidence of predation on breeding females or of Brown-Headed Cowbird (*Molothrus ater*) nest parasitism. Rates of apparent nest predation did not vary among years, study sites, and consecutive nesting attempts (Table 3), and s_d was not different between the incubation and nestling stages (mean = 0.953; $z = 0.70$, $P = 0.48$). Nesting success was estimated at $p_s = 0.310$ (range: 0.266–0.362) (Table 4).

Annual female survival.—Nineteen of the 30 captured and marked breeding females were ASY birds. Therefore, our estimate of annual adult female survival, $P_A = 0.633 \pm 0.088$, and of annual juvenile female survival, $P_J = 0.317 \pm 0.044$ (Table 4).

Multiple breeding attempts and annual fecundity.—For the SRDB model, we computed probabilities of renesting and double-brooding from our data: $p_r = 28 \div (62 \times 0.69) = 0.655$, $p_d = 20 \div 40 = 0.5$ (Table 5). For the MR model, we computed $p_{r1} = 0.818$, $p_{r2} = 0.667$, and $p_{r3} = 0.333$ from Hann's (1937) data (Table 1). However, because nesting chronology approximates rather than estimates p_r and because we did not observe any evidence of multiple renesting in our populations, we

TABLE 2. Reproductive parameters of Ovenbirds in Great Smoky Mountains National Park, 1999–2001.

Parameter	Mean	SE	N	Range	Mean – SE	Mean + SE
Clutch size	4.49	0.073	89	3–6	4.42	4.56
Hatched brood size	4.12	0.121	64	1–6	4.00	4.24
Fledged brood size	3.79	0.193	43	1–6	3.60	3.98
Construction (days) ^a						
First nest	7.1	0.09	11	7–8	7.0	7.2
Additional nest	5.8	0.20	5	5–6	5.6	6.0
Egg-laying (days)	2.5	0.07	89	1–4	2.4	2.6
Incubation (days)	13.2	0.19	21	11–14.5	13.0	13.4
Egg stage (days)	15.6	0.20	21	14–17	15.4	15.8
Nestling stage (days)	8.7	0.17	36	7–11	8.5	8.9
Active contents (days) ^b	24.3	0.33	9	23–26	24.0	24.7
Nesting cycle (days) ^c						
First nesting	31.4					
Additional nesting attempts	30.1					

^a Estimated from our study (assuming 4–6 days for nest construction followed by 1–2 days before egg laying).

^b Calculated only for successful nests found before egg laying.

^c Average number of days from nest initiation until fledging.

