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# Juvenile Survival in a Population of Neotropical Migrant Birds

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**Abstract:** *Determination of population productivity of Neotropical migrant birds and assessment of breeding habitat quality have been based on population densities and nesting success. Data on juvenile survival improve our estimates of population productivity, provide information on factors during the post-fledging period that affect this productivity and, with comparative data, enable us to better assess breeding habitat quality. We present the first estimate of post-fledging juvenile survival in a population of Neotropical migrant birds. We studied post-fledging survival in a population of Wood Thrush (*Hylocichla mustelina*) in southern Missouri, (U.S.) an area hypothesized to contain source populations. Nesting success during our study period was 0.266, and individual survival within the nest was 0.245. Post-fledging survival during the first 8 weeks after fledging was 0.423. Survival varied significantly between post-fledging weekly age classes, with survival of weeks 1, 2, 3, and 4 through 8 being 0.716, 0.930, 0.637, and 1.00, respectively. Probability of predation after fledging was 0.506. Probability of mortality by other causes was 0.071. Probability of predation varied by weekly age class and may have been related to behaviors occurring at different developmental stages. Post-fledging survival was not correlated with nestling mass and did not change throughout the course of the breeding season. Analysis of the source/sink status of the population based on our estimates of nesting success and post-fledging survival indicates that young were being produced below replacement levels during our study period. Large-scale management decisions should take into account potential fluctuations in the productivity of Neotropical migrant populations over time. Data on post-fledging juvenile survival are needed from other populations of Neotropical migrant birds to more accurately assess differential productivity between populations and better assess breeding habitat quality.*

Supervivencia de Juveniles en una Población de Aves Migratorias Neotropicales

**Resumen:** *La determinación de la productividad poblacional de aves migratorias Neotropicales y la evaluación de la calidad del hábitat para reproducción se han basado en densidades poblacionales y éxito de nidificación. Datos de supervivencia de juveniles mejoran las estimaciones de productividad poblacional, proporcionan información sobre los factores que afectan la productividad durante el período posterior al emplumamiento y mediante datos comparativos permiten una mejor evaluación de la calidad del hábitat de reproducción. Presentamos la primera estimación de supervivencia juvenil posterior al emplumamiento en una población de aves migratorias Neotropicales. Estudiamos la supervivencia después del emplumamiento del zorzal (*Hylocichla mustelina*) en el sur de Missouri (E.U.A.), una zona que hipotéticamente contiene poblaciones "fuente". El éxito de nidificación fue 0.266 durante el período de estudio, la supervivencia individual dentro del nido fue 0.245. La supervivencia después del emplumamiento en las ocho primeras semanas después de emplumar fue 0.423. La supervivencia varió significativamente entre las clases de edad semanal*

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posteriores al emplumamiento, con supervivencia en las semanas 1, 2, 3, y 4-8 de 0.716, 0.930, 0.637 y 1.00 respectivamente. La probabilidad de depredación después de emplumar fue de 0.506. La probabilidad de morir por otras causas fue de 0.071. La probabilidad de depredación varió por clase de edad semanal, quizá en relación con conductas que ocurren en las diferentes etapas del desarrollo. La supervivencia posterior al emplumamiento no se correlacionó con la masa de los pollos y no varió a lo largo de la época de reproducción. El análisis del estatus fuente/receptor de la población con base en nuestras estimaciones del éxito de nidificación y en la supervivencia posterior al emplumamiento indica la producción de jóvenes por debajo de niveles de reemplazo durante el período de estudio. La toma de decisiones de manejo a gran escala debería considerar potenciales fluctuaciones en la productividad de población migratorias Neotropicales. Se requieren datos de supervivencia de juveniles posterior al emplumamiento de otras poblaciones de aves migratorias Neotropicales a fin de poder evaluar con precisión las diferencias en la productividad entre poblaciones, así como mejorar la evaluación de la calidad del hábitat.

## Introduction

Breeding populations of many species of Neotropical migrant birds vary in productivity such that source/sink interactions between populations occur (Donovan et al. 1995; Robinson et al. 1995). Conservation of these species is dependent upon our identification and protection of habitats that support source populations. Thus, accurate assessment of the source or sink status of populations and the factors contributing to their status is critical (Pulliam & Danielson 1991; Donovan et al. 1995; Freemark et al. 1995; Brawn & Robinson 1996). To date, determination of source/sink status and the factors affecting this status and subsequent assessment of breeding habitat quality have been based on population densities and rates of nesting success (Hagan & Johnston 1992; Finch & Stangel 1993). Juvenile survival, a potentially key factor in the differential productivity between populations, has been treated as a constant because of a lack of empirical data.

