

Applying songbird population dynamics models to conservation biology needs

© 2018. A. L. Podolsky^{1,2} ORCID 0000-0001-7617-0709,

¹North Carolina State University,
USA, Raleigh, NC 27695-7313,

²Yuri Gagarin State Technical University of Saratov,
77, Politekhnikeskaya St., Saratov, Russia, 410054,
e-mail: andrei.podolsky@mail.ru

Proper understanding of the reproductive biology traits and population dynamics patterns of declining songbird species is crucial for ensuring their effective protection and recovery. Metapopulation dynamics may cause the extinction of local populations in some landscape patches regardless of the habitat quality and undertaken conservation measures. At the same time, the source-sink type of the population dynamics could saturate lower quality habitat patches with dispersing individuals from the population sources. Hence, poorer quality habitats presumed to yield population sinks could eventually maintain population sources. Consequently, an effective recovery strategy for declining species should include high quality suitable habitats along with some poorer quality patches in the regional network of protected natural areas.

I developed the mathematical model for songbird reproductive strategy based on the case study of my three-year field research conducted on the Ovenbird (*Seiurus aurocapilla* L.) in the Great Smoky Mountains National Park (U.S.A.). Breeding Bird Survey detected multiannual negative population trends in this species in pristine landscapes of the Southern Appalachians, whereas its growing populations were found in some of the adjacent areas strongly affected by human activities. I modified basic Pulliam's (1988) model of population growth rates for this species by including assumptions about annual female survival and annual fecundity. I also applied productivity data from 110 active nests to determine an average successful brood size and nesting success. Finally, I added probabilistic variables accounting for reneating rates after unsuccessful breeding attempt and double-brooding rates to the model while assuming equal sex ratio among the breeding individuals. Computer simulations based on actual data and assumed range of values of the model variables yielded population growth rates well below 1, thus confirming the declining status of the national park populations. Therefore, the best pristine habitats in the study area were not ecologically significant sources, and in fact they were ecological traps for this species. Such unpredictable population dynamics in high quality habitats vs. low quality patches could be caused by the "paradox of predation": high quality landscapes of the national park attracted, in addition to birds, a variety of mammalian and reptilian nest predators. Most of these predators were absent or scarce in low quality patches.

Keywords: annual fecundity, annual survival, reneating rate, double-brooding rate, population growth rate, *Seiurus aurocapilla*.

УДК 574.34 + 004.94

Применение моделей динамики популяций певчих птиц для сохранения биоразнообразия

© 2018. А. Л. Подольский^{1,2}, PhD по зоологии и экологии, профессор,

¹ Государственный университет Северной Каролины (США),
27695, США, Сев. Каролина, г. Роли, п/я 7313,

²Саратовский государственный технический университет им. Ю.А. Гагарина,
410054, Россия, Саратов, ул. Политехническая, 77,
e-mail: andrei.podolsky@mail.ru

Правильное понимание репродуктивной биологии и популяционной динамики певчих птиц чрезвычайно важно для обеспечения их эффективной охраны и восстановления популяционной численности. Метопопуляционная динамика может привести к исчезновению локальных популяций в некоторых участках ландшафта, независимо от их качества и проводимых охранных мер. В то же время, динамика популяций по типу «источники–раковины» может привести к насыщению местообитаний низкого качества излишком особей, выселяющихся из популяций-источников, а значит, популяции-раковины в менее качественных местообитаниях могут трансформироваться в популяции-источники. Следовательно, эффективная стратегия восстановления видов со снижающейся численностью должна предусматривать включение в региональную сеть охраняемых природных территорий, как высококачественных местообитаний, так и ландшафтов более низкого качества.

Я разработал математическую модель репродуктивной стратегии певчих птиц, основанную на трёхлетних полевых исследованиях певуна-печника (*Seiurus aurocapilla* L.) в национальном парке Грейт-Смоки-Маунтинс (США).

Американский национальный проект по учёту гнездящихся птиц выявил многолетний спад его популяционной численности в нетронутых ландшафтах Южных Аппалачей, тогда как растущие популяции этого вида были обнаружены в смежных районах с преобладанием антропогенных ландшафтов. Я модифицировал базовую модель скорости популяционного роста (Pulliam, 1988), включив в неё годовую выживаемость самок, годовую плодовитость, вероятность повторного размножения после неудачной первой попытки, вероятность второго репродуктивного цикла после успешного первого при условии равного соотношения полов среди размножающихся птиц. Данные по продуктивности 110 активных гнёзд были использованы для расчёта среднего размера успешного выводка и успешности гнездования. Компьютерное моделирование на основе фактических данных и предполагаемого диапазона значений модельных переменных дало темпы роста популяций значительно ниже 1, что объяснило неблагоприятный популяционный статус певуна в национальном парке. Поэтому лучшие нетронутые местообитания в районе исследований не были экологически значимыми источниками, а скорее оказались экологическими ловушками для этого вида. Такая непредсказуемая динамика популяций в высококачественных местообитаниях в сравнении с низкокачественными зонами может быть вызвана «парадоксом хищничества»: высококачественные ландшафты национального парка привлекали разнообразных хищных млекопитающих и рептилий, разоряющих птичьи гнёзда. Большинство из этих хищников отсутствовали или были малочисленны в ландшафтах более низкого качества.