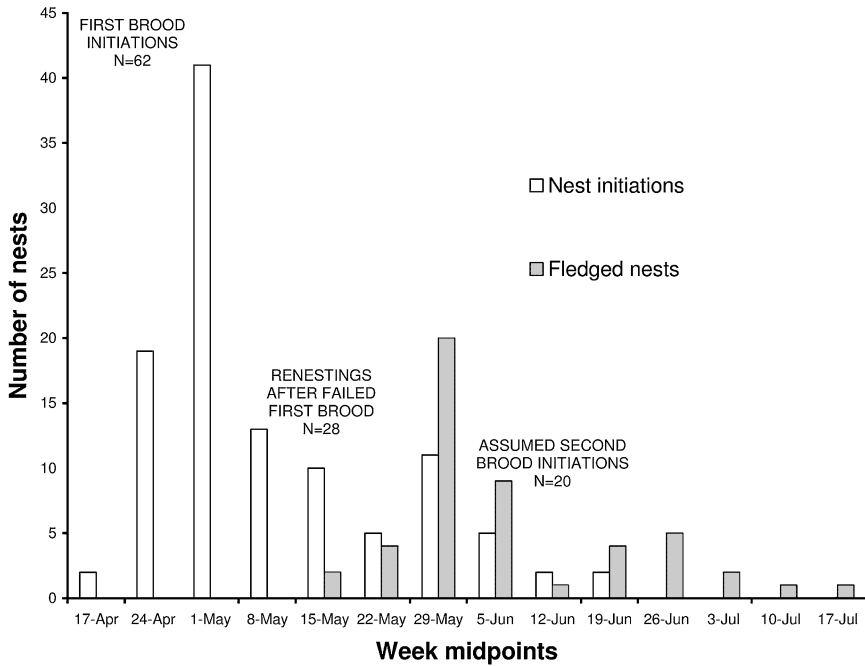


FIG. 2. Chronology of Ovenbird reproduction in Great Smoky Mountains National Park, 1999–2001. Initiated and fledged nests are shown on a weekly basis. The earliest nest initiation was observed on 14 April, the latest on 19 June. The earliest fledging occurred on 15 May, and the latest on 18 July. For modeling purposes (single-renesting–double-brooding model), the first three weeks were assumed to represent the initiation of the first broods, renesting attempts were assumed to have started on weeks 4–6, and the initiation of the second broods following successful first broods and successful renesting attempts were assumed to occur during weeks 7–10.

TABLE 3. Spatial and temporal homogeneity of Ovenbird reproductive parameters and apparent predation. Predation rates are expressed as the ratios of depredated nests to all nests.

Parameters	Comparisons ^a											
	Among years ^b				Among study sites				Among broods ^c			
	χ^2	F	df	P	χ^2	F	df	P	χ^2	F	df	P
Clutch size	–	5.62	2	<0.01	–	0.43	6	0.86	–	20.06	2	<0.001
Hatched brood size	–	0.83	2	0.44	–	0.59	5	0.71	–	7.47	2	<0.01
Fledged brood size	–	0.02	2	0.98	–	1.25	5	0.31	–	1.14	2	0.33
Predation rates	0.40	–	2	0.82	0.74	–	4	0.95	0.27	–	2	0.88

^aChi-square test and ANOVA: general linear model.

^b1999, 2000, and 2001.

^cFirst broods (nests initiated early in the season), renesting after the first nest failure, and assumed second broods (nest initiations late in the season).

used both the p_r estimate from our study and the p_{r1} estimate from Hann (1937) to calculate lambda in scenarios *c* and *e* of the SRDB model. More specifically, our estimate of p_r was used in scenarios c_1 and e_V whereas the estimate of p_{r1} was applied to scenarios c_2 and e_2 (Table 5). Our

estimate of p_d was used in scenarios *d*, e_V , and e_2 . We used mean, low, and high estimates of B , P_A , P_V , and p_s for estimating annual fecundity (Table 4). Mean $F_{SRDB\ e} = 0.99–1.06$, depending on the assumed value of renesting probability, and $F_{MR} = 1.11$ (range: 0.94–1.29) female offspring

TABLE 4. Estimated annual survival of adult (P_A) and juvenile (P_j) females, and annual fecundity (F) in Ovenbird populations with and without double-brooding. The single-renesting–double-brooding (SRDB) model (scenario e) includes single renesting ($p_r = 0.655$), and double-brooding ($p_d = 0.5$) rates estimated from this study (e_1), or from Hann (1937) $p_r = 0.818$ (e_2). The multiple-renesting (MR) model, assuming triple renesting after failure but no double-brooding, is based on estimates from Hann (1937), where $p_{r1} = 0.818$, $p_{r2} = 0.667$, and $p_{r3} = 0.333$. All other model parameters (successful brood size [B], daily nest survival rate [s_d], nesting success [p_s]) are estimated from the present study.

Estimates	P_A	P_j	B	s_d	p_s	F^{*a}	SRDB		MR
							$F(e_1)$	$F(e_2)$	F
Mean	0.633	0.317	3.79	0.953	0.310	1.16	0.99	1.06	1.11
Low ^b	0.545	0.273	3.60	0.947	0.266	1.67	0.80	0.87	0.94
High ^b	0.721	0.361	3.98	0.959	0.362	0.77	1.21	1.30	1.29

^aEquilibrium fecundity for SRDB and MR models of Ovenbird population growth rate (annual fecundity corresponding to $\lambda = 1$).