The current method used to estimate juvenile survival in Neotropical migrant populations is to divide adult mortality by the average number of offspring fledged (Ricklefs 1973). An implicit assumption of this method is that productivity equals adult mortality; in other words, the population is assumed to be producing young at replacement levels. Such an assumption contradicts the use of these estimates in source/sink models. Nevertheless, researchers continue to use a value obtained by this method (0.310; Greenberg 1980) in modeling source/sink dynamics (Temple & Cary 1988; Howe et al. 1991; Donovan et al. 1995). Empirical data on juvenile survival improve our estimates of population productivity, and they provide information on factors beyond nesting success that affect this productivity. With comparative data from other populations, information on juvenile survival will enable us to more accurately assess breeding habitat quality.

The only data on juvenile survival in avian populations consist of information on nonmigratory species or short-

distance migrants (Woolfenden 1978; Dhondt 1979; Perrins 1980; Wolf et al. 1988; Krementz et al. 1989; Sullivan 1989; Zann & Runciman 1994). These data have been obtained by mark/recapture or resighting techniques, methods that work poorly for Neotropical migrants because of their extensive post-fledging movements and lack of natal site fidelity. Radio telemetry is a useful tool in gaining information on juvenile survival in these species because it enables us to locate individuals daily, even after dispersal from the natal territories has occurred. Telemetry allows us to confirm the survival or mortality of study individuals daily, estimate survival based on observed mortality events, make behavioral observations relating to survival probability, and identify specific causes of mortality.

We obtained estimates of post-fledging juvenile survival in a population of Wood Thrush (*Hylocichla ustulata*) in the Ozark Mountains of southern Missouri. This area has been hypothesized to be a source for sink populations of Wood Thrush based on rates of nesting success (Donovan et al. 1995; Robinson et al. 1995). We obtained estimates of nesting success and survival of individuals within the nest, and we estimated post-fledging survival by radio-tracking individuals from the time of fledging. We estimated rates of cause-specific post-fledging mortality and identified specific predators when possible. We tested for a correlation between nestling condition and length of post-fledging survival and tested for seasonal changes in post-fledging survival. Using our estimates of nesting success and post-fledging survival, we determined the source/sink status of the southern Missouri Wood Thrush population during our study period.

## Methods, Study Species, and Area

Wood Thrush breed in mid- to late-successional deciduous forest. Forest-dwelling migratory songbirds have become of particular concern lately as forests are increas-

ingly fragmented and sink populations are identified (Askins et al. 1990; Robinson 1992; Donovan et al. 1995; Faaborg et al. 1995; Robinson et al. 1995). Wood Thrush are large enough to carry radio transmitters with a battery life of several months (average adult body mass is 47.4 g; Dunning 1993), and they nest low enough in many parts of their range that transmitters can be placed on individuals prior to fledging. Life history characteristics of Wood Thrush are similar to those of many forest-interior migrants: clutch size averages three to four, incubation and nestling periods are 13 and 12 days, respectively; and adults attempt two to three broods per season (Ehrlich et al. 1988). Wood Thrush are typical of many species of Neotropical migrants in that they appear to be increasing or remaining stable in some parts of their range but severely declining in others (Peterjohn et al. 1995). Accurate productivity estimates are critical in determining the source/sink status of populations of these species and in assessing breeding habitat quality (Brawn & Robinson 1996).

Our study sites were located in Carter, Reynolds, and Shannon counties in the Ozark Mountains of southern Missouri. This area is typified by contiguous mature and managed forest habitats, with over 80% forest cover in a 2 million ha area (Geissman et al. 1986). Initial study areas were located on nine, 400-ha sites that had been mapped and gridded for the Missouri Ozark Forest Ecosystem Project (Kurzejeski et al. 1993). These sites consisted of state-owned mature oak-hickory forest, and existed within a mosaic of managed forest habitats. Study areas were expanded to include managed forest habitats on federal and private land as study individuals moved prior to migration.

### Nesting Success

During the summers of 1994 and 1995, we located Wood Thrush nests in conjunction with the Missouri Ozark Forest Ecosystem Project. Nests were monitored every 3 to 4 days, until fledging or total nest failure occurred. We calculated nesting success for the population using the Mayfield method (Mayfield 1961, 1975). We divided the nesting period into four intervals: laying, incubation, nestling days 1–6, and nestling days 7–12. The average clutch size in our study was 3.4 eggs, such that the average egg laying period was 3 days. Wood Thrush initiate incubation when the penultimate egg is laid. To avoid overlap of the laying and incubation intervals, we used a laying interval of 1 day and an incubation interval of 13 days in the Mayfield analysis. The nestling period was divided into two intervals based on the a priori hypothesis that increased nestling noise during the second half of the nestling period may increase predation risk. We assumed risk of nest loss to be constant within each interval, where nest loss was defined as death of the entire brood.

