

ЧАСТЬ 2.

Серия «ГЕОГРАФИЯ» Т.26 (65) №3, 2013

УДК 574.34 + 004.94

DESIGNING PROTECTED NATURAL AREAS ON THE BASIS OF MODELING POPULATION DYNAMICS OF RARE SPECIES

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An effectiveness of protection and recovery of rare species depends on proper understanding of their ecological characteristics and population dynamics. Metapopulation dynamics could lead to the extinction of local populations in selected landscape patches regardless of the habitat quality and conservation measures. On the other hand, source-sink dynamics could result in lesser quality habitat patches to be saturated by dispersing individuals from population sources. Therefore, an effective strategy for the protection of rare species at the regional level should include both high quality pristine landscapes and some lower quality habitat patches in the regional network of protected areas for the species in question. I studied reproductive ecology of declining songbird species, the Ovenbird (*Seiurus aurocapilla* L.), in the Great Smoky Mountains National Park (U.S.A.) to develop parsimonious computer models describing its population dynamics. These models can be used to propose a proper bioserve design for this species to ensure the source status of its populations.

Keywords: annual fecundity, annual survival, multiple brooding, population growth models, reneating, *Seiurus aurocapilla*.

INTRODUCTION

An effectiveness of protection and recovery of rare species depends on proper understanding of their ecological characteristics and population dynamics. Habitats suitable for a certain species alternate with unfavorable habitat patches. The common misconception is that effective protection of a declining species can be accomplished only by protecting the 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 conservation measures. According to the source-sink concept [2], habitat patches supporting population sources can produce a surplus of individuals to disperse to adjacent poor quality patches of sink habitats.

Population declines of migratory terrestrial birds in eastern North America are explained mainly by habitat fragmentation, and higher rates of predation and brood parasitism in fragmented landscapes [3]. These findings initiated numerous studies of bird reproductive success and source-sink dynamics in contiguous vs. fragmented landscapes [4, 5].

It is important to properly estimate annual fecundity in birds. Hundreds of published studies did not distinguish between nesting success and productivity [6]. Some species of passerines are multibrooded while some breed only once a year. It was found that certain proportion of individuals in populations of single-brooded species can undertake second

broods at southern extremes of their breeding ranges [7]. Often ignored by population-growth models, renesting after a nest failure and double-brooding may account for up to 40% of annual fecundity in birds [8]. Therefore, failing to consider additional breeding attempts in demographic models can result in underestimates of annual fecundity and population growth rate [9, 10].

Being a common model species for songbird source-sink relationships, the Ovenbird (*Seiurus aurocapilla* L.) is generally considered a single-brooded species [11]. The objectives of my study were to model a source-sink dynamics of the Ovenbird *populations in the* Great Smoky Mountains National Park (NC / TN, 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 [12]. To explain this paradox, I developed a probabilistic model of Ovenbird annual fecundity based on my field estimates of nesting success and brood size and both observed and published estimates of female survival, and rates of renesting and double-brooding. I also wanted to assess how assumptions about these parameters influence estimated population growth rates.

1. METHODS

1.1 Building the model

My seven study sites, cumulatively covering >700 ha, were located in the Great Smoky Mountain National Park 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 [13] defined annual fecundity (F) as the number of juvenile females produced annually per breeding female. Assuming 100% pairing success of females, equal fledgling sex ratio, and a single reproductive cycle 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 [14] as:

$$F = \frac{1}{2} B p_s. \tag{1}$$

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

$$\lambda = P_A + P_J F = 1 \tag{2}$$

for a population at equilibrium, and $\lambda > 1$ for a source population, where P_A and P_J are annual survival of adult and juvenile females, correspondingly. Published Ovenbird population models include a variety of assumptions about renesting and double-brooding: some studies assumed mono-cyclic reproduction with no renesting [15], while others assumed one renesting after failure [16], or even a 5-10% possibility of double-brooding [17].