^b“Low” values of P_A , P_j , B , s_d , and p_s , correspond to the lower limits of the estimated 95% confidence intervals, ‘high’ values of these parameters correspond to the upper limits of the estimated confidence intervals. ‘Low’ and ‘high’ values of F and F^* were computed from either “low” or “high” values of parameters in equations (1) and (2). They approximate their lower and upper confidence limits.

TABLE 5. Ovenbird population growth rates from single renesting–double-brooding (SRDB) model (scenarios a – e) and multiple renesting (MR) model.

Model scenarios ^a	p_r ^b	p_d ^c	λ_{low}	λ_{mean}	λ_{high} ^d
SRDB model					
a	0	0	0.675	0.819	0.981
b	1	0	0.771	0.947	1.146
c_1	0.655	0	0.739	0.903	1.089
c_2	0.818	0	0.754	0.924	1.116
d	1	0.5	0.801	0.996	1.223
e_1	0.655	0.5	0.764	0.945	1.156
e_2	0.818	0.5	0.782	0.969	1.188
MR model					
	(0.818 0.667 0.333) ^e	0	0.802	0.983	1.186

^aModel scenarios use estimates of annual adult female survival ($P_A = 0.63 \pm 0.09$), fledged brood size ($B = 3.79 \pm 0.19$), and nesting success ($p_s = 0.31_{mean}$, 0.27_{low} , and 0.36_{high}) from this study. Annual survival of juvenile females assumed half of P_A ($P_j = 0.32 \pm 0.04$). Scenarios c and e of the SRDB model use estimates of renesting rate (p_r) after the first nest failure from both this study and Hann (1937): 0.655 and 0.818, respectively.

^bRenesting rate (ratio of renesting attempts to previously failed nests).

^cDouble-brooding rate (ratio of second broods to successful first broods).

^dRanges of lambda values represent approximate 95% confidence intervals.

per female. The corresponding value of equilibrium fecundity was $F^* = 1.16$ female offspring per reproducing female (range: 0.77–1.67).

Models of population growth.—At $P_A = 0.63$, scenario SRDB d was the only model to yield lambda approaching 1 (Table 5). The MR model produced negative population growth ($\lambda = 0.983$). All other scenarios of the SRDB model resulted in even lower population growth rates. For all scenarios of both models except SRDB a , increasing P_A to 0.70 and P_j to 0.35 yielded $\lambda \geq 1$ (Fig. 3).

DISCUSSION

Components of annual fecundity.—Our daily nest survival rates (0.953 ± 0.006) and average fledged brood size (3.79 ± 0.19) were derived from large samples, and they are within the range of published rates for contiguous forested habitats. Published values of s_d and B range from 0.945 to 0.985 and from 2.94 to 4.30, respectively (Donovan et al. 1995b, Porneluzi and Faaborg 1999, Flaspohler et al. 2001, Ford et al. 2001,

Manolis et al. 2002). Although Faaborg et al. (1998) reported that late-season nests of songbirds were more successful than early-season nests, other studies (e.g., Farnsworth et al. 2000, Wood Thrush [*Hylocichla mustelina*]) report homogeneity of s_d over the breeding season. We found no evidence of seasonal variability in successful brood size and daily nest survival rates.

Contrary to the assumption that songbirds re-nest more readily if nests fail early in the nesting period (Payevsky 1985, Van Horn and Donovan 1994), our calculations from Hann’s (1937) data imply similar probabilities of re-nesting at all stages of the nesting cycle: 0.75 at nest-construction stage ($n = 12$), 0.67 at egg stage ($n = 15$), and 0.70 ($n = 10$) at nestling stage ($\chi^2 = 0.04$, $df = 2$, $P = 0.98$). Although direct measurements of p_r and p_d based on observations of marked birds would be more conclusive, the task of following individual birds between nesting attempts is daunting. We did not have a sufficient sample size of marked female Ovenbirds to reliably estimate rates of re-nesting and double-brooding (we observed three clear instances of double-brooding and one instance of re-nesting next to a failed nest). Thus, our indirect estimates, $p_r = 0.655$ and $p_d = 0.5$,

were based solely on nesting chronology. It is difficult to evaluate the validity of these estimates, because published data on re-nesting probabilities of Ovenbirds are limited (Hann 1937). Within-season dispersal and incomplete site fidelity may further confound estimates (Hann 1937, Howlett and Stutchbury 1997). It is also possible that our Ovenbird populations, located at the southern boundary of the species’ breeding range, may have a higher p_d than populations farther north because of a longer breeding season.

