

A PRODUCTIVITY MODEL FOR PARASITIZED, MULTIBROODED SONGBIRDS

LARKIN A. POWELL^{1,3} AND MELINDA G. KNUTSON²

¹*School of Natural Resources, 202 Natural Resources Hall, University of Nebraska, Lincoln, NE 68583-0819*

²*U.S. Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, La Crosse, WI 54603*

Abstract. We present an enhancement of a simulation model to predict annual productivity for Wood Thrushes (*Hylocichla mustelina*) and American Redstarts (*Setophaga ruticilla*); the model includes effects of Brown-headed Cowbird (*Molothrus ater*) parasitism. We used species-specific data from the Driftless Area Ecoregion of Wisconsin, Minnesota, and Iowa to parameterize the model as a case study. The simulation model predicted annual productivity of 2.03 ± 1.60 SD for Wood Thrushes and 1.56 ± 1.31 SD for American Redstarts. Our sensitivity analysis showed that high parasitism lowered Wood Thrush annual productivity more than American Redstart productivity, even though parasitism affected individual nests of redstarts more severely. Annual productivity predictions are valuable for habitat managers, but productivity is not easily obtained from field studies. Our model provides a useful means of integrating complex life history parameters to predict productivity for songbirds that experience nest parasitism.

Key words: American Redstart, Brown-headed Cowbird, productivity, seasonal fecundity, simulation model, Wood Thrush.

Un Modelo de Productividad para Aves Canoras que son Parasitadas y Tienen Puestas Múltiples

Resumen. Presentamos un modelo de simulación mejorado para predecir la productividad anual de *Hylocichla mustelina* y *Setophaga ruticilla* que considera el efecto del parasitismo por *Molothrus ater*. Utilizamos datos especie-específicos de la ecorregión “Driftless Area” de Wisconsin, Minnesota y Iowa para determinar los parámetros del modelo como un caso de estudio. El modelo de simulación predijo una productividad anual de 2.03 ± 1.60 DE para *H. mustelina* y de 1.56 ± 1.31 DE para *S. ruticilla*. El análisis de sensibilidad mostró que altos niveles de parasitismo disminuyeron la productividad anual de *H. mustelina* en un mayor grado que la de *S. ruticilla*, a pesar de que el parasitismo a nivel de cada nido afectó de forma más severa a *S. ruticilla*. Las predicciones de productividad anual son valiosas para el manejo de hábitats, pero las medidas de productividad no son obtenidas fácilmente mediante estudios de campo. Nuestro modelo provee una herramienta útil para integrar parámetros de historia de vida para predecir la productividad de aves canoras que son parasitadas en sus nidos.

INTRODUCTION

Biologists commonly seek to determine the annual reproductive performance of avian populations (Ricklefs and Bloom 1977, Anders and Marshall 2005). To this end, nest monitoring data are routinely collected during a variety of avian studies, but Thompson et al. (2001) and Underwood and Roth (2002) found that daily nest survival is not a useful metric for predicting songbird annual productivity. Instead, biologists should attempt to calculate annual fecundity (B ; mean number of females

produced per adult female per year) or annual productivity (p ; total juveniles per female alive at the end of the breeding season). Anders and Marshall (2005) suggested that accurate assessments of annual productivity are critical, given the need for data to direct conservation and management decisions.

Calculations of annual productivity are not easy to obtain (Ricklefs and Bloom 1977). Conceptually, annual songbird productivity (p) is a simple function of three random variables, defined as: $p = f \times ns \times nests$; where f equals mean number of fledglings per successful nest, ns equals nest survival probability, and $nests$ equals the average number of nests built per female per year. Many biologists have calculated

Manuscript received 30 June 2005; accepted 2 February 2006.

³ E-mail: lpowell3@unl.edu

annual productivity in this manner; however, following individual females throughout a breeding season is not possible in large-scale studies (Donovan et al. 1995). Furthermore, a prediction of the variance of p ($\text{var}[p]$) is not easily obtained via this method. When temporally complete data are not available for each female for a breeding season, the calculation of p requires a best-guess estimate of the number of nests attempted by females, and this is often not provided. Thompson et al. (2001) reported that more than two-thirds of avian demographic articles, reviewed from 1984–1997, failed to compensate for multiple brooding or renesting.