We calculated a daily survival rate (DSR) for each interval based on number of nest failures versus number of nest exposure days within the interval. We calculated interval survival rates by raising the daily survival rate for each interval to the power of the number of days within the interval. Nesting success for the population was calculated by multiplying the four interval survival rates (Mayfield 1961). We computed standard error (SE) for each daily survival rate and calculated 95% confidence intervals (CI) as  $DSR \pm 1.96 SE$ . Ninety five percent confidence intervals for each interval survival rate were then calculated by raising the 95% CI of each daily survival rate to the power of the number of days within the interval (Johnson 1979). We tested for pairwise differences in interval survival rates using CONTRAST, a program that utilizes a chi-square statistic to test for homogeneity of survival estimates by creating a linear contrast of the rate estimates (Sauer & Williams 1989). Alpha values were not Bonferroni-adjusted because interval comparisons were based on a priori hypotheses.

### Individual Survival within the Nest

Nesting success is based on the survival of entire broods rather than individuals. To obtain statistically comparable pre- and post-fledging survival rates based on the survival of individuals, we analyzed the survival of individuals within the nest. This analysis consisted of using a modified Mayfield technique that incorporates information on partial brood loss (Flint et al. 1995). This method was developed to estimate survival of precocial young, but it is useful in estimating survival of altricial birds when the fate of individuals is of interest. For this analysis we divided the nesting period into the same four intervals, and risk of mortality was again assumed to be constant within each interval. We calculated daily survival rates of individual eggs and nestlings by dividing number of individual deaths by number of exposure days of individuals within each interval. We then calculated interval survival rates by raising the daily survival rate for each interval to the power of the number of days within the interval. Individual survival during the nesting period, from laying to fledging, was calculated by multiplying the four interval survival rates. Nonindependence of survival of eggs and nestlings within a nest was accounted for in this analysis in the calculation of standard errors of the daily survival rates (Flint et al. 1995). Ninety-five percent confidence intervals for the daily and interval survival rates were calculated using the same methods employed in the unmodified Mayfield analysis.

### Post-Fledging Survival

To assess post-fledging survival, we placed radio transmitters on 26- to 37-g nestlings on day 9, 10, or 11 of the 12-day nestling period. Transmitters weighing 1.3 g with

a battery life of 35 days were used in 1994, and 1.6-g transmitters with a battery life of 60 days were used in 1995 (Advanced Telemetry Systems, Bethel, Minnesota). A transmitter was placed on a bird's back with the antenna pointing toward the tail. A harness of nylon elastic string was then tied under each wing leaving room for growth of the bird's wings and pectoral muscles. We radio-tagged one to three nestlings in each nest in 1994 and all nestlings within each nest in 1995. We banded all nestlings with U.S. Fish and Wildlife Service numbered leg bands and two color bands and took measurements of mass.

We located individuals using programmable receivers and three-element hand-held Yagi antennas (Advanced Telemetry Systems, Bethel, MN). We sighted each individual daily until radio failure, death, or migration from the study area occurred. We defined radio failure as the inability to locate the transmitter signal at a time when age of the individual indicated that movement out of the study area was not possible. Migration from the study area was assumed when the transmitter signal could not be located and age of the bird indicated that movement out of the study area was probable.

For all statistical analyses of post-fledging data, we assumed that survival times of individuals were independent. Were post-fledging survival within a brood not actually independent, our survival estimates would remain the same, but the variation around those estimates would decrease (Flint et al. 1995). Handling and radio-tagging birds may have affected their probability of survival (White & Garrott 1990), but it was not possible for us to quantify this effect. We calculated post-fledging survival using MICROMORT, a program that utilizes a modified Mayfield technique to obtain survival rates of individuals (Heisey & Fuller 1985). Daily survival rates were calculated for intervals within which risk of mortality was assumed to be constant. To define these intervals we treated all individuals as a single cohort and calculated a survivorship function using the life table procedure in SPSS (Norusis/SPSS, Inc. 1992). Intervals of constant slope on this survivorship function indicate the intervals in which risk of mortality is constant (White & Garrott 1990). We used MICROMORT to calculate a daily survival rate for each interval based on number of deaths versus number of exposure days of individuals within each interval. Interval survival rates and 95% confidence intervals were then calculated using the same methods employed for estimates of Mayfield nesting success. We tested for pairwise differences in post-fledging interval survival rates using the chi-square statistic in CONTRAST.

#### CAUSE-SPECIFIC MORTALITY

We calculated rates of cause-specific mortality of post-fledging juveniles using the program MICROMORT (Heisey & Fuller 1985). We identified two agents of mortality: predation and death by other means. We assumed

predation to have occurred if (1) a bird was found dead and was not intact, (2) a transmitter was located amidst juvenile Wood Thrush feathers, (3) a transmitter alone was found and exhibited signs of having been chewed by a predator, or (4) a transmitter was located inside the body or nest of a predator. In this analysis daily probability of mortality by each agent was calculated for each interval. These probabilities are based on number of deaths due to each mortality agent versus number of exposure days of individuals in each interval. Cause-specific interval mortality rates were calculated from daily rates as the product of the relative risk of mortality by a given agent and the overall probability of death within each interval. The overall, or span rates of mortality due to each agent, were calculated from interval rates in this same manner (Heisey & Fuller 1985). We tested for pairwise differences in interval cause-specific mortality rates using the chi-square statistic in CONTRAST.