Annual female survival.—Schmutz et al. (1997) suggested that population growth rates are more sensitive to variations in P_A and P_J than they are to variations in annual fecundity. Nevertheless, only a few studies have measured annual survival rates of adult songbirds directly (Holmes et al. 1996, Perkins and Vickery 2001, Sandercock and Jaramillo 2002, Sillett and Holmes 2002, Jones et al. 2004). Fewer still have estimated annual survival rates of Ovenbirds (Hann 1937, Savidge and Davis 1974, Faaborg and Arendt 1995, DeSante et al. 2001), and only one study specifically estimated the survival of female Ovenbirds (Bayne and Hobson 2002), presumably because territorial males are much

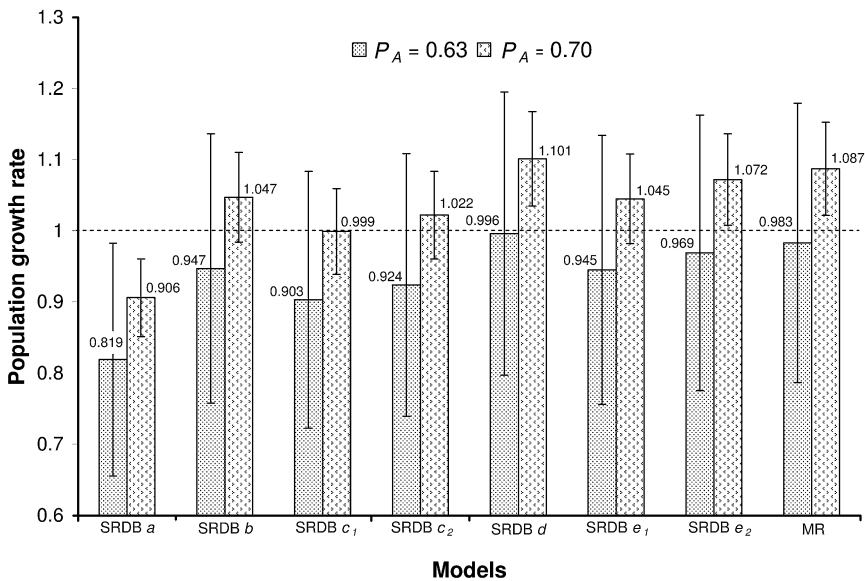


FIG. 3. Sensitivity of lambda to varying probabilities of female survival in seven scenarios of the single-re-nesting–double-brooding (SRDB) model and in the multiple re-nesting (MR) model assuming different values of re-nesting and double-brooding (model details summarized in Table 5). Increasing adult female survival (P_A) from our empirical estimate of 0.63 to a hypothetical value of 0.70 resulted, on average, in a 10.6% increase in population growth rates (λ) for all models.

easier to detect and capture (Porneluzi and Faaborg 1999). In general, survival estimates based on the recapture of marked birds are negatively biased because of interannual dispersal (Nichols et al. 1981, Nagy and Holmes 2004) and incomplete site fidelity (Hann 1937, Marshall et al. 2004). Faaborg et al. (1998) pointed out that survival estimates of passerines based solely on band return rates should be viewed with caution because of the bird's short life-span (on average, 2.4 years in female Ovenbirds; Hann 1937). Our estimate of adult female survival from the age ratios (0.63 ± 0.09) agrees with recent published estimates from unfragmented landscapes based on band returns (0.61 ± 0.09 , Porneluzi and Faaborg 1999; 0.60 ± 0.06 , Bayne and Hobson 2002) and appears to be on the high end of published estimates reported in 16 other available publications ranging from 0.02 to 0.85 (e.g., table 3 in Bayne and Hobson 2002).

