



SURVIVAL OF FLEDGLING HOODED WARBLERS (*WILSONIA CITRINA*) IN SMALL AND LARGE FOREST FRAGMENTS

SCOTT A. RUSH¹ AND BRIDGET J. M. STUTCHBURY

York University, 4700 Keele Street, North York, Ontario M3J 1P3, Canada

ABSTRACT.—Studies on the effects of forest fragmentation on the reproductive ecology of forest songbirds have focused almost exclusively on the egg and nestling stages. Little is known about survival or habitat use of fledglings in their first weeks out of the nest. We radiotracked adult Hooded Warblers (*Wilsonia citrina*) attending fledglings from large (>150-ha) and small (<30-ha) forest fragments during 2002 and 2003. Mark–recapture models were used to assess the effects of forest-fragment size and age of the attending adult on the survival of young. We also examined the structure of nesting- versus postfledging-habitat used by fledglings. Only 19% of fledgling Hooded Warblers survived the 28-day fledgling period prior to independence, and fledglings' daily survival probability was lowest in the first four days after they left the nest (1–2 days postfledging: 0.72; 3–4 days postfledging: 0.69). Fledgling survival did not differ between large and small forest fragments. Large fragments were more likely to contain older adults, and age of parent had a positive influence on fledgling survival, independent of fragment size. As in many other studies, overall productivity was higher within larger fragments; this was largely attributable to differences in number fledged rather than fledgling survival. Habitat used by fledglings was more structurally complex than habitat at nest sites, which indicates that fledglings may seek habitat with high cover to avoid predation. Fledgling survival was much lower than estimates used in demographic models, which suggests that for many species, these models may need re-evaluation. Received 7 October 2006, accepted 28 April 2007.

Key words: fledgling survival, habitat use, Hooded Warbler, mark–recapture, songbird, *Wilsonia citrina*.

Supervivencia de Volantones de *Wilsonia citrina* en Fragmentos de Bosque Pequeños y Grandes

RESUMEN.—Los estudios sobre los efectos de la fragmentación del bosque sobre la ecología reproductiva de las aves canoras de bosque se han enfocado casi exclusivamente en las etapas de huevo y pichón. Poco se conoce sobre la supervivencia o el uso del hábitat de los volantones durante las primeras semanas afuera del nido. Monitoreamos con radiotransmisores individuos adultos de *Wilsonia citrina* que estaban asistiendo a volantones en fragmentos de bosque grandes (>150 ha) y pequeños (<30 ha), durante 2002 y 2003. Se usaron modelos de marca y recaptura para determinar los efectos del tamaño del fragmento de bosque y de la edad del adulto asistente sobre la supervivencia del juvenil. También examinamos la estructura del hábitat de nidificación versus la del hábitat post emplumamiento usado por los volantones. Sólo el 19% de los volantones de *W. citrina* sobrevivieron el período de volantón de 28 días previo a la independencia, y la probabilidad diaria de supervivencia de los volantones fue menor durante los primeros cuatro días luego de que dejaron el nido (1–2 días post emplumamiento: 0.72; 3–4 días post emplumamiento: 0.69). La supervivencia de los volantones no difirió entre los fragmentos de bosque grandes y pequeños. Los fragmentos grandes tuvieron mayor probabilidad de contener adultos de mayor edad, y la edad de los padres tuvo una influencia positiva sobre la supervivencia del volantón, independientemente del tamaño del fragmento. Como en muchos otros estudios, la productividad general fue mayor en los fragmentos mayores; esto fue atribuible principalmente a las diferencias en el número de individuos emplumados más que en la supervivencia de los volantones. El hábitat usado por los volantones fue más complejo estructuralmente que el hábitat de los sitios de nidificación, lo que indica que los volantones pueden buscar ambientes con alta cobertura para evitar la depredación. La supervivencia de los volantones fue mucho menor que las estimaciones usadas en los modelos demográficos, lo que sugiere que para muchas especies, estos modelos pueden requerir reevaluaciones.