To determine whether changes in cause-specific mortality were associated with juvenile behaviors occurring at different developmental stages, we made daily behavioral observations. We carried out observations for as long as possible without disturbing the individual, usually from 2-5 minutes per day. Observations included noting the occurrence of parental feeding, foraging by the juvenile, parental response to our presence near the juvenile, and dispersal of the juvenile from the parental territory. We calculated the median and mean number of days after fledging at which juveniles were last seen fed, first seen foraging, last seen in the presence of a parent, and first located consistently outside of the parental territory.

#### NESTLING CONDITION AND SURVIVAL

We tested for a relationship between nestling condition and length of post-fledging survival using a Cox regression model (Cox & Oakes 1984). Because primary feathers were still emerging from their tracts and tarsi were still developing at the time that we obtained morphometric data, we used mass as the indicator of nestling condition. Mass was measured on day 9, 10, or 11 of the 12-day nestling period. Because all broods were not measured at the same time during development, we ranked mass within each nest and then converted the ranks to standardized ranks (standardized rank = rank-1/brood size-1) to correct for unequal brood sizes. Measurement of length of post-fledging survival was necessarily truncated for individuals who survived to migrate from the study area. We analyzed length of post-fledging survival versus standardized mass rank using the Cox model procedure in SPSS (Emrich et al. 1981).

#### SEASONAL CHANGES IN SURVIVAL

To test for age-independent changes in post-fledging survival through the 1995 breeding season, we used the

Kaplan-Meier technique (Kaplan & Meier 1958) generalized to the staggered entry case (Pollock et al. 1989). We assumed that censoring mechanisms (transmitter failure or departure from the study area) were independent of animal fate. We calculated cumulative survival of the population over time, where survival at time 1 was  $s(t_1) = 1 - (\text{no. dead/no. at risk})$ . Survival at time 2 was  $s(t_2) = 1 - [s(t_1) (\text{no. dead since } t_1/\text{no. at risk})]$ , and so on (Kaplan & Meier 1958). The staggered entry technique was utilized in order to enter individuals into analysis on the date that they fledged and censor individuals on the date at which radio failure or migration from the study area occurred.

To remove effects of age on survival from this analysis, we analyzed survival throughout the season separately for each age class. Results of the modified Mayfield analysis of post-fledging survival indicate that post-fledging survival varied by weekly age class, so we calculated a separate Kaplan-Meier staggered entry function for each 1-week age class. To determine whether there were differences in survival through the breeding season for each age class, we converted the Kaplan-Meier staggered entry survival function for each age class to a hazard function, which displays relative risk of mortality versus time (White & Garrott 1990) and tested the null hypothesis of a zero slope for each hazard function using the PROC REG procedure in SAS (SAS Institute Inc. 1989). In addition, to determine whether risk of mortality peaked at particular times during the breeding season, we checked for synchronous increases in the hazard functions across age classes.

#### SOURCE/SINK STATUS

We used our estimates of nesting success and post-fledging survival to determine the source/sink status of our

study population. We used the model employed by Pulliam (1988), in which the population is determined to be producing individuals at replacement levels if recruitment (which is mean number of female offspring per female per year  $\times$  juvenile survival) equals adult mortality. We calculated mean number of female offspring per female per year based on the number of female offspring per successful nest (assuming a 1:1 sex ratio), our estimate of nesting success, and the assumption that all pairs would attempt to raise two broods per season and would re-nest if their first or second brood was depredated (Donovan et al. 1995).

To estimate juvenile survival we multiplied our estimate of post-fledging survival by a winter survival estimate for juveniles of two warbler species of 0.680 (Holmes et al. 1989). Rappole et al. (1989) calculated a wintering daily survival rate of 0.974 for a group of non-sedentary Wood Thrush in Mexico, which they hypothesized to be juvenile birds. If we raise this rate to a period of 120 days, however, we obtain an overwinter survival rate of 0.042 for juvenile birds. This estimate seems too low to be plausible. The estimate found by Holmes et al. (1989) is similar to that found by Conway et al. (1995) for wintering Wood Thrush of unknown age in Belize. We used the mean of published estimates, 0.380, for adult mortality (reviewed in Donovan et al. 1995).