Annual productivity (p) and its variance ($\text{var}[p]$) can be directly determined by using samples of color-marked or radio-marked females. For example, Underwood and Roth (2002) were able to effectively calculate annual productivity from color-marked Wood Thrush females in an intensely studied, isolated forest fragment. However, Lang et al. (2002) reported long movements of females between nests within a breeding season in a larger forested landscape; incomplete detections caused by similar movements or other reasons limited the sample size of color-marked Wood Thrush females used by Trine (1998) for calculations of annual productivity.

Simulation models are useful when it is difficult to monitor individual females for an entire breeding season (Anders and Marshall 2005). Pease and Grzybowski (1995) and Powell et al. (1999) used stochastic simulation models that predicted p by incorporating field estimates of nest survival, frequency of renesting, length of breeding season and renesting interval, and other life history components. The two simulation models also provided estimates of variance for the predicted productivities; variance estimates are critical for population growth models (Conroy et al. 1995).

Powell et al.'s (1999) model did not include the effects of Brown-headed Cowbird (*Molothrus ater*) parasitism, as <5% of Wood Thrushes in Georgia experienced parasitism. However, many songbirds experience high levels of parasitism in portions of their range, and parasitism can negatively affect annual productivity for many avian species (Donovan et al. 1995, Robinson et al. 1995). Thus, our goal was to enhance Powell et al.'s (1999)

simulation model to predict annual productivity for songbird species that experience brood parasitism. We parameterized the enhanced model with data obtained from field studies and the literature for Wood Thrushes (*Hylocichla mustelina*) and American Redstarts (*Setophaga ruticilla*); both species are multi-brooded, Neotropical migrants that experience cowbird parasitism in forests of the Driftless Area Ecoregion of Wisconsin, Minnesota, and Iowa. We used the resulting annual productivity model to explore potential interactive effects of nest survival and parasitism on annual productivity of our focal species.

METHODS

We modified Powell et al.'s (1999) dynamic, stochastic, individual-based model to predict annual productivity (p) for multibrooded songbirds that experience parasitism. Our model's structure and function was identical to that of Powell et al. (1999), in that it incorporated female and fledgling dynamics; however, we added a parasitism module (Fig. 1), and we created species-specific models for Wood Thrushes and American Redstarts. We constructed the model using the Interactive Matrix Language in SAS (IML; SAS Institute 2000), and the model followed one female and her offspring on a "random walk" through the breeding season (Fig. 1). We assumed that a mate was available for the female during the entire summer; we did not include adult males in our model.

We based the breeding season length (Table 1) on our field data from the Driftless Area. We used field or literature data for time needed to build a nest, nesting interval, and fledgling care interval (Table 1). The model followed fledglings until mid-September, the normal start of migration for the Driftless Area; at this time, the number of living fledglings produced by each female were summed to derive her annual productivity.

We obtained daily nest survival rates from nest monitoring data from the Driftless Area Ecoregion of Wisconsin, Minnesota, and Iowa (upland sites: Knutson et al. 2004; Mississippi River floodplain sites: Knutson et al. 2006). We used Powell et al.'s (1999) estimates of weekly adult and juvenile survival to calculate daily survival of Wood Thrushes. We calculated daily adult and juvenile survival probabilities for