Ключевые слова: годовая плодовитость, годовая выживаемость, вероятность повторного размножения, вероятность бицикличности размножения, скорость популяционного роста, *Seiurus aurocapilla*.

An effectiveness of protection and recovery of declining species depends on proper understanding of their reproductive biology traits and population dynamics patterns. Habitats suitable for a certain species alternate with unfavorable habitat patches. The common misconception is that an effective protection of a declining species can be accomplished solely by protecting its best available pristine habitats. According to the theoretical metapopulation paradigm, the regional population is composed of local populations undergoing constant stochastic exchange of individuals [1]. This pattern can lead to the extinction of local populations in selected landscape patches regardless of the habitat quality and undertaken conservation measures. According to the Pulliam's (1988) source-sink concept [2], habitat patches supporting population sources can produce a surplus of individuals dispersing to adjacent poorer quality patches of sink habitats.

Population declines of migratory terrestrial birds in eastern North America are explained mainly by higher rates of predation and brood parasitism in fragmented landscapes [3]. These findings initiated studies of bird reproductive success and source-sink dynamics in contiguous vs. fragmented landscapes [4]. It is important to properly estimate annual fecundity in birds. Hundreds of published studies did not distinguish between nesting success and productivity [5]. Some species of passerines are multibrooded, while some breed only once per year, but certain proportion of individuals in populations of single-brooded species can undertake second broods at the southern extremes of their breeding ranges. Often ignored by population-growth models, reneesting after a nest failure and double-brooding may account for up to 40% of annual

fecundity in birds [6]. Hence, failing to consider additional breeding attempts in demographic models can result in underestimates of annual fecundity and population growth rate [7, 8].

Being a common model species for songbird source-sink relationships, the Ovenbird (*Seiurus aurocapilla* L.) is generally considered a single-brooded species [9]. The objectives of my study were to model a source-sink dynamics of the Ovenbird populations in the Great Smoky Mountains National Park (GSMNP), U.S.A., near the southern extent of the species' range, where a longer breeding season may provide greater opportunities for double-brooding. Breeding Bird Survey detected multiannual negative population trends in this species in pristine landscapes of the Southern Appalachians, whereas growing populations were found in some of the adjacent areas affected by human activities [10]. To explain this paradox, I developed a probabilistic model of the Ovenbird annual fecundity based on my field estimates of nesting success, brood size, along with both observed and published estimates of female survival, and rates of reneesting and double-brooding. I also wanted to assess how assumptions about these parameters influence estimated population growth rates.

Methods

Building the model

My seven study sites, cumulatively covering > 700 ha, were located in GSMNP between Gatlinburg, Tennessee, and Waterville, North Carolina. They supported large contiguous tracts of mixed deciduous forest 75–100 years old at elevations from 400 m to 1,100 m above the sea level.

Ricklefs [11] defined annual fecundity (F) as the number of juvenile females produced an-

nually per breeding female. Assuming 100% pairing success of females, equal fledgling sex ratio, and a single reproductive cycle with no reneating 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 [12] as:

$$F = \frac{1}{2} B p_s \quad (1)$$

Pulliam [2] defined the finite rate of population growth (λ) as:

$$\lambda = P_A + P_J F, \quad (2)$$

where P_A and P_J are annual survival of adult and juvenile females, correspondingly. For a population at equilibrium $\lambda = 1$, and $\lambda > 1$ for a source population. Published Ovenbird population models include a variety of assumptions about reneating and double-brooding: some studies assumed mono-cyclic reproduction with no reneating [13], while others assumed one reneating after the nest failure [14], or even a 5–10% possibility of double-brooding [15].

I developed a probabilistic single-reneating-double-brooding (SRDB) model of the Ovenbird annual fecundity to explore how variations in rates of reneating (p_r) and double-brooding (p_d), influence predictions about the population growth rates. Consequently, estimates of λ will vary according to the assumptions about p_r and p_d . In this model, females could undertake reneating after previously failed nests and double-brooding after successful nesting with any probability between 0 and 1. A modification of the Pulliam's model [2] to incorporate reneating and double-brooding can be expressed as:

$$\begin{aligned} \lambda &= P_A + \frac{1}{2} P_J [p_s B + p_r (1-p_s) p_r B + p_s^2 p_d B + p_s^2 p_d (1-p_s) p_r B] = \\ &= P_A + \frac{1}{2} P_J B p_s [1 + p_r - p_s p_r + p_s p_d + p_s p_d (1-p_s) p_r] \quad (3) \end{aligned}$$