SINCE THE 1960s, many populations of forest-nesting Neotropical migrant songbirds have experienced significant declines (Askins et al. 1990, Newton 2004). Small forest fragments in eastern North America can act as population “sinks” where low productivity attributable to increased predation or parasitism results in a

negative intrinsic growth rate for that population (e.g., Robinson et al. 1995, Burke and Nol 2000). For these subpopulations to persist, they require immigration from population sources where the intrinsic growth rate is positive (Pulliam 1988, Simons et al. 2000). Historically, for most songbird populations, the basis for

¹Present address: D. B. Warnell School of Forest and Natural Resources, University of Georgia, Athens, Georgia 30602, USA. E-mail: rushs@warnell.uga.edu

classification as a “source” or “sink” has relied on productivity estimates based on the number of young that fledge from nests, because few studies have directly measured fledgling survival up to the point of independence from parents (reviewed in Anders and Marshall 2005). Juvenile survival over the first year is assumed to be 50% of adult survival (Greenberg 1980), or is simply set at 0.31 on the basis of Temple and Cary’s (1988) calculations. Some studies have found that small forest fragments are not sinks (e.g., Friesen et al. 1999, Fauth 2001), but if actual fledgling survival is very low, this conclusion may be premature. Few studies of forest-nesting Neotropical migrants have directly measured the survival of young during the postfledging period (Anders and Marshall 2005), and none has compared large and small fragments. It is reasonable to expect that if nests in small forest fragments experience higher predation on eggs and nestlings, fledglings may also suffer higher predation in small fragments.

The postfledging period has received little attention, largely because young birds are cryptically colored and highly mobile, which makes repeated observations difficult. Few studies have used radiotelemetry or systematically collected resighting information to estimate fledgling survival of forest birds (Anders et al. 1997, Vega Rivera et al. 1998). Recent studies using periodic observations of fledgling songbirds throughout the parental-care period have established that the survival of juvenile songbirds can differ over time, study site, and habitat types (Krementz et al. 1989, Anders et al. 1997, Vega Rivera et al. 1998). For Wood Thrushes (*Hylocichla mustelina*) in Missouri, fledgling survival was only 0.42 for the 8-week postfledging period, whereas in Georgia, 75% of fledglings survived a 14-week period (Anders et al. 1997, Powell et al. 2000). Fledgling-survival estimates in migratory songbirds can be as low as 0.32 over just a three-week period, which suggests that the typical annual survival estimate of 0.31 may greatly overestimate juvenile survival (Anders and Marshall 2005). We radiotracked Hooded Warbler (*Wilsonia citrina*) parents to systematically measure survival of their fledglings in forest fragments.

The settlement of older, more experienced birds into large forest tracts may push the younger, less-experienced breeders into smaller forest fragments (Fretwell and Lucas 1970, Holmes et al. 1996, Bayne and Hobson 2002). Therefore, fledglings raised in smaller forest fragments may suffer a decrease in survivorship because of high predation risk, but also as a result of having inexperienced parents. Parental experience (i.e., age) in some songbirds is positively related to nesting success (Porneluzi and Faaborg 1999, Zanette 2001), more experienced adults being able to locate more or better-quality prey or lower the risk of predation on their young. For instance, experienced male and female Eastern Yellow Robins (*Eopsaltria australis*) breeding in forest fragments in Australia produced 10–20% more independent young than inexperienced parents (Zanette 2001).