## Results

### Nesting Success and Individual Survival within the Nest

We monitored 35 Wood Thrush nests in 1994 and 51 in 1995. Nesting success did not vary significantly between years ( $\chi^2 < 1.09, p > 0.29$  for all interval pairwise compar-

**Table 1.** Nesting success, individual survival within the nest, and post-fledging survival rates of juvenile Wood Thrush in southern Missouri, 1994-1995.

	Interval	Length (days)	Daily survival rate	95% CI	Interval survival rate*	95% CI
Nesting success ( $n = 86$ nests)	laying	1	0.950	0.854-1.00	0.950 <sup>a</sup>	0.854-1.00
	incubation	13	0.964	0.945-0.982	0.617 <sup>b</sup>	0.482-0.786
	nestling days 1-6	6	0.918	0.883-0.954	0.600 <sup>b</sup>	0.475-0.752
	nestling days 7-12	6	0.954	0.927-0.982	0.755 <sup>b</sup>	0.633-0.897
					overall rate = 0.266	0.180-0.393
Individual survival within the nest ( $n = 262$ individuals from 78 nests)	laying	1	0.936	0.869-1.00	0.936	0.869-1.00
	incubation	13	0.962	0.945-0.980	0.608	0.479-0.769
	nestling days 1-6	6	0.903	0.864-0.942	0.541	0.416-0.699
	nestling days 7-12	6	0.963	0.935-0.991	0.796	0.668-0.947
					overall rate = 0.245	
Post-fledging survival ( $n = 49$ individuals)	week 1	7	0.953	0.928-0.979	0.716 <sup>a</sup>	0.591-0.863
	week 2	7	0.990	0.975-1.00	0.930 <sup>b</sup>	0.840-1.00
	week 3	7	0.938	0.898-0.977	0.637 <sup>a</sup>	0.471-0.850
	weeks 4-8	35	1.00	1.00-1.00	1.00 <sup>b</sup>	1.00-1.00
					overall rate = 0.423	0.294-.610

\*Interval survival rates indicated by different letters (a and b) are significantly different (all  $\chi^2 > 5.51, p < 0.019$  for nesting success intervals; all  $\chi^2 > 6.48, p < 0.011$  for post-fledging survival intervals).

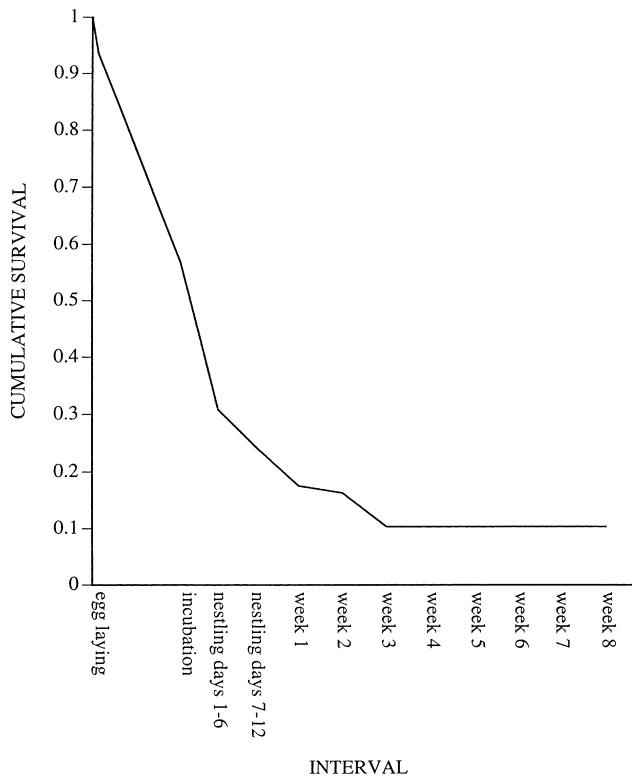


Figure 1. Cumulative probability of Wood Thrush survival from egg stage to initiation of fall migration. Weeks 1 through 8 refer to intervals of the post-fledging period.

isons), nor did individual survival within the nest ( $\chi^2 < 3.00$ ,  $p > 0.08$  for all interval pairwise comparisons), so we pooled data from both years. Nest survival during the laying, incubation, and first and second halves of the nestling periods was 0.950, 0.617, 0.600, and 0.755, respectively. Overall nesting success for the population was 0.266 (Table 1). In the analysis of individual survival within the nest, in which partial brood loss was taken into

account, survival during these same intervals was 0.936, 0.608, 0.541, and 0.796. Probability of survival from laying to fledging was 0.245 (Table 1). Partial brood loss was attributable in four nests to failure of eggs to hatch, in three nests to removal of eggs by Brown-headed Cowbirds (*Molothrus ater*), and in three nests to depredation of chicks.

POST-FLEDGING SURVIVAL

We placed radio transmitters on 7 individuals from 4 nests in 1994 and 42 individuals from 13 nests in 1995. Over the entire study period four transmitters failed within 1 week after the individuals fledged from the nest. In these cases the individuals were censored from the survival analysis at the age at which the transmitters failed.