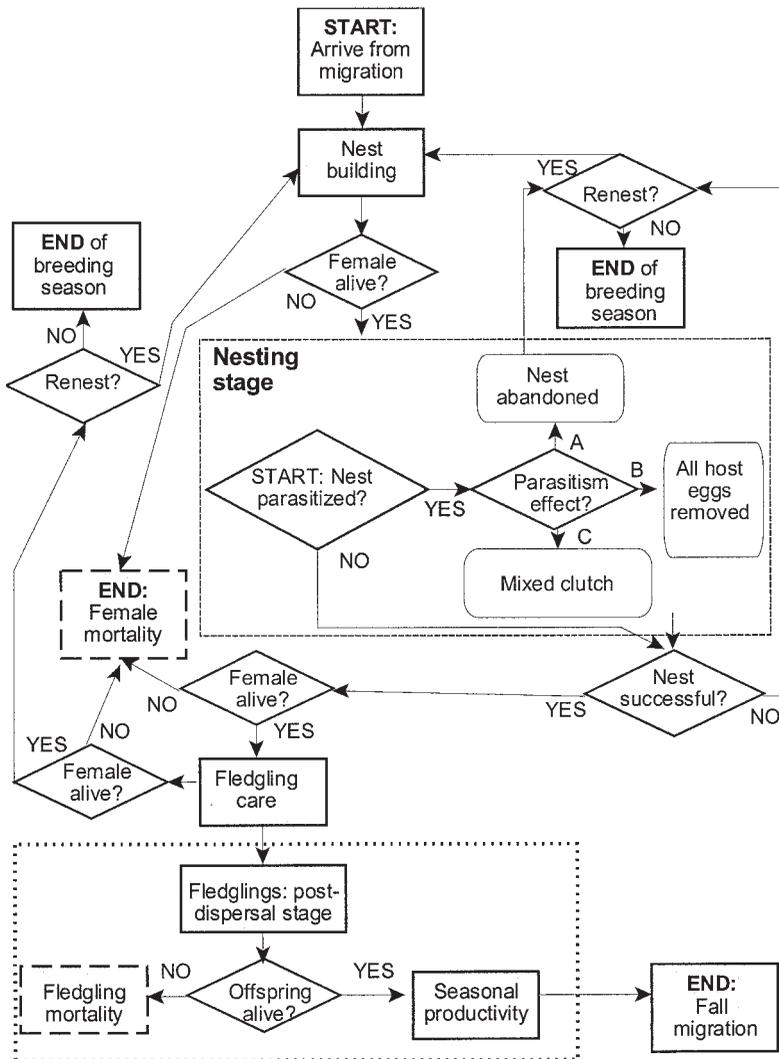


FIGURE 1. Flow chart summary of individual-based, annual productivity model. The diagram describes states (shaded boxes) through which a female songbird transitions during the breeding season, along with several decision points (diamond boxes). The model includes a parasitism module during the nesting stage with three effects of nest parasitism on the nesting process: (A) nest abandonment, (B) complete host egg reduction (cowbird-only clutches), and (C) partial host egg reduction (mixed host and parasite clutches). The model follows an adult female and her offspring (dotted box) to the end of the breeding season; see Powell et al. (1999) for comparison to model without parasitism module. For simplicity, this figure summarizes the model structure in stages within the breeding season; however, daily demographic parameters were used in the model (Table 1).

American Redstarts from apparent annual survival estimates (Sherry and Holmes 1997). Changes in the time scales of survival rates necessitated adjustments of variance, so we used the delta method (Williams et al. 2002) to approximate the variance of these parameters.

We considered biological limitations on female renesting attempts to realistically model

the nesting strategy of both species during the breeding season. Wood Thrush females renest at every opportunity during the breeding season regardless of prior success (Roth et al. 1996, Powell et al. 1999). Most American Redstart females do not renest after a successful nest and will only attempt four nests during the breeding season (Sherry and Holmes 1997). We defined

TABLE 1. Parameter estimates \pm SE or SD used in estimation of annual productivity and annual population growth rates for Wood Thrushes ($n = 40$ nests) and American Redstarts ($n = 267$); if no reference is listed, estimate is either extrapolated from existing data or from field data from the Driftless Area in Wisconsin, Minnesota, and Iowa (1992–1998). AHY = after-hatch-year (adult); HY = hatch-year (juvenile); and S_A = adult annual survival.

Parameter	Wood Thrush		American Redstart	
	Estimate	Reference	Estimate	Reference
Daily survival, AHY	0.997 ± 0.006	Powell et al. (1999)	0.999 ± 0.001	$S_A^{(1/365)}$, Sherry and Holmes (1997), Petit (1999)
Daily survival, HY	0.997 ± 0.001		0.997 ± 0.001	$[0.5 \times S_A]^{(1/365)}$
Daily nest survival	0.966 ± 0.008	Powell et al. (1999)	0.945 ± 0.004	
Parasitism probability	0.525 ± 0.079		0.169 ± 0.023	
Abandonment ^a	0.00 (0 of 21)		0.067 (3 of 45)	
Raise cowbirds only ^a	0.00 (0 of 21)		0.311 (14 of 45)	
Raise mixed clutch ^{a,b}	1.00 (21 of 21)		0.622 (28 of 45)	
Breeding season (days) ^c	66	Roth et al. (1996)	53	Sherry and Holmes (1997)
Nest building interval (days) ^c	5	Powell et al. (1999)	5	Sherry and Holmes (1997)
Nesting period (days) ^{c,d}	24	Powell et al. (1999)	20	Sherry and Holmes (1997)
Fledgling care interval (days) ^c	18	Powell et al. (1999)	21	Sherry and Holmes (1997)
Clutch size	2.78 ± 1.31		2.89 ± 1.16	

^a If nest parasitized.