For adult songbirds, much information exists on habitat selection during the nesting period; however, once the young have fledged, this habitat preference may change (Anders et al. 1998, Vega Rivera et al. 1998, King et al. 2006). Once they are mobile, fledglings may seek out habitat that differs from the nesting site to maximize their own survival. Several studies of forest-interior songbirds have noted that these species use forest edge extensively during the postfledging period (Anders et al. 1998, Vega Rivera et al. 1998). Forest edges or patches of dense vegetation

may be preferred habitat, particularly during the molt period (Vega Rivera et al. 1998, Marshall et al. 2003), and may lower the risk of predation by providing cover (Anders et al. 1998). In Hooded Warblers, parents sometimes move far from the nesting site while caring for fledglings (Evans Ogden and Stutchbury 1994). Small forest fragments could constrain these movements because of forest-field boundaries and relatively poor-quality habitat in corridors linking forest patches.

Here, we investigate differences in nesting success and the survival of fledgling Hooded Warblers in small and large forest fragments during their 28-day postfledging period. Specifically, the goals of the present study were to (1) provide estimates of fledgling survival and movements in large and small forest fragments, (2) examine the effects of parental age on fledgling survival, and (3) compare habitat at the nest versus that at fledgling locations.

METHODS

The study was conducted in Erie and Crawford counties (41°46′N, 79°56′W) in northwestern Pennsylvania during the summers of 2002 and 2003. We radiotracked 19 families of Hooded Warblers from 13 forest fragments: 8 families from 8 small forest fragments (<30 ha) and 11 families from 5 large forest fragments (>155 ha) (Table 1).

Selection of forest fragments was made using the following criteria: large forest fragments (1) must constitute a continuous patch of forest >150 ha in area and (2) must not have been logged during the 25 years preceding the study. Small forest fragments were chosen if they were <30 ha in area. These size categories reflect the end-points of the range of extant forests in our study area. All forest fragments had hard edges on all sides. “Hard edge” is defined as a lack of gradual transition between abutting ecological communities (e.g., field and forest). During mid-May to early June of each year, we located candidate forest fragments within the study area. Different forest fragments were studied each year; candidate forest fragments were selected on the basis of size criteria and the presence of Hooded Warblers. We confirmed the presence of Hooded Warblers through observations of territorial males, nesting females, or both. Once the presence of Hooded Warblers was confirmed, aerial photographs for each forest fragment were obtained through the web-based program TERRASERVER (TerraServer, Raleigh, North Carolina). The aerial photographs were then imported into IMAGEJ (Abramoff et al. 2004). Using a Wacom Tablet, version 4.72 (Wacom, Saitama, Japan), IMAGEJ’s measurement tool was calibrated against a known linear distance in each photograph. After calibration, the perimeter of each forest fragment was measured and the area calculated.

“Landscape composition” was defined as the percentage of forest cover within 5 km of the center of each forest fragment. We chose to use this metric of landscape composition because a meta-analysis (Hartley and Hunter 1998) indicated that the percentage of forest cover at the 5-km scale was significantly related to daily nest survival for other forest songbird species. The percentage of forest cover within 5 km of each forest fragment was measured using the aerial photographs and IMAGEJ. A radius of 5 km from the geographic center of each forest fragment was measured. Total forested area within this circle was measured using the same

TABLE 1. Forest-fragment and landscape measurements.

Fragment name	Area (ha)	Perimeter length (km)	Distance (m) to nearest forest fragment ≥ 3 ha	Forest cover within 5 km of forest-fragment center (%)
Small forest fragments				
Bancroft*	29.00	2.66	71.86	32
Tarof Small	5.50	0.97	13.4	31
Ripple	6.97	1.24	17.87	31
Mystery	3.53	0.93	28.67	32
Henry Road	22.59	3.12	27.74	43
DC	10.72	1.46	48.47	37
GC*	8.07	2.02	10.74	23
PES*	6.50	1.29	10.74	26
Large forest fragments				
Farm	231.84	13.16	16.52	53
ORNG*	155.20	9.48	8.98	42
SBM*	212.34	12.30	38.43	43
SCOT*	163.00	9.42	33.56	43
FRXT	203.64	8.28	10.22	48

*Indicates forest fragments studied in 2003.

methods employed to measure the forest area of each candidate forest fragment. We then divided the area of the circle by the estimate of total forested area to obtain the percentage of forest cover. To identify the relative isolation of the forest fragments used, we measured the distance from each forest fragment to the nearest neighboring forest fragment (Table 1). The aerial photographs used were taken during 1993 and 1994. To assess the reliability of measurements, we located each forest fragment on the ground and compared the existing boundaries of the forest fragment to those in the photograph, ensuring that the dimensions were comparable.