The SRDB model (Fig. 1) presumes that there are successful (p_s) and unsuccessful ($1-p_s$) first nests. While some successful females ($p_s [1-p_d]$) will stop reproducing, other females ($p_s p_d$) will double-brood, and some of those ($p_s^2 p_d$) will succeed. Females that are unsuccessful on their first nesting attempt will reneat with a probability p_r . Females that reneated 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, independently of its outcome. The model also assumes a closed population (no dispersal and no recruitment), equal sex ratios, independence of P_A of p_s , p_r and p_d , and homogeneity of fledged brood sizes among consecutive breeding attempts. I examined five scenarios of this model based on setting reneating and double-brooding probabilities to 1 or 0, or by using values estimated from the field study:

- (a) $p_r = 0, p_d = 0$;
- (b) $p_r = 1, p_d = 0$;
- (c) $p_r = \{\text{estimated value}\}, p_d = 0$;
- (d) $p_r = 1, p_d = \{\text{estimated value}\}$;
- (e) $p_r = \{\text{estimated value}\}, p_d = \{\text{estimated value}\}$.

Estimating model parameters

In order to estimate annual reproductive success, we searched study sites for nests from mid-April until the end of July following the existing guidelines to collect a representative sample of nests [16, 17]. 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. Nests were considered successful only if signs of successful fledging were observed [18]. Reproductive success was estimated by using daily survival rates (s_d) and nesting success (p_s) *sensu* Mayfield [12] and estimating an average successful brood size (B).

$$p_s = s_d^n, \quad (4)$$

where n is a duration of the period from the beginning of egg-laying to fledging of the offspring. As an alternative, the apparent, or naive, nest depredation was estimated as:

$$D = \frac{N_D}{N_T}, \quad (5)$$

where D is apparent nest depredation rates, N_D is No. of depredated nests, N_T is No. of all nests.

Standard errors of s_d and test-statistics (z) for evaluating variability of s_d among years, sites, and consecutive breeding attempts were calculated [19]. The confidence interval for p_s was approximated as a range of values between high and low estimates. I used chi-square tests to evaluate variations of apparent nest depredation, computed from the equation (5), among years, consecutive breeding attempts, and sites. To account for possible effects of temporal and spatial heterogeneity on average clutch size, hatched

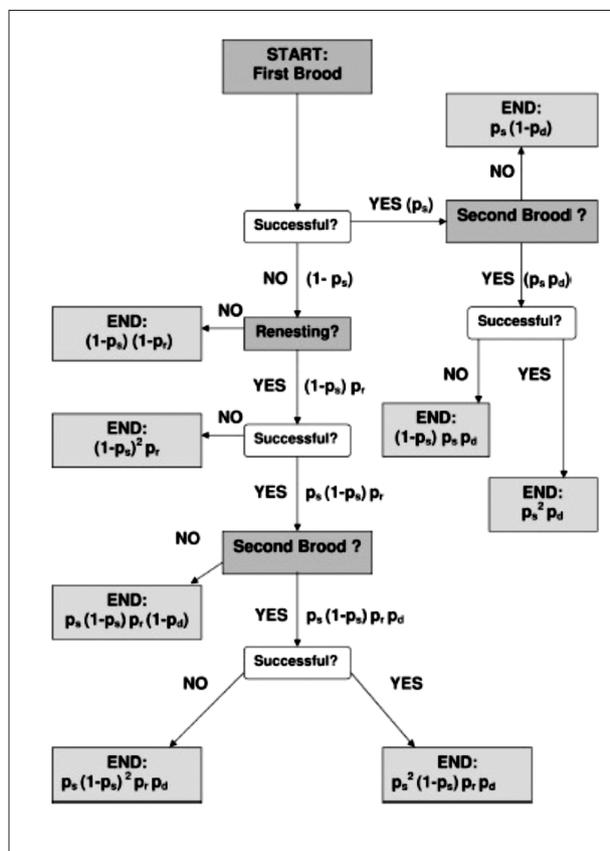


Fig. 1. Flow-chart summary of the SRDB model of annual fecundity

brood size, and fledged brood size, I conducted ANOVA, general linear model. The SRDB model (Fig. 1) is described by the equation (3). It assumes homogeneity of Ovenbird nesting success (p_s) and is limited by one reneating attempt after nest failure (p_r) while successful first broods and successful reneating attempts after the failed first broods are followed by a second breeding with a probability p_d .