^b Nest contents not depleted by parasite; reduced by 0.90 nestlings per nest (Donovan et al. 1995).

^c Parameter not stochastic in the model.

^d American Redstart simulations allowed no more than one successful nest or four attempts (Sherry and Holmes 1997).

a successful nest as one that produced at least one fledgling, and p was defined as the number of simulated fledglings that survived until the end of the breeding season (Powell et al. 1999).

Following Powell et al. (1999), daily survival rates for females and juveniles, daily nest survival, and the number of fledglings per successful nest were chosen randomly from the appropriate distributions (see below), based on our field estimate of each demographic parameter and its variance (Table 1). We also employed this process to simulate parasitism of nests, using field data to provide the parameter's distribution.

During the breeding season, the model randomly selected a parasitism probability for each female (θ_i , % nests parasitized) from a beta distribution to ensure parameter values from 0.0 to 1.0; population-level parasitism probabilities and SD were obtained from field data (Knutson et al. 2004; Table 1). Each beta random variable was a function of two gamma-distributed random variables (SAS Institute 2000). Once selected, the model used the same parasitism probability (θ_i) for the entire breeding season, and each nest, i , was classified as parasitized or not (Fig. 1). We used SAS IML's random number generator to choose a uniformly distributed random number, x_i , where $x = 0-1$, for each simulated nest i , $i = 1, \dots, n$. If x_i was lower than the previously selected probability of parasitism (θ_i), nest i was classified as parasitized (e.g., $\theta_i = 0.45$; $x_1 = 0.353$, $x_2 = 0.888$; nest 1 was parasitized, but nest 2 was not). The model determined the fate of the simulated nest (parasitized or not) on the first day of incubation.

Once parasitized, a nest may have one of three outcomes: (1) the female may abandon the nest, (2) the host female's clutch may be completely lost, and only cowbird nestlings are raised, or (3) the host female's clutch may be partially reduced, resulting in a mixed nest of host and parasite nestlings. We incorporated the probability of each of these outcomes into our model by using relative proportions of the three conditions from our sample of nests. Similar to our approach for assigning parasitism status, we used SAS IML's random number generator to choose a uniformly distributed random number, x_i , where $0 \leq x \leq 1$, for each simulated nest i , $i = 1, \dots, n$. We created ranges between 0 and 1 from our field

estimates of the proportion of parasitized nests that were abandoned (A), cowbird-only clutches (C), or mixed clutches with reduced host clutch size (M). For example, if parasitism resulted in 20% of host females abandoning nests, 30% raising reduced, mixed clutches, and 50% raising cowbirds only, the three ranges would be: $0 \leq A \leq 0.2$, $0.2 < M \leq 0.5$; and $0.5 < C \leq 1.0$. We then compared the random number, x_i , with the three ranges, and applied a status to the nest based on the value of x_i (e.g., given the example ranges, if $x_1 = 0.183$, the nest would be abandoned; if $x_2 = 0.634$, all contents of the nest would be cowbird nestlings). The model determined the status of each simulated nest on the first day of incubation. If the nest was classified as abandoned, the female could potentially build another nest. In cases where the host young in the nest were partially or completely reduced, the simulated female continued to nest (Fig. 1). Cowbird-only nests produced no host young, even if successful, and we reduced the model-established clutch size of mixed clutches by 0.9 nestlings (Donovan et al. 1995).

Survival and nest success rates were chosen from beta distributions. We selected the number of fledglings per successful nest from a normal distribution, and the random variable was rounded to the nearest integer to allow the model to follow individual offspring during the postfledging period.