Once the size of a candidate forest fragment was determined and a territorial male was found, attempts were made to capture the male using a "target banding" approach, whereby the bird was lured into a mist net using tape playback of a male Hooded Warbler's song and a model of a male Hooded Warbler. Once captured, males were banded with a federal band and up to three uniquely colored plastic leg bands. Observations of color-banded males allowed us to identify the specific territories of each male within each forest fragment. We aged captured birds as either second-year (SY; <2 years old) or after-second-year (ASY; >2 years old) according to the criteria outlined by Pyle (1997) and validated by Evans Ogden and Stutchbury (1996).

Nests were located by searching suitable nesting habitat within each territory or by locating breeding females through their vocalizations and following them to their nest site. Within large forest fragments, nests were selected for inclusion in the study only if they were >150 m from a forest edge. Many of the smaller forest fragments had only one or two Hooded Warbler territories within them, so only the first of these nests to fledge young was selected for the study. During each year of the study, all selected nests were associated with the first known breeding attempt of each Hooded Warbler pair. Within several of the large forest fragments, up to three different nests were selected. These nests met the above distance-from-edge criteria and were ≥ 250 m apart.

Once a nest was located, it was monitored every four days to determine the clutch-initiation date and clutch size. Typically,

female Hooded Warblers incubate eggs for 12 days and the young hatch on the 12th day (Evans Ogden and Stutchbury 1994). On the seventh day posthatching, we returned to each nest site, observed the adults feeding the young in each nest, and identified the male attending each nest through observation of his color bands. The adults were then captured using mist nets set up around the nest site. The adult female was banded and aged using the same methods employed for the male. We then fitted both adults with Holohil BD-2B (0.67-g) radiotransmitters (Holohil, Carp, Ontario). Transmitters had a battery life of ~ 28 days and were attached using a figure-eight harness made with lightweight cotton embroidery thread (for details on harness construction and attachment, see Rappole and Tipton 1991). The transmitter and harness system weighed $\sim 7\%$ of the adult's body mass and has been shown not to adversely affect the movement and survival of Hooded Warblers during the breeding season (Neudorf and Pitcher 1997).

The one- to two-day lag between adults being fitted with radiotransmitters and the fledging event allowed the parents to become accustomed to the radiotransmitters before fledging their young. Once both adults were captured, we removed the nestlings from the nest and banded each with a federal band and two individual-specific colored leg bands. One day later, we returned to each nest site and radiotracked the adults to ensure that their radiotransmitters were functioning and they were still caring for their young.

We determined the date of fledging by visiting the nest daily after the eighth day posthatching. If the young disappeared from the nest before fledging, they were considered to have been depredated and the nest was used in the calculation of nesting success but was excluded from any further analysis. Once the young had fledged from the nest, we radiotracked the adults and located the young by visually following the adults when they fed them. When the young fledge from the nest, the brood is divided between the parents, and each parent provides exclusive care for its part of the brood (Evans Ogden and Stutchbury 1997). Brood division facilitated monitoring of each parent-offspring

group and its movement during the postfledging period. Each group was monitored every two days postfledging, the time of the observation periods randomized to avoid any time-related bias. Parent-offspring groups were observed until a fledgling was first resighted and successfully identified; however, if no fledglings were observed and identified within 45 min of the start of the observation period, the observation period lasted for 1 h. We made these observations while sitting quietly near the suspected location of the fledglings. During each period, we attempted to resight and identify each fledgling through its colored bands while also noting the identity of the adult caring for it. If, during the course of an observation, a fledgling remained in the same location for ≥ 10 min, we recorded its position using a global positioning system device (GPS 12XL; Garmin, Olathe, Kansas) to set a waypoint for that location.