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

$$\lambda = P_A + P_J^{1/2} [p_s B + p_s (1-p_s) p_r B + p_s p_d p_s B + p_s p_d p_s (1-p_s) p_r B] = P_A + P_J^{1/2} B p_s [1 + p_r - p_s p_r + p_s p_d + p_s p_d (1-p_s) p_r] \quad (3)$$

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, 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, 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 renesting and double-brooding probabilities to 1 or 0, or by using values estimated from our 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) $p_r = \{\text{estimated value}\}, p_d = \{\text{estimated value}\}$.

1. 2 Estimating model parameters

In order to estimate *annual reproductive success, my field crew and I* searched study sites for nests from mid-April until the end of July following the existing guidelines to collect a representative sample of nests [18, 19]. 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 [20].

Reproductive success was estimated by using daily survival rates (s_d) and nesting success (p_s) *sensu* Mayfield [14] 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 naïve, nest epre ati on was estimate as:

$$\begin{aligned} & \text{apparent nest depredation rates} = \\ & = (\text{number of predated nests}) \div (\text{number of all nests}). \end{aligned} \quad (5)$$

Standard errors of s_d and test-statistics (z) for evaluating variability of s_d among years, sites, and consecutive breeding attempts were calculated [21]. I approximated a confidence interval for p_s 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 brood size, and fledged brood size, I conducted analysis of variance (ANOVA, general linear model).

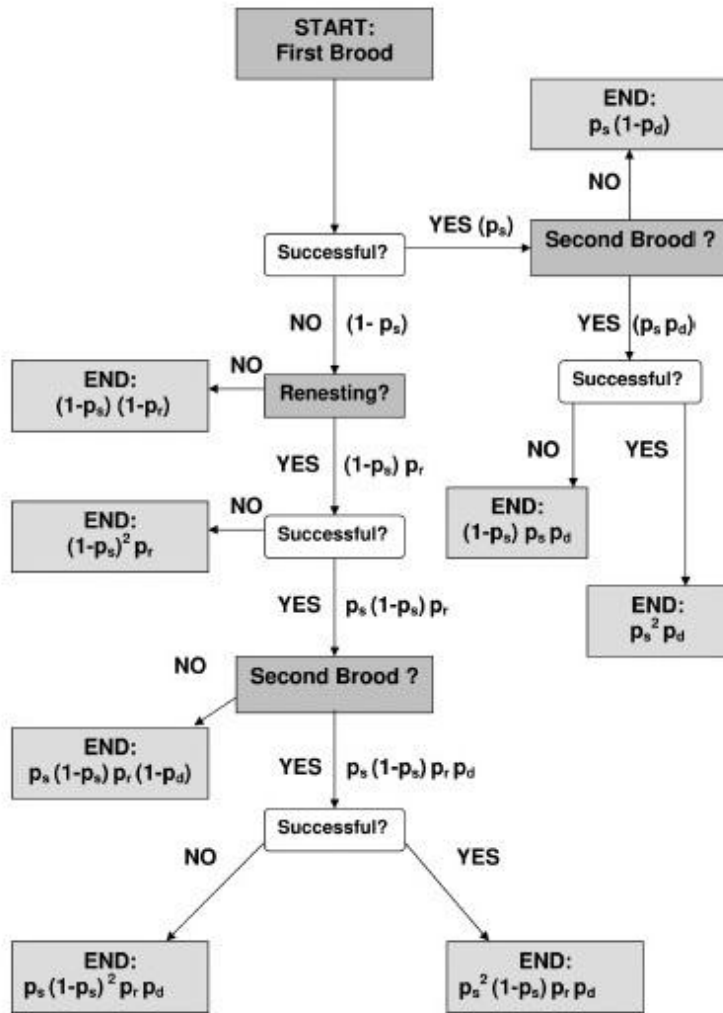


Fig. 1. Flow-chart summary of the single-renesting-double-brooding model of annual fecundity.