Estimation of the annual survival of adult and juvenile females was conducted as follows. 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 [20]. An alternative method based on ratios of after-second-year (ASY) to second-year (SY) birds was used [11]:

$$P_A = \frac{ASY}{ASY+SY} \tag{6}$$

Females were captured on nests using a butterfly net and their age was identified by the shape of the third rectrix [21]. Following Ricklefs [11], I considered the probability of juvenile female survival:

$$P_J = \frac{1}{2} P_A \tag{7}$$

To estimate the probabilities of reneating and double-brooding in SRDB model, I 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 [8]. I used the field data from three years of research 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. I estimated the number of potential successful reproductions per season (N) as:

$$N = \frac{T_B}{T_N + \Delta T} \tag{8}$$

where T_B is the breeding-season length, T_N is duration of the nesting cycle, ΔT is the interval between two consecutive cycles.

Female Ovenbirds arrive on their breeding grounds over an average interval of seven days and start their nests over seven days from the date of arrival [9]. Nests initiated within the first three weeks of the breeding season were considered first broods, nests initiated within the next three weeks were assumed to represent reneating, and nests started from week 7 on were attributed to the second broods. Assuming an independence of nests in my study and constant nest-searching effort, I estimated the probability of reneating as:

$$p_r = \frac{RA}{FB \cdot (1 - p_s)} \tag{9}$$

where RA is No. of reneating attempts, FB is No. of first broods.

Using same assumptions, I assessed the probability of double-brooding p_d in Ovenbird populations at my study sites as the ratio of second broods to all preceding successful nesting attempts:

$$p_d = \frac{SB}{FB_s + RA_s} \tag{10}$$

where SB is No. of second broods, FB_s is No. of successful first broods, RA_s is No. of successful reneating attempts.

Results

Reproductive chronology

In three years of field work, 110 Ovenbird nests were found and monitored in GMSNP.

On average among three years, the earliest nest initiation took place on 14 April, while the latest on 20 June, with fledging on 18 July. Therefore, the breeding season of the Ovenbird lasted 96 days. The average nesting cycle lasted 31 days for first broods and 30 days for renesting birds and second broods. Assuming a conservative renesting interval of seven days, the duration of the breeding season at the study sites, according to the equation (8), would allow for two successful broods in a season: $\frac{96}{38} = 2.5$. Fig. 2 illustrates how nests in my study were classified among consecutive reproductive attempts. 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). Renesting peaked on 14 May ± 1.1 days ($n = 28$) with a peak of fledging on 11 June ± 2.3 days. Second broods were estimated to start on 3 June ± 1.7 days ($n = 20$) and fledge on 2 July ± 2.9 days.

In the Figure 2, initiated and fledged nests are shown on a weekly basis. It is clear that the first three weeks represent the initiation of the first broods, renesting started during the weeks

4–6, and the initiation of the second broods following successful first broods and successful renesting attempts occurred during the weeks 7–10.

Model parameterization

Annual reproductive success was estimated as follows. 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. I found no significant site effect on clutch size, brood size, or number of young fledged. Although clutch size varied significantly among years, and both clutch and hatched brood sizes declined significantly over the breeding season (Tables 1 and 2), I found no spatial or temporal heterogeneity in fledged brood sizes and therefore used the same brood size (B) for all consecutive reproductive attempts in the SRDB model.

Rates of apparent nest predation did not vary among years, study sites, and consecutive nesting attempts (Tables 1 and 2), and s_d was not different between the incubation and nestling stages (mean = 0.953; $z = 0.70$, $P = 0.48$). Nest-