Stochastic demographic parameters, once selected, were held constant for one simulated "breeding season" of n days. Mortality of individuals and nests was simulated in the same manner in which we determined the parasitism status of each nest. Individual and nest mortality was simulated daily by choosing a uniformly distributed random number, x_i , where $0 \leq x \leq 1$, for each simulated day i , $i = 1, \dots, n$. If x_i was greater than the stochastic demographic parameter value, \hat{S} , the nest failed or the individual died on day i (e.g., $\hat{S} = 0.998$; $x_1 = 0.553$, $x_2 = 0.999$; individual survived on day 1 when $x_1 < \hat{S}$, but died on day 2 when $x_2 > \hat{S}$). A different x_i was chosen for adult survival, juvenile survival, and nest success.

The model outputs for breeding season annual productivity were: (1) the average number of nests initiated per female during a breeding season, (2) the average number of successful nests per female during a breeding

TABLE 2. Model-predicted parameter estimates \pm SD for Wood Thrush and American Redstart females, derived from nesting data collected in the Driftless Area in Wisconsin, Minnesota, and Iowa from 1992–1998, under three model structures: juvenile (HY) and adult (AHY) breeding season mortality incorporated, AHY breeding season mortality only (no HY mortality), and no breeding season mortality. Predictions are annual averages for 200 simulated females. Parameter estimates are given per female, per year. Annual productivity is measured as the total number of fledglings (male and female) produced per female that survived to the end of the breeding season. “No-mortality” model results are analogous to the annual production of Ricklefs and Bloom (1977) or the seasonal fecundity of Pease and Grzybowski (1995).

Parameter	Wood Thrush model			American Redstart model		
	HY and AHY mortality	AHY mortality only	No mortality	HY and AHY mortality	AHY mortality only	No mortality
Attempted nests	2.79 \pm 1.01	2.78 \pm 0.82	2.95 \pm 0.83	2.53 \pm 1.41	2.60 \pm 1.39	2.63 \pm 1.34
Parasitized nests	1.49 \pm 0.99	1.48 \pm 0.88	1.57 \pm 1.02	0.43 \pm 0.66	0.46 \pm 0.70	0.47 \pm 0.63
Successful nests	1.15 \pm 0.65	1.29 \pm 0.62	1.34 \pm 0.59	0.75 \pm 0.44	0.77 \pm 0.43	0.79 \pm 0.41
Annual productivity	2.03 \pm 1.60	3.04 \pm 1.98	3.29 \pm 1.86	1.56 \pm 1.31	2.21 \pm 1.59	2.21 \pm 1.51

season, (3) the average number of fledglings produced per female that survived to the end of a breeding season, and (4) the average number of parasitized nests per female during the breeding season. Because the model incorporated several stochastic components, we performed 200 simulations (following Powell et al. 1999) to obtain estimates of the mean and variance for the model outputs. Our model can also be used to predict “annual production” (Ricklefs and Bloom 1977) or “seasonal fecundity” (Pease and Grzybowski 1995) by setting female and juvenile survival to 1.00 (no mortality).

Powell et al. (1999) examined sensitivity of the annual productivity model to varying nest, adult, and juvenile survival rates. We performed a sensitivity analysis of the new parasitism module to determine the effect of varying levels of nest parasitism (% nests parasitized) on annual productivity and population growth rates. During the 200 simulations of these analyses, parasitism probabilities were held constant. Roth et al. (1996) suggested that low nest survival could mask the effects of parasitism; therefore, we used the model to predict annual productivity at four daily nest survival rates: 0.975, 0.951, 0.935, and the overall daily nest survival rate reported in our study for each species (Table 1). The model predicted p and a 95% confidence interval for p under each sensitivity test permutation of nest survival and parasitism probabilities. Model predictions are presented as mean \pm SD.

RESULTS

Our model predicted annual productivity of 2.03 ± 1.60 fledglings (male and female) per year for Wood Thrush females and 1.56 ± 1.31 for American Redstarts (Table 2). When juvenile and adult breeding season mortality were ignored, model predictions of annual productivity rose to 3.29 ± 1.86 for Wood Thrushes and 2.21 ± 1.51 for American Redstarts (Table 2).