Results of the post-fledging survivorship function generated with SPSS indicate that daily survival of juvenile Wood Thrush was constant within each week after fledging, so we calculated Mayfield interval survival rates that correspond to weekly post-fledging survival. Survival varied significantly between weeks, or weekly age classes, with survival of weeks 1, 2, 3, and 4-8 being 0.716, 0.930, 0.637, and 1.00 respectively (Table 1). Probability of survival from fledging to initiation of migration was 0.423. Combining the estimates of pre- and post-fledging survival rates calculated by modified Mayfield techniques, we obtained an overall survival rate of 0.104 for individual Wood Thrush from laying to 8 weeks post-fledging (Fig. 1).

Our analysis of cause-specific mortality indicates that overall probability of post-fledging predation was 0.506. Probability of predation during post-fledging weeks 1, 2, 3, and 4-8 was 0.213, 0.070, 0.364, and 0, respectively (Table 2).

Twenty juvenile Wood Thrush were depredated. We were able to identify four species of predators. In one case we tracked a transmitter to a Cooper's Hawk (*Accipiter cooperii*) nest approximately 2.5 km from the home

Table 2. Cause-specific post-fledging mortality rates of juvenile Wood Thrush in southern Missouri, 1994-1995.

Cause of mortality	Post-fledging interval	Daily mortality rate	95% CI	Interval mortality rate*	95% CI
Predation	week 1	0.035	0.013-0.058	0.213 <sup>a</sup>	0.090-0.337
	week 2	0.010	0.00-0.025	0.070 <sup>b</sup>	0.00-0.164
	week 3	0.063	0.023-0.102	0.364 <sup>a</sup>	0.176-0.551
	weeks 4-8	0.00	0.00-0.00	0.00 <sup>b</sup>	0.00-0.00
				overall rate = 0.506	0.349-0.662
Other	week 1	0.012	0.00-0.025	0.071 <sup>a</sup>	0.00-0.149
	week 2	0.00	0.00-0.00	0.00 <sup>b</sup>	0.00-0.00
	week 3	0.00	0.00-0.00	0.00 <sup>b</sup>	0.00-0.00
	weeks 4-8	0.00	0.00-0.00	0.00 <sup>b</sup>	0.00-0.00
				overall rate = 0.071	0.00-0.149

\*Interval mortality rates indicated by different letters (a and b) are significantly different (all  $\chi^2 > 3.27$ ,  $p < 0.071$  for interval rates of predation;  $\chi^2 = 3.23$ ,  $p = 0.0721$  for interval rates of mortality by other causes).

range of the depredated Wood Thrush. The juvenile had been out of its nest for 15 days at the time of predation. We found a transmitter from a juvenile of a different brood below this same nest 5 days later. The hawk nest was approximately 2.9 km from the home range of this depredated individual, and this bird had been out of the nest for 7 days at the time of predation. In another case we tracked a transmitter to a timber rattlesnake (*Crotalus horridus*) that had swallowed the transmitter along with the juvenile bird. The predated individual in this case had been out of the nest for 17 days. In a third case we found a secondary feather from a Broad-winged Hawk (*Buteo platypterus*) approximately 1 m from several feathers and the removed transmitter of a depredated Wood Thrush. This juvenile bird had been out of the nest for 16 days at the time of predation. Finally, we observed a predation attempt by an eastern chipmunk (*Tamias striatus*) on a radiomarked juvenile that had been out of the nest for 1 day. This predation attempt failed because of intervention by the Wood Thrush parents.

Overall probability of mortality by causes other than predation was 0.071 (Table 2). All mortalities that were not due to predation occurred during the first week after fledging. Three such mortalities were identified. In one case a radio-marked nestling appeared to have been abandoned in the nest after its two radio-marked siblings had fledged. Two other individuals were found dead on the ground with no obvious signs of predation. One of the juveniles had been out of the nest for 2 days, and the other had been out of the nest for 5 days.

There was one case in which the mortality of a study individual appeared to be caused by the presence of the transmitter harness. On day 20 after fledging the individual was discovered caught on a branch by the harness string and was freed from the branch. The next day the individual was found dead below this same branch. In the modified Mayfield analyses of post-fledging survival and cause-specific mortality, we included the survival days but not the death of this individual. In the Kaplan-Meier analysis of changes in survival throughout the season, the individual was censored at the age of 21 days.

Behavioral observations indicate that juveniles were last fed by their parents an average of 13.3 days after fledging. Juveniles were first observed foraging for themselves an average of 15.3 days after fledging. Parents were last seen in the presence of their offspring an average of 15.5 days after fledging. Juveniles were last located on the parental territory an average of 22.3 days after fledging (Table 3).