The model presented at Fig. 1 is described by the equation (3). It assumes homogeneity of Ovenbird nesting success (p_s) and is limited by one renesting attempt after nest failure (p_r) while successful first broods and successful renesting 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 [22]. I used an alternative method based on ratios of after-second-year (ASY) to second-year (SY) birds [13]:

$$P_A = \text{ASY} \div (\text{ASY} + \text{SY}). \quad (6)$$

Females were captured on nests using a butterfly net and their age was identified by the shape of the third rectrix [23]. Following Ricklefs [13], I considered probability of juvenile female survival:

$$P_J = 0.5 P_A. \quad (7)$$

To estimate probabilities of renesting 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 [10]. I used 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:

$$N = (\text{breeding-season length}) \div (\text{duration of the nesting cycle} + \text{interval between two consecutive cycles}). \quad (8)$$

Female Ovenbirds arrive on breeding grounds over an average interval of seven days and start their nests over seven days from the date of arrival [11]. 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 renesting, and nests started from week 7 on were attributed to second broods [24]. Assuming an independence of nests in my study and constant nest-searching effort, I estimated the probability of renesting as:

$$p_r = \text{renesting attempts} \div [\text{first broods} \times (1-p_s)] \quad (9)$$

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

$$p_d = \text{second broods} \div (\text{successful first broods} + \text{successful renesting attempts}). \quad (10)$$

2. RESULTS

2.1. Reproductive chronology

From 1999 to 2001, 110 Ovenbird nests were found and monitored in the Great Smoky Mountain National Park. On average among three years, the earliest nest initiation took place on 14 April and 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 my study sites (according to the equation [8]) would allow for two successful broods in a season: $96 \div 38 = 2.5$.

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 fledged on 2 July ± 2.9 days.

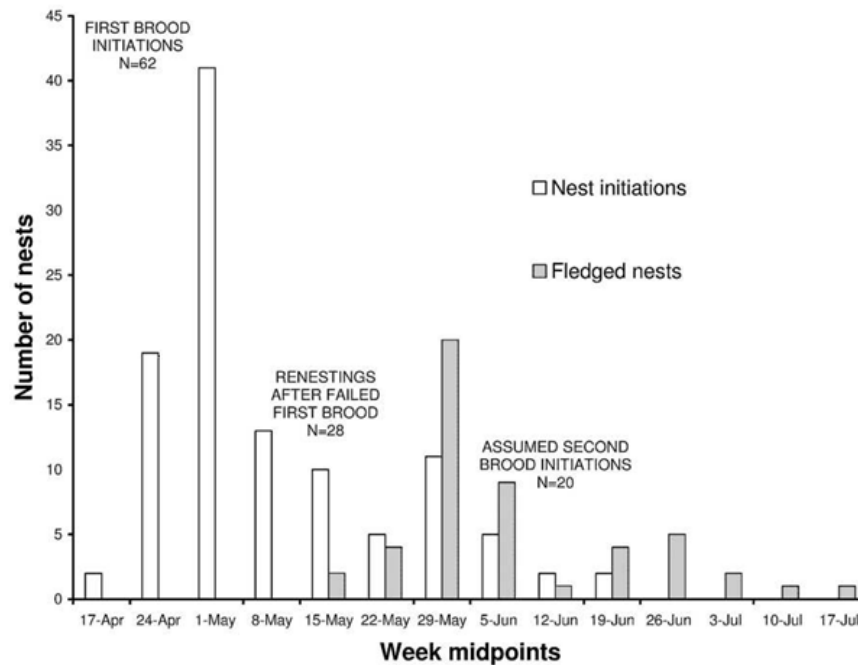


Fig. 2. Timing of Ovenbird reproduction in the Great Smoky Mountains National Park, 1999 – 2001.

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

2.2. 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 raise 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 SRDB model.

Table 1.

Temporal variation in Ovenbird reproductive parameters and nest depredation rates.

Statistical comparisons ^a								
Parameters	Among years ^b				Among consecutive broods ^c			
	χ^2	F-value	df	P	χ^2	F-value	df	P
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 ^d	0,40	—	2	0,82	0,27	—	2	0,88

^a Chi-square test and ANOVA: general linear model.