Our annual productivity model predicted that Wood Thrushes attempted an average of 2.79 ± 1.01 nests, of which 1.15 ± 0.65 were successful, compared to 2.53 ± 1.41 and 0.75 ± 0.44 , respectively, for American Redstarts. On average, 1.49 ± 0.99 Wood Thrush nests were parasitized during the breeding season, compared with an average of 0.43 ± 0.66 redstart nests (Table 2). However, sensitivity analyses showed that at the higher nest success rates of 0.975 and 0.951, Wood Thrushes produced more fledglings than redstarts (Fig. 2).

Higher levels of nest parasitism resulted in trends of lower annual productivity for both species (Fig. 2). However, at the extremes (no parasitism and 100% parasitism), the 95% confidence intervals for American Redstart annual productivity overlapped for all four nest survival rates. As parasitism probabilities increased, Wood Thrushes showed a significant decline in annual productivity at the highest daily nest survival rates of 0.975, 0.966, and 0.951 (Fig. 2). For each 20% increase in the probability of parasitism at a daily nest survival rate of 0.975, our model predicted a drop in

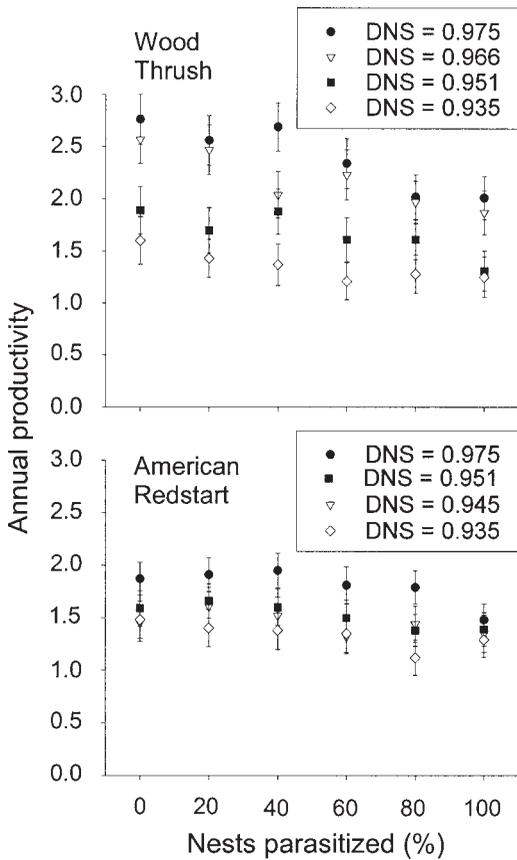


FIGURE 2. Sensitivity analysis of model predictions of annual productivity (p) under a range of parasitism probabilities (% nests parasitized) and daily nest survival (DNS) rates. Actual DNS rates from field data collected in the Driftless Area in Minnesota, Wisconsin, and Iowa (1992–1998) used in the productivity model are 0.966 for Wood Thrush and 0.945 for American Redstart. Error bars are 95% confidence intervals.

Wood Thrush annual productivity of approximately 0.15 fledglings (no parasitism: $p = 2.76$; 100% parasitism: $p = 2.01$; Fig. 2). At the same daily nest survival rate, redstart annual productivity dropped by approximately 0.08 fledglings for each 20% increase in parasitism probability (no parasitism: $p = 1.87$; 100% parasitism: $p = 1.48$).

DISCUSSION

Our modeling exercise emphasizes that daily nest survival alone should not be used to assess annual productivity for Wood Thrushes and American Redstarts in the Driftless Area. As

noted earlier, annual productivity is a complicated parameter for biologists to calculate. Wood Thrushes have higher nest survival (24-day survival: 44%) than redstarts (20-day survival: 32%), but redstarts have higher apparent annual adult survival rates (67%) than Wood Thrushes (58%). Wood Thrushes were parasitized more than redstarts (53% vs. 17%, respectively), but redstarts had higher rates of nest abandonment and parasite-only clutches. In sum, our model predicted that Wood Thrushes annually produce approximately 0.5 more fledglings than redstarts ($p = 2.03$ vs. $p = 1.56$, respectively) in the Driftless Area. We believe our individual-based simulation model is an effective method to synthesize life history parameters in an attempt to provide a rigorous prediction of annual productivity.