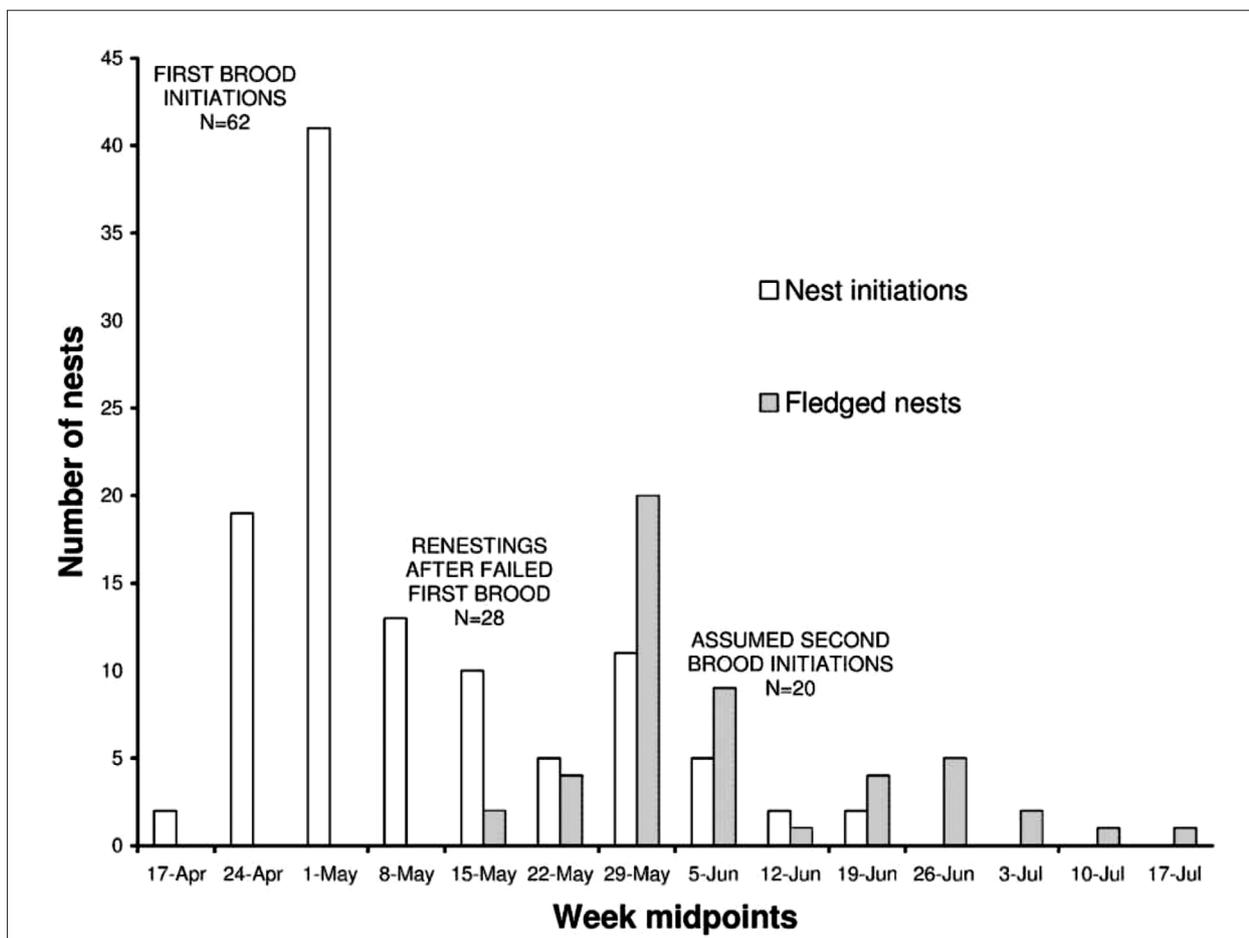


Fig. 2. Timing of Ovenbird reproduction in GSMNP ($n = 110$ nests)

Table 1

Temporal variation in Ovenbird reproductive parameters and nest depredation rates

Parameters	Statistical comparisons ^a							
	among three years of study				among consecutive broods ^b			
	χ^2	<i>F</i> -value	<i>df</i>	<i>P</i>	χ^2	<i>F</i> -value	<i>df</i>	<i>P</i>
Clutch size	–	5.62	2	< 0.01	–	20.06	2	< 0.001
Hatched brood size	–	0.83	2	0.44	–	7.47	2	< 0.01
Fledged brood size	–	0.02	2	0.98	–	1.14	2	0.33
Nest depredation rates ^c	0.40	–	2	0.82	0.27	–	2	0.88

Note: ^a Chi-square test and ANOVA: general linear model; ^b First broods, reneating after the first nest failure, and second broods; ^c Apparent nest depredation (expressed as the ratios of depredated nests to all nests).

Table 2

Spatial variation in Ovenbird reproductive parameters and nest depredation rates

Parameters	Statistical comparisons among study sites			
	χ^2	<i>F</i> -value	<i>df</i>	<i>P</i>
Clutch size	–	0.43	6	0.86
Hatched brood size	–	0.59	5	0.71
Fledged brood size	–	1.25	5	0.31
Nest depredation rates	0.74	–	4	0.95

Table 3

Annual survival of adult (P_A) and juvenile (P_J) females, and annual fecundity (F) in Ovenbird populations with single reneating and double-brooding (SRDB model)

Estimates ^a	P_A	P_J	B	s_d	p_s	F^* ^b	F_{SRDBe} ^c
Mean	0.633	0.317	3.79	0.953	0.310	1.16	0.99
Low ^d	0.545	0.273	3.60	0.947	0.266	1.67	0.80
High ^d	0.721	0.361	3.98	0.959	0.362	0.77	1.21

Note: ^a Successful brood size (B), daily nest survival rate (s_d) and nesting success (p_s) were estimated from this study; ^b Equilibrium fecundity of Ovenbirds (i. e. annual fecundity corresponding to $\lambda = 1$); ^c SRDB model-scenario *e* includes rates of reneating ($p_r = 0.655$) and double-brooding ($p_d = 0.5$) estimated from this study; ^d ‘Low’ and ‘high’ values of P_A , P_J , B , s_d , and p_s correspond to the lower and upper limits of their estimated 95% confidence intervals, respectively. ‘Low’ and ‘high’ values of F and F^* approximate their lower and upper confidence limits. They were computed from either ‘low’ or ‘high’ values of all other parameters in the equation (3).

ing success was estimated from the equation (4) at $p_s = 0.310$ (range: 0.266–0.362) (Table 3).