Population trends and models of population growth.—Although Breeding Bird Survey data for the Ovenbird suggest consistent population declines in the southern Appalachian region at an average annual rate of 1.5% (Sauer et al. 2005), we observed no evidence of large population changes during six years of population monitoring in Great Smoky Mountains National Park (Simons and Shriner 2000, Podolsky 2003). Nevertheless, only one of our models (SRDB *d*) produced population growth rates close to 1; other scenarios (including *e*, based on empirical estimates) yielded rapidly declining populations (Table 5).

Given our strict monitoring protocol, the criteria used to assess nest fates, and large sample sizes, we feel that our estimates of p_s and B are accurate. It is possible that high immigration rates into our study sites were sustaining our populations. However, the National Park and adjacent National Forests are surrounded by more fragmented landscapes, and it seems highly unlikely that these surrounding habitats were serving as population sources. Therefore, we believe that other parameters of population growth models (annual female survival and rates of renesting and double-brooding) must be considered to explain observed population trends. Because we detected no population declines on our study sites, we believe that one or more of these parameters must be higher than our empirical estimates.

We initially believed that single renesting–double-brooding was the most likely scenario

on our study sites, but our empirical estimate of population growth rates approached or exceeded 1 only under an assumed annual survival of adult females of 0.70 (model SRDB e_1). Furthermore, at $P_A = 0.7$, all models and scenarios except SRDB *a* yielded population sources (Fig. 3). An 11.1% increase in P_A (from 0.63 to 0.70) and P_f (from 0.32 to 0.35) caused proportional increases in lambda of 10.6% (0.906–1.101 vs. 0.819–0.996). This result and Roberts's (1971) report of $P_A = 0.85 \pm 0.07$ suggest that survival rates of adult Ovenbird females may exceed 70% in some populations.

Similarly, even minor changes in renesting and double-brooding rates caused smaller but consistent changes in population growth rates. For example, increasing the p_r by 24.9% (from 0.655 to 0.818) resulted in a 2.3–2.5% increase in lambda (SRDB models c_2 vs. c_1 , and e_2 vs. e_1 ; Table 5). The MR model, based on empirical estimates of the likelihood of three consecutive renesting attempts, yielded a 6.4% higher lambda than a single renesting model c_2 (Table 5). In the model SRDB *d*, a combination of $p_r = 1$ and $p_d = 0.5$ produced a stable population at our empirical estimate of P_A . Pairwise comparisons of SRDB models (c_1 vs. e_1 and c_2 vs. e_2) demonstrated that an increase in p_d from 0% to 50% increased lambda by only 4.3–4.6% (Table 5). Because double-brooding rates exceeding 0.5 are highly improbable in Ovenbird populations, we conclude that both P_A and p_r were underestimated in our study. We believe that this negative bias is a result of estimating annual female survival from the age ratio of reproducing females and estimating renesting probabilities indirectly.

Implications for conservation and future research.—Studies of source–sink dynamics are often prompted by concerns about negative population trends. Although accurate assessments of population status are vital for developing demographic models for conservation and management (Ruth et al. 2003), current population models of migratory songbirds are usually based on assumptions about female survival rates and empirical measures of fecundity. They generally ignore the potential influence of variations in rates of renesting and double-brooding. Of all model parameters in our study, annual female survival had the greatest proportional effect on lambda, followed by rates of renesting and rates of double-brooding. Direct methods

for estimating these parameters should be used whenever feasible. Accurate empirical estimates of these parameters will significantly improve existing songbird population models.

ACKNOWLEDGMENTS

The study would not have been possible without the support of Great Smoky Mountains National Park staff and personnel, and the help of many dedicated field assistants (especially, T. Maness, C. Causey, D. Martin, M. Miller, J. Zoller, C. Grubenmann, J. Garcia, R. Staffen, and A. Sanfaçon). We thank S. G. Sealy, D. B. Lank, R. F. Rockwell, J. Gilliam, K. Pollock, and two anonymous reviewers for helpful comments on this manuscript. Funding was provided by the Biological Resources Division, U.S. Geological Survey, and by the Russel B. and Eugenia C. Walcott Endowment.

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Associate Editor: D. B. Lank