Our sensitivity analyses revealed that Wood Thrush annual productivity was more sensitive to changes in levels of parasitism than that of American Redstarts. Wood Thrush annual productivity dropped markedly with higher parasitism, especially at higher nest success rates, as predicted by Roth et al. (1996). However, our field data showed that if redstarts were parasitized, they suffered higher abandonment (7% vs. 0%) and more complete host clutch losses (31% vs. 0%) than Wood Thrushes. Although parasitism affected the outcome of individual redstart nests more severely, increased probabilities of parasitism resulted in sharper declines in annual productivity for Wood Thrushes as increased parasitism could affect more than one successful nest per year.

Calculations of productivity from previous studies are more prevalent for Wood Thrushes than for American Redstarts. Roth et al. (1996), Trine (1998), Weinberg and Roth (1998), Fauth (2001), and Phillips et al. (2005) estimated seasonal fecundity of Wood Thrushes in Delaware, southern Illinois, Delaware, Indiana, and southern Ontario, as 2.6, 0.5–1.5, 3.6, 2.6–4.0, and 2.4 fledglings per female, respectively. Roth et al. (1996), Trine (1998), and Weinberg and Roth (1998) estimated productivity by following females through the breeding season, and their estimates are conservative as some fledglings may have escaped detection. Phillips et al. (2005) placed limits on the number of annual nest attempts by a female, following methods similar to Donovan et al.

(1995). However, Powell et al. (1999) and Fauth (2001) reported a mean of 3.1 nests per female from radio-marked and color-banded females, with some females nesting as many as five times per season (Powell et al. 1999).

Individual-based simulation models of productivity can limit the number of nest attempts, as we did for American Redstarts. Alternatively, for species such as Wood Thrushes that have less predictable patterns of nesting (Powell et al. 1999), simulation models may use breeding season length to realistically limit the number of nest attempts and to incorporate natural variability exhibited by radio-marked females. For example, Dececco et al. (2000) relied on empirical data from Wood Thrushes in Virginia and West Virginia to define the renesting periods used in simulations; they used Pease and Grzybowski's (1995) model to predict seasonal fecundity of 3.5 fledglings per female. Simons et al. (2000), in a modification of Pease and Grzybowski's (1995) model, allowed Wood Thrushes to renest until the end of the breeding season and predicted annual productivity of 2.7 fledglings per female. Powell et al. (1999) also allowed renesting to the end of the breeding season and estimated annual productivity of 3.0 fledglings per female. We suspect that calculations of annual productivity may be negatively biased when limits are placed on Wood Thrush nesting attempts. Our modeling exercise reveals the need for more data from radio-marked females, as these calculations are critical for assessments of habitat quality; many authors use fecundity calculations similar to Donovan et al. (1995) to determine possible source or sink status of populations. Because productivity is a complex function of many factors, biologists should consider using simulation models to predict annual productivity (Anders and Marshall 2005), and individual-based productivity models should tally the number of nesting attempts during the breeding season as a comparative statistic.

The structure of our enhanced annual productivity model is flexible to allow incorporation of life history traits for any avian species. Knutson et al. (2006) created multiple, species-specific versions of our model to predict annual productivity for 27 species of forest songbirds. Our model may be used by managers to determine potential benefits of management strategies designed to reduce parasitism. The

model may also be used by evolutionary biologists as they examine life history trade-offs and decision-making by birds in response to parasitism. Regardless of its application, our model's usefulness is constrained by the availability of site- and species-specific data. For example, we were unable to use local survival data for adults and juveniles in our modeling exercise. Thus, we support the recommendation of Anders and Marshall (2005), and call for further studies that estimate breeding season survival.

ACKNOWLEDGMENTS

J. Lang, M. Conroy, and D. Kremetz contributed to the development of the earlier version of this model. G. Niemi and M. Friberg supplied a portion of the nesting data used in our modeling exercise. We thank S. Bourassa, L. Pfannmuller, R. Hines, C. Sveum, C. Korschgen, and over 25 field staff and volunteers for their assistance. Project support was provided by the U.S. Geological Survey Upper Midwest Environmental Sciences Center and the BBIRD program, the U.S. Fish and Wildlife Service Region 3 Nongame Bird Program, the University of Minnesota Natural Resources Research Institute, Minnesota Environment and Natural Resources Trust Fund, the Minnesota Department of Natural Resources, Wisconsin Department of Natural Resources, the Iowa Department of Natural Resources, the University of Dubuque, and the University of Nebraska-Lincoln. R. Johnson, J. McCarty, E. Kirsch, and B. Gray made helpful comments on an earlier version of this manuscript. This is Journal Series No. 14434 from the University of Nebraska Agricultural Research Division. The SAS IML code for the Wood Thrush and American Redstart annual productivity models is available on request from LAP.