Nestling mass, measured on day 9, 10, or 11 of the 12-day nestling period, ranged from 26.1 g to 36.8 g ( $\bar{x} = 31.5$  g). Observed length of post-fledging survival ranged from 1 day to 59 days, although this measurement was truncated for 17 individuals due to migration from the study area. Analysis of the relationship between length of post-fledging survival and standardized mass rank indicates that

**Table 3.** Timing of developmental behaviors of juvenile Wood Thrush.

	Last seen fed	First seen foraging	Last seen with parent	Dispersed
Median*	13.0	15.5	15.0	22.0
Mean*	13.3	15.3	15.5	22.3
SD	3.66	3.29	2.97	1.99
<i>n</i>	13	18	22	15

\*Number of days since fledging.

there was no correlation between these two variables ( $\chi^2 = 0.218$ ;  $df = 1$ ;  $p = 0.6404$ ).

In our analysis of seasonal changes in post-fledging survival, slopes of the hazard functions generated from the Kaplan-Meier staggered entry survival functions were not significantly different from zero (all  $p > 0.14$ ). In addition, there were no instances of synchronous peaks in hazard functions between age classes. These results indicate that probability of post-fledging survival did not change throughout the course of the breeding season.

#### SOURCE/SINK STATUS

For our model of the source/sink status of our study population, we calculated the mean number of female offspring per successful nest as 1.57. With a nesting success rate of 0.266, each adult female produced an average of 1.21 female offspring per season. Multiplying our post-fledging survival estimate of 0.423 by a winter survival estimate of 0.680, we obtained an overall juvenile survival rate of 0.290. Multiplying this rate by 1.21 female offspring per female, we obtained an annual recruitment estimate of 0.350. This estimate does not include juvenile mortalities that occurred during migration. If we compare this recruitment estimate to the average of published estimates of adult mortality, 0.380, the Wood Thrush population in southern Missouri was not producing enough juveniles to compensate for adult mortality during our study period.

#### Discussion

Results of our analysis of post-fledging survival indicate that the productivity of the southern Missouri Wood Thrush population was notably affected by mortalities that occurred during the post-fledging period. No other estimates of post-fledging survival of Neotropical migrants exist for comparison with our results. Our estimate of 0.423, however, is higher than that found for several species of nonmigratory birds and short-distance migrants. Dhondt (1979) found a survival probability of 0.252 for Great Tits (*Parus major*) during the first 10 weeks after fledging. Sullivan (1989) found a survival

probability of 0.321 for Yellow-eyed Juncos (*Junco phaeotus*) from fledging to parental independence, and Zann and Runciman (1994) found a survival probability of 0.33 for Zebra Finches (*Taeniopygia guttata*) during the first 35 days after fledging. Krementz et al. (1989) found a mean survival rate of 0.429 for European Starlings (*Sturnus vulgaris*) during the first 7 weeks after fledging, a rate similar to that of juvenile Wood Thrush in our study. Although post-fledging survival of our study individuals was higher than that of several species of nonmigratory birds and short-distance migrants, it was low enough to affect productivity, such that factors affecting survival should be of concern.

Results of our analyses of cause-specific mortality and effect of nestling condition provide information on factors that affected post-fledging survival in our study population. Predation, the main cause of nest failure in open-nesting passerine birds (Ricklefs 1969; Martin 1992), was the main cause of post-fledging mortality in our study. However, the suite of predators of post-fledging juvenile birds differed from that of nest predators. Although common forest nest predators include American Crows (*Corvus brachyrhynchos*), Blue Jays (*Cyanocitta cristata*), raccoons (*Procyon lotor*), squirrels (*Tamiasciurus* and *Sciurus* spp.), and mice (*Peromyscus* spp.; Yahner & Scott 1988; Reitsma et al. 1990; Leimgruber et al. 1994; Haskell 1995), predators of post-fledging juveniles in our study included the Cooper's Hawk, Broad-winged Hawk, timber rattlesnake, and eastern chipmunk. Of these, only the chipmunk has also been observed to depredate nests in this habitat type (Reitsma et al. 1990; Haskell 1995).

Risk of mortality of post-fledging juveniles varied with age and probability of predation may have been correlated with developmental behaviors occurring at different ages. Risk of predation the first week after fledging was relatively high. During this period individuals remained near the ground, could not fly quickly or for long distances, and attempted to avoid predation by remaining completely still when threatened. During the second week after fledging, risk of predation decreased. By this time juveniles could fly apparently as quickly as adult birds, and they were still being fed by their parents. Escape from predators may have been more likely at this time, and mortality associated with initial foraging attempts was not yet a factor.