Annual Ovenbird female survival was computed using equation (6) from the sample of 30 captured and marked breeding females: $P_A = 0.633 \pm 0.088$, $P_J = 0.317 \pm 0.044$. Probabilities of reneating and double-brooding were estimated from my field data using equations (9) and (10):

$$p_r = \frac{28}{62 \cdot (1 - 0.31)} = 0.655;$$

$$p_d = \frac{20}{40} = 0.5 \text{ (Table 3).}$$

I then used the empirical values of p_r for computing annual fecundity and population

growth rates in the SRDB model scenarios *c* and *e*, while empirical values of p_d were used for computation of F and λ in the scenarios *d* and *e*. I applied mean, low, and high estimates of B , P_A , P_J , and p_s for estimating annual fecundity (Table 4). Mean $F_{SRDBe} = 0.99$ (range: 0.80–1.21) female fledglings per breeding female. The corresponding value of equilibrium fecundity was $F^* = 1.16$ female offspring per reproducing female (range: 0.77–1.67).

Computer simulations of Ovenbird population growth rates on my study sites in GSMNP based on the SRDB model yielded the following results. Scenario *d* with assumed 100% reneating rate after the nest failure and empirical estimate of double-brooding rate at 50% was

the only scenario to yield lambda approaching 1 ($\lambda = 0.996$; range: 0.801–1.223), i. e. a population at equilibrium. However, assumptions of the scenario *d* can be hardly expected to occur in the Ovenbird populations.

All other scenarios of the SRDB model resulted in much lower population growth rates (Table 4). For example, monocyclic reproduction without reneating (scenario *a*) yielded the lowest $\lambda = 0.819$ (range: 0.675–0.981), while scenario *e* based on empirical estimates of both reneating and double-brooding rates resulted in $\lambda = 0.945$ (range: 0.764–1.156).

Discussion

Annual female survival and components of annual fecundity

Survival estimates based on the recapture of birds marked in previous years are negatively biased because of dispersal [22] and incomplete site fidelity [23]. Of a very few studies that measured annual survival rates of adult Ovenbirds directly, only one study specifically estimated female survival [24], because territorial males are much easier to detect and capture than females. My indirect estimate of adult female survival from the age ratios ($P_A = 0.633 \pm 0.088$) agreed with recent published estimates from unfragmented landscapes based on the band returns (0.61 ± 0.09 [13]; 0.60 ± 0.06 [24]). It appeared to be on the high end of the published estimates that range from 0.02 to 0.85, as reported in Table 3 in Bayne and Hobson [24].

Contrary to some findings, stating that later in the season Ovenbirds breed more successfully [25], I found no evidence of seasonal variability in successful brood size and daily nest survival rates on my study sites. Therefore, I was able to

use the same empirically derived values of these model parameters for consecutive reproductive attempts. Both daily nest survival rates ($s_d = 0.953 \pm 0.006$) and average fledged brood size ($B = 3.79 \pm 0.19$) in my study were derived from large samples, and they were within the range of the published rates for contiguous forested habitats (s_d and B ranging 0.945–0.985 and 2.94–4.30, respectively [13–15, 26]).

Direct measurements of reneating and double-brooding rates based on observations of marked birds are very complicated. Within-season dispersal and incomplete site fidelity are poorly studied in this species. They may further confound the estimates [27]. Published data on reneating probabilities of Ovenbirds are virtually non-existent. In my study, there were only three clear instances of double-brooding and one instance of reneating next to a failed nest. My indirect estimates, $p_r = 0.655$ and $p_d = 0.5$, were based solely on nesting chronology. Typically, the Ovenbird is considered a monocyclic species with only a few instances of true second broods ever encountered [9]. Therefore, it was highly unlikely that my computed values of p_d and, consequently, of annual fecundity were underestimated, even though it was quite possible that, at the southern boundary of the species' breeding range, Ovenbird populations might have a higher p_d than populations farther north, due to a longer breeding season.

Population growth models and population trends vs. depredation rates

Breeding Bird Survey data for the Ovenbird in the southern Appalachian region suggest consistent population declines at an average annual rate of 1.5% while surrounding areas sustain

Table 4

Ovenbird population growth rates from the SRDB model (scenarios *a-e*)

Model scenarios ^a	p_r ^b	p_d ^c	λ_{low}	λ_{mean}	λ_{high} ^d
<i>a</i>	0	0	0.675	0.819	0.981
<i>b</i>	1	0	0.771	0.947	1.146
<i>c</i>	0.655	0	0.739	0.903	1.089
<i>d</i>	1	0.5	0.801	0.996	1.223
<i>e</i>	0.655	0.5	0.764	0.945	1.156