LITERATURE CITED

- ANDERS, A. D., AND M. R. MARSHALL. 2005. Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conservation Biology* 19:66–74.
- CONROY, M. J., Y. COHEN, F. C. JAMES, Y. G. MATSINOS, AND B. A. MAURER. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* 5:17–19.
- DECECCO, J. A., M. R. MARSHALL, A. B. WILLIAMS, G. A. GALE, AND R. J. COOPER. 2000. Comparative seasonal fecundity of four Neotropical migrants in middle Appalachia. *Condor* 102: 653–663.
- DONOVAN, T. M., F. R. THOMPSON III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- FAUTH, P. T. 2001. Wood Thrush populations are not all sinks in the agricultural Midwestern United States. *Conservation Biology* 15:523–527.

- KNUTSON, M. G., G. J. NIEMI, W. E. NEWTON, AND M. A. FRIBERG. 2004. Avian nest success in Midwestern forests fragmented by agriculture. *Condor* 106:117–131.
- KNUTSON, M. G., L. A. POWELL, R. K. HINES, M. A. FRIBERG, AND G. J. NIEMI. 2006. An assessment of bird habitat quality using population growth rates. *Condor* 108:301–314.
- LANG, J. D., L. A. POWELL, D. G. KREMENTZ, AND M. J. CONROY. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *Auk* 119:109–124.
- PEASE, C. M., AND J. A. GRZYBOWSKI. 1995. Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. *Auk* 112:343–363.
- PETIT, L. J. 1999. Prothonotary Warbler (*Protonotaria citrea*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 408. The Birds of North American, Inc., Philadelphia, PA.
- PHILLIPS, J., E. NOL, D. BURKE, AND W. DUNFORD. 2005. Impacts of housing developments on Wood Thrush nesting success in hardwood forest fragments. *Condor* 107:97–106.
- POWELL, L. A., M. J. CONROY, D. G. KREMENTZ, AND J. D. LANG. 1999. A model to predict breeding-season productivity for multibrooded songbirds. *Auk* 116:1001–1008.
- RICKLEFS, R., AND G. BLOOM. 1977. Components of avian breeding productivity. *Auk* 94:86–96.
- ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- ROTH, R. R., M. S. JOHNSON, AND T. J. UNDERWOOD. 1996. Wood Thrush (*Hylocichla mustelina*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 246. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- SAS INSTITUTE [ONLINE]. 2000. SAS OnlineDoc, version 8. SAS Institute, Inc., Cary, NC. <<http://v8doc.sas.com/sashtml/>> (5 February 2006).
- SHERRY, T. W., AND R. T. HOLMES. 1997. American Redstart (*Setophaga ruticilla*). In A. Poole and F. Gill [EDS.], *The birds of North America*, No. 277. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- SIMONS, T. R., G. L. FARNSWORTH, AND S. A. SHRINER. 2000. Evaluating Great Smoky Mountains National Park as a population source for the Wood Thrush. *Conservation Biology* 14:1133–1144.
- THOMPSON, B. C., G. E. KNADLE, D. L. BRUBAKER, AND K. S. BRUBAKER. 2001. Nest success is not an adequate comparative estimate of avian reproduction. *Journal of Field Ornithology* 72:527–536.
- TRINE, C. L. 1998. Wood Thrush population sinks and implications for the scale of regional conservation strategies. *Conservation Biology* 12:576–585.
- UNDERWOOD, T. J., AND R. R. ROTH. 2002. Demographic variables are poor indicators of Wood Thrush productivity. *Condor* 104:92–102.
- WEINBERG, H. J., AND R. R. ROTH. 1998. Forest area and habitat quality for nesting Wood Thrushes. *Auk* 115:879–889.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, CA.