During the third week after fledging, predation risk increased. At this age juveniles were no longer attended regularly by the parents, and they began to forage for themselves. Initial foraging attempts were relatively loud and conspicuous as juveniles threw leaf litter while searching for invertebrates. Increased detectability may have led to increased predation at this time. Approximately 3 weeks after fledging, juveniles dispersed individually from the forest-interior natal territories and moved into areas of dense vegetation, such as mature

wooded riparian habitat, young deciduous and pine forests (clearcuts), and forest/field edges (Anders 1996). Probability of predation up to 5 weeks after this dispersal event was zero. A similar pattern of age-dependent post-fledging survival has been seen in Yellow-eyed Juncos: survival was low before juveniles could fly and increased after flight ability had been attained. Survival then decreased just after independence from the parents and increased again as juveniles matured (Sullivan 1989).

In addition to developmental behaviors, a factor that has the potential to affect probability of post-fledging predation is the condition of individuals in the nest. Although nestlings may be healthy enough to fledge, poor body condition during the nestling period could lead to low survival probability after fledging. This situation has been seen to occur in Great Tits and European Starlings (Perrins 1963; Dhondt 1979; Krementz et al. 1989). Results of our analysis of post-fledging survival versus nestling body mass indicate that nestling condition did not affect survival probability in our study. It is possible that because we had to rank the mass of individuals within each nest, we obscured existing differences in survival. Measuring broods at the same time during development would alleviate this concern.

Factors that affect survival can show seasonal changes in the severity of their effects. Several studies of nesting success have shown changes in rates of nest predation throughout the breeding season (Nolan 1963; Thompson & Nolan 1973; Caccamise 1978; Schaub et al. 1992), and studies of Great Tits and European Starlings have shown seasonal changes in post-fledging survival (Perrins 1963; Dhondt 1979; Krementz et al. 1989). Food availability and predation pressure have the potential to vary over the course of the breeding season, causing differences in post-fledging survival between juveniles of early and late broods. Our analysis of seasonal changes in post-fledging survival indicate that risk of mortality did not change throughout the course of the breeding season. Survival probability thus remained constant for juveniles from early and late broods.

Because post-fledging mortality has the potential to differ between populations of Neotropical migrant birds, determination of the source/sink status of populations and assessment of breeding habitat quality should take into account the effect of this mortality on population productivity. We determined the source/sink status of the southern Missouri Wood Thrush population using our estimates of nesting success and post-fledging survival. Whereas Donovan et al. (1995) and Robinson et al. (1995) concluded that the Wood Thrush population in southern Missouri was a source from 1991 to 1993, results of our analysis indicate that the population was not a source in 1994 and 1995.

It is not the inclusion of our post-fledging survival estimate, however, that causes the discrepancy in these results. Donovan et al. (1995) and Robinson et al. (1995)



used a theoretical juvenile survival value of 0.31 in their analyses. Our estimate of juvenile survival is similar at 0.29, although this estimate does not include mortalities occurring during migration. The main factor affecting the change in this population's source/sink status is nesting success. From 1991 through 1993 the nesting success of this population was 0.414 ( $n = 56$ ; Donovan et al. 1995). In contrast, nesting success during our study period was only 0.266. Data obtained by the Missouri Ozark Forest Ecosystem Project in 1994 and 1995 indicate that predation rates on nests of many forest-interior species were higher in those years than in 1991 through 1993. Combined with these data, results of our analysis suggest that the source status of the southern Missouri Wood Thrush population is highly variable between years. This population has apparently produced excess young for immigration into sink populations in some years, but has produced young below replacement levels in other years.

Although our estimate of post-fledging survival did not greatly affect our conclusions concerning this population's source/sink status, differential post-fledging survival between populations has the potential to affect our understanding of population productivity and source/sink interactions. Data on post-fledging survival from other populations of Neotropical migrant birds will enable us to better quantify source/sink interactions and more accurately assess breeding habitat quality.

## Conclusions

To date, determination of the productivity of Neotropical migrant bird populations and assessment of breeding habitat quality have focused on population densities and nesting success. Results of our study indicate that the productivity of the southern Missouri Wood Thrush population was also affected by post-fledging mortality. Predation was the main cause of post-fledging mortality. Just as nesting success varies between populations, so may post-fledging survival and the factors affecting survival vary between populations, leading to differences in productivity. Data on post-fledging survival from other populations of Neotropical migrant birds are needed in order to better quantify the differential productivity between populations, further identify factors during the post-fledging period that can be managed to improve productivity, and more accurately assess breeding habitat quality.

The Wood Thrush population in southern Missouri has been considered a source population. Our analysis of the source/sink status of this population, however, indicates that young were being produced below replacement levels during our study due to a decline in nesting success. The identification of a population as a source thus does not necessarily imply that excess individuals are being produced for immigration into sink popula-

tions consistently over time. Large-scale management decisions concerning source and sink populations should take into account potential fluctuations in the productivity and source/sink status of populations over time.

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