Note: ^a Model scenarios use the estimates of annual adult female survival ($P_A = 0.633 \pm 0.088$), fledged brood size ($B = 3.79 \pm 0.19$), and nesting success ($p_s = 0.310_{mean}$, 0.266_{low} , and 0.362_{high}) from this study. Annual survival of juvenile females is assumed half of P_A ($P_J = 0.317 \pm 0.044$): see the equation (7); ^b Reneating rate (ratio of reneating attempts to previously failed nests). Scenarios *c* and *e* use the estimates of p_r from this study (0.655); ^c Double-brooding rate (ratio of second broods to the sum of successful first broods and successful reneating attempts). Scenarios *d* and *e* use the estimates of p_d from this study (0.5); ^d Ranges of λ -values represent approximate 95% confidence intervals.

growing populations [10]. Although I observed no evidence of large Ovenbird population changes over three years of research in GSMNP, my data on population growth rates implied negative population trend in this species: all scenarios of the single-renesting-double-brooding model, but one, yielded λ considerably less than 1. Scenario *d* produced population approaching equilibrium, although the assumption of 100% renesting rate seemed highly unrealistic (Table 4). Given strict monitoring protocol, the criteria used to assess nest fates, and large sample sizes, my estimates of p_s and B were quite accurate. My indirect empirical estimate of annual female survival complied with published data [24], and along with computed renesting and double-brooding rates, it did not seem to be understated. Therefore, the model parameter causing $\lambda < 1$ was likely to be the nest survival rate.

Nest depredation is the most common cause of ground-nesting songbird nest failure [28]. Except for two instances of parental birds taken by predators, all other reproductive failures in my study were caused by nest depredation. In most published studies, higher rates of predation are attributed to higher degrees of forested habitat fragmentation [29]. However, this is not always true due to the “paradox of predation” [30]: high quality forests in GSMNP attracted a variety of abundant reptilian, avian, and mammalian predators ranging from voles, wood rats, flying squirrels, and opossums to various snakes, Blue Jays, and even black bears [31]. Therefore, the best pristine habitats of GSMNP were not ecologically significant sources but rather “ecological traps” [32] for the Ovenbird. This species obviously evaluates the habitat quality mainly from visual cues. On the other hand, in some of the affected by human activities adjacent landscapes, breeding success and annual productivity could have been higher, which would explain growing Ovenbird populations reported by Breeding Bird Survey [10], because many of the above predators were absent or scarce in lower quality fragmented forests.

Implications for future conservation strategies

Although accurate assessment of the population status is crucial for developing demographic models for conservation and management [33], 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 variation in the rates of renesting and double-brooding. Accurate empirical estimates of these parameters could significantly improve an accuracy of the existing songbird population models. Direct methods for estimating these parameters should be used, whenever possible.

The “paradox of predation” could potentially lead to unpredictable population dynamics. Therefore, besides *a priori* assignment of the protected status to the high quality pristine landscapes, an effective strategy for the protection of declining species at the regional level should also include an examination of the specifics of spatial and temporal dynamics of its populations and possible inclusion of the lower quality habitats in the regional network of protected natural areas.

Logically, it could be even necessary to actively protect suitable patches, not inhabited by the species, but which could be subsequently colonized by it as a result of its metapopulation and source-sink dynamics.

References

1. Hanski I. Metapopulation ecology. New York: Oxford University Press, 1999. 328 p.
2. Pulliam H.R. Sources, sinks, and population regulation // *American Naturalist*. 1988. V. 132. P. 652–661.
3. Askins R.A. Restoring North America’s birds: lessons from landscape ecology. New Haven: Yale University Press, 2000. 320 p.
4. Murphy M.T. Habitat-specific demography of a long-distance, neotropical migrant bird, the Eastern Kingbird // *Ecology*. 2001. V. 82. P. 1304–1318.
5. Thompson B.C., Knadle G.E., Brubaker D.L., Brubaker K.S. Nest success is not an adequate comparative estimate of avian reproduction // *Journal of Field Ornithology*. 2001. V. 72. P. 527–536.
6. Murray Jr. B.G. Measuring annual reproductive success, with comments on the evolution of reproductive behavior // *Auk*. 1991. V. 108. P. 942–952.
7. Nagy L.R., Holmes R.T. To double-brood or not? Individual variation in the reproductive effort in Black-Throated Blue Warblers (*Dendroica caerulescens*) // *Auk*. 2005. V. 122. P. 902–914.
8. Grzybowski J.A., Pease C.M. Renesting determines seasonal fecundity in songbirds: What do we know? What should we assume? // *Auk*. 2005. V. 122. P. 280–291.
9. Van Horn M.A., Donovan T.M. Ovenbird (*Seiurus aurocapillus*) // *Birds of North America* / Eds. A. Poole, F. Gill, D.C. Washington. Academy of Natural Sciences and American Ornithologists’ Union, 1994. No. 88. 23 p.
10. Sauer J.R., Hines J.E., Fallon J. The North American breeding bird survey, results and analysis,