^b 1999, 2000, and 2001.

^c First broods, renesting after the first nest failure, and second broods.

^d Apparent nest depredation (expressed as the ratios of depredated nests to all nests).

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; $z = 0.70$, $P = 0.48$). Nesting success was estimated from the equation (4) at $p_s = 0.310$ (range: 0.266–0.362) (Table 3).

Table 2.
Spatial variation in Ovenbird reproductive parameters and nest depredation rates.

Parameters	Statistical comparisons among study sites			
	χ^2	F-value	df	P
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

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 renesting and double-brooding were estimated from my field data using equations (9) and (10): $p_r = 28 \div [62 \times (1-0.31)] = 0.655$; $p_d = 20 \div 40 = 0.5$ (Table 3).

Table 3.
Annual survival of adult (P_A) and juvenile (P_J) females, and annual fecundity (F) in Ovenbird populations with single renesting and double-brooding (SRDB model).

Estimates ^a	P_A	P_J	B	s_d	p_s	F^* ^b	$F_{SRDB e}$ ^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

^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 renesting ($p_r = 0.655$) 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).

I then used 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 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 $F_{SRDB} = 0.99$ (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).

Table 4.
Ovenbird population growth rates from the single-renesting-double-brooding 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

^a Model scenarios use estimates of annual adult female survival ($P_A = 0.633 \pm 0.088$), fledgling 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 equation (7).

^b Renesting rate (ratio of renesting attempts to previously failed nests). Scenarios c and e use 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 renesting attempts). Scenarios d and e use estimates of p_d from this study (0.5).

^d Ranges of λ -values represent approximate 95% confidence intervals.

Computer simulations of Ovenbird population growth rates on my study sites in the Great Smoky Mountain National Park based on the SRDB model yielded the following results. Scenario d with assumed 100% renesting rate after 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 renesting (scenario a) yielded the lowest $\lambda = 0.819$ (range: 0.675–0.981) while scenario e based on empirical estimates of both renesting and double-brooding rates resulted in $\lambda = 0.945$ (range: 0.764–1.156).

3. DISCUSSION

3.1. 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 [25] and incomplete site fidelity [26]. Of a very few studies that measured annual survival rates of adult Ovenbirds directly, only one study

specifically estimated female survival [27], because territorial males are much easier to detect and capture than females. My indirect estimate of adult female survival from the age ratios ($P_A = 0.633 \pm 0.088$) agree with recent published estimates from unfragmented landscapes based on band returns (0.61 ± 0.09 [15]; 0.60 ± 0.06 [27]). It appears to be on the high end of published estimates that range from 0.02 to 0.85, as reported in Table 3 in Bayne and Hobson [27].

Contrary to some findings that later in the season Ovenbirds breed more successfully [28], 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 fledgling brood size ($B = 3.79 \pm 0.19$) in my study were derived from large samples, and they are within the range of published rates for contiguous forested habitats (s_d and B ranging 0.945–0.985 and 2.94–4.30, respectively [15–17, 29]).

Direct measurements of *re-nesting and double-brooding rates* based on observations of marked birds are very complicated. Within-season dispersal and incomplete site fidelity that are poorly studied in this species may further confound estimates [30]. Published data on re-nesting probabilities of Ovenbirds are virtually non-existent. In my study, there were only three clear instances of double-brooding and one instance of re-nesting 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 [11]. Therefore, it was highly unlikely that my computed values of p_d and, consequently, of annual fecundity were underestimated, even though it is quite possible that at the southern boundary of the species' breeding range, Ovenbird populations may have a higher p_d than populations farther north because of a longer breeding season.

3.2. 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 growing populations [12]. Although I observed no evidence of large Ovenbird population changes during three years of research in the Great Smoky Mountain National Park [24], my data on population growth rates implied negative population trend in this species: all scenarios of the single-re-nesting-double-brooding model but one yielded λ considerably less than 1. Scenario *d* produced population approaching equilibrium, although the assumption of 100% re-nesting rate seemed highly unrealistic (Table 4). Given strict monitoring protocol, the criteria used to assess nest fates, and large sample sizes, I feel that my estimates of p_s and B are quite accurate. My indirect empirical estimate of annual female survival complied with published data [27], and along with computed re-nesting and double-brooding rates, it does not seem to be understated. Therefore, I believe that the model parameter causing $\lambda < 1$ is the nest survival rate.

Nest depredation is the most common cause of ground-nesting songbird nest failure [31]. 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 [32]. However, this is not always true due to the “paradox of predation” [33]: high quality forests in Great Smoky Mountain National Park 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 [34]. Therefore, the best pristine habitats of the Great Smoky Mountain National Park were not ecologically significant sources but rather “ecological traps” [35] for the Ovenbird that evaluates 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 [12], because many of the above predators were absent or scarce in lower quality fragmented forests.

CONCLUSIONS: IMPLICATIONS FOR FUTURE CONSERVATION STRATEGIES

Although accurate assessment of population status is vital for developing demographic models for conservation and management [36], 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 rates of renesting and double-brooding. Accurate empirical estimates of these parameters will significantly improve existing songbird population models. Direct methods for estimating these parameters should be used whenever feasible.

The “paradox of predation” could potentially lead to unpredictable population dynamics. Therefore, besides assigning to the high quality pristine landscapes protected status a priori, an effective strategy for the protection of rare species at the regional level should also include 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 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 source-sink dynamics and metapopulation dynamics.

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Подольский А.Л. Организация охраняемых природных территорий на основе моделирования популяционной динамики редких видов / А.Л. Подольский // Ученые записки Таврического национального университета имени В. И. Вернадского. – Серия «География». – 2013. – Т. 26 (65), № 3. – С. 179 – .

Эффективность сохранения биоразнообразия зависит от правильного понимания популяционной структуры и пространственно-временной динамики охраняемых видов. Метопопуляционная динамика может привести к вымиранию локальных популяций в отдельных парцеллах ландшафта независимо от качества местообитаний и проводимых природоохранных мер. С другой стороны, популяционная динамика по принципу «источников и раковин» может вызвать перенасыщение благоприятных местообитаний размножающимися особями и сделать эти участки «источниками» излишка особей для заселения близлежащих участков худшего качества («раковин»). В этом экологическом сценарии охрана менее качественных участков ландшафта должна быть включена в общую приоритетную стратегию охраны редких видов.

Ключевые слова: годовая продуктивность, годовая выживаемость, полициклическое размножение, модели популяционного роста, повторное гнездование, *Seiurus aurocapilla*.

Подольскій А.Л. Організація захищених природних територій на основі моделювання динаміки населення рідкісних видів / А.Л. Подольскій // Вчені записки Таврійського національного університету імені В.І.Вернадського. – Серія «Географія». – 2013. – Т. 26 (65), № 3. – С. 179 – 191..

Ефективність збереження біорізноманіття залежить від правильного розуміння структури популяцій, а також тимчасової і просторової динаміки рідкісних видів. Метопопуляційна динаміка може привести до зникнення місцевих популяцій у деяких районах краєвиду, незалежно від якості місця проживання та природоохороняємих зусиль. З іншого боку, популяційна динаміка типу "джерел і раковин" може привести до присутності надто багатого розведення тварин у сприятливому середовищі проживання. Як результат, ці території можуть стати "джерелами" надлишки фізичних осіб поблизу ділянок низької якості ("раковини"). У цьому випадку захист навколишнього середовища меншої якості районів краєвиду повинні бути включені в пріоритетну стратегію захисту рідкісних видів.

Ключові слова: щорічна продуктивність, щорічне виживання, поліциклічне відтворення, моделі зростання популяцій, неодноразові вкладення, *Seiurus aurocapilla*.

Статья поступила в редакцию 13.09.2013 г