- 1966–2004, version 2005.2. Laurel: U.S. Geological Survey Patuxent Wildlife Research Center, 2005. [Internet resource] <https://www.mbr-pwrc.usgs.gov/bbs/bs2004.html> (Accessed: 01.07.2018).
11. Ricklefs R.E. Fecundity, mortality, and avian demography // *Breeding Biology of Birds* / Ed. D.S. Farner. Philadelphia: National Academy of Sciences, 1973. P. 366–435.
 12. Mayfield H.F. Suggestions for calculating nest success // *Wilson Bulletin*. 1975. V. 87. P. 456–466.
 13. Porneluzi P.A., Faaborg J. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes // *Conservation Biology*. 1999. V. 13. P. 1151–1161.
 14. Donovan T.M., Thompson III F.R., Faaborg J., Probst J.R. Reproductive success of migratory birds in habitat sources and sinks // *Conservation Biology*. 1995. V. 9. P. 1380–1395.
 15. Flaspohler D.J., Temple S.A., Rosenfield R.N. Effects of forest edges on Ovenbird demography in a managed forest landscape // *Conservation Biology*. 2001. V. 15. P. 173–183.
 16. Martin T.E., Geupel G.R. Nest-monitoring plots: methods for locating nests and monitoring success // *Journal of Field Ornithology*. 1993. V. 64. P. 507–519.
 17. Rodewald A.D. Nest-searching cues and studies of nest-site selection and nesting success // *Journal of Field Ornithology*. 2004. V. 75. P. 31–39.
 18. Manolis J.C., Andersen D.E., Cuthbert F.J. Uncertain nest fates in songbird studies and variation in Mayfield estimation // *Auk*. 2000. V. 117. P. 615–626.
 19. Johnson D.H. Estimating nesting success: the Mayfield method and an alternative // *Auk*. 1979. V. 96. P. 651–661.
 20. Greenwood P.J., Harvey P.H. The natal and breeding dispersal of birds // *Annual Review of Ecology and Systematics*. 1982. V. 13. P. 1–21.
 21. Donovan T.M., Stanley C.M. A new method of determining Ovenbird age on the basis of rectrix shape // *Journal of Field Ornithology*. 1995. V. 66. P. 247–252.
 22. Nichols J.D., Noon B.R., Stokes S.L., Hines J.E. Remarks on the use of mark-recapture methodology in estimating avian population size. Estimating Numbers of Terrestrial Birds / Eds. C.J. Ralph, J.M. Scott // *Studies in Avian Biology*. 1981. No. 6. P. 121–136.
 23. Marshall M.R., Diefenbach D.R., Wood L.A., Cooper R.J. Annual survival estimation of migratory songbirds confounded by incomplete breeding site-fidelity: study designs that may help // *Animal Biodiversity and Conservation*. 2004. V. 27. P. 59–72.
 24. Bayne E.M., Hobson K.A. Annual survival of adult American Redstarts and Ovenbirds in the southern boreal forest // *Wilson Bulletin*. 2002. V. 114. P. 358–367.
 25. Faaborg J., Thompson III F.R., Robinson S.K., Donovan T.M., Whitehead D.R., Brawn J.D. Understanding fragmented Midwestern landscapes: the future / Eds. J.M. Marzluff, R. Sallabanks // *Avian Conservation: Research and Management*. Washington, D.C.: Island Press, 1998. P. 193–207.
 26. Manolis J.C., Andersen D.E., Cuthbert F.J. Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape // *Auk*. 2002. V. 119. P. 955–970.
 27. Howlett J.S., Stutchbury B.J.M. Within-season dispersal, nest-site modification, and predation in re-nesting Hooded Warblers // *Wilson Bulletin*. 1987. V. 109. P. 643–649.
 28. Thompson III F.R. Factors affecting nest predation on forest songbirds in North America // *Ibis*. 2007. V. 149. P. 98–109.
 29. Chalfoun D., Thompson III F.R., Ratnaswamy M.J. Nest predators and fragmentation: a review and meta-analysis // *Conservation Biology*. 2002. V. 16. P. 306–318.
 30. Wilcove D.S. Nest predation in forest tracts and the decline of migratory songbirds // *Ecology*. 1985. V. 66. P. 1211–1214.
 31. Farnsworth G.L., Simons T.R. Observations of Wood Thrush nest predators in a large contiguous forest // *Wilson Bulletin*. 2000. V. 112. P. 82–87.
 32. Robertson B.A., Hutto R.L. A framework for understanding ecological traps and an evaluation of existing evidence // *Ecology*. 2006. V. 87. P. 1075–1085.
 33. Ruth J.M., Petit D.R., Sauer J.R., Samuel M.D., Johnson F.A., Fornwall M.D., Korschgen C.E., Bennett J.P. Science for avian conservation: priorities for the new millennium // *Auk*. 2003. V. 120. P. 204–211.