Estimates of daily nest survival prior to fledging were calculated using logistic-exposure models (GENMOD in SAS; SAS Institute, Cary, North Carolina; Shaffer 2004). To quantify fragment-size-specific survival and resighting probabilities for fledglings, we used Cormack-Jolly-Seber (CJS) models in MARK (White and Burnham 1999). The benefit of using CJS models is that resighting probability is incorporated when modeling the loss of individuals from a sample population (Williams et al. 2001). Thus, the presence or absence of an individual during one sampling event does not govern survival estimated for the entire study period. MARK is highly versatile, providing estimates for parameters such as survival and recapture for marked animals from biological studies. MARK can be used to develop models addressing the survival and recapture probabilities of marked animals from multiple attribute groups as well as how individual-specific covariates may affect these probabilities, allowing evaluation of the plausibility of different biological hypotheses.

Model notation followed Lebreton et al. (1992), where survival probability is denoted as ϕ and recapture probability as ρ . Subscripts used in model notation indicate whether the parameters in the model vary with fragment size (e.g., ϕ_{frag} , ρ_{frag}), are dependent on time since fledging (ϕ_t , ρ_t), are constant over time (ϕ_c , ρ_c), or describe an interaction in fledgling survival between fragment size and time since fledging ($\phi_{\text{frag}t}$). Thus, in modeling the influence of group and time on fledgling survival, we developed a suite of 13 candidate models incorporating these variables in different combinations. Additionally, as noted above, several previous studies have found that in songbirds, parental experience (i.e., parental age) can be positively related to nesting success (Porneluzi and Faaborg 1999, Zanette 2001), more experienced adults being able to locate more or better-quality prey or lower the risk of predation experienced by the young. Accordingly, we expected that adult age would also be related positively to the survival of fledglings. To model the influence of adult age on fledgling survival, we used separate covariates for the ages of the adult male and the adult female in the modeling process. We then applied these covariates to the best-fitting model, using a common intercept term but differing slopes. We used the beta estimates derived from the individual covariates in a logistic function to calculate relative effect sizes for the relationships between the age of the adults and fledgling survival.

We compared the fit of the different competing models using Akaike's Information Criterion (AIC); Akaike 1974, Lebreton et al.

1992, Burnham and Anderson 2002) corrected for sample size (AIC_c), as provided by MARK. Theoretically, selection of the model with the lowest AIC_c value out of all candidate models should result in the selection of the most parsimonious model that best fits the data to which it has been applied. To correct for the possibility of overdispersion, we used MARK to calculate the mean deviance of the global model (the model containing all parameters) through 1,000 bootstrap simulations. This estimated deviance was then compared with the deviance observed for the global model, dividing the observed by the simulated deviance to obtain a variance-inflation factor (\hat{c}). This variance-inflation factor was then applied to the AIC_c as an adjustment through quasi-likelihood, resulting in the $QAIC_c$ value of each model (Burnham and Anderson 2002). We considered all models with a $\Delta QAIC_c$ value ≤ 2 in relation to the best-fitting model as part of a confidence set of best-supported models (Burnham and Anderson 2002).

We defined "productivity" as the number of young that survived to independence. We used the number of young fledged per successful nest and daily survival estimates, obtained for the postfledging period, to calculate the productivity of Hooded Warblers nesting within large and small forest fragments.

We collected quantitative information on the habitat used by Hooded Warblers for nesting and during the postfledging period. We used 0.1-ha circular sampling plots centered on the nest site and on fledgling locations following the methods of James and Shugart (1970). Two 22.5-m rope transects were laid out to delineate the plots, with one rope running north-south and the other running east-west. Within each plot, we collected data on five habitat variables: (1) number of shrubs that were > 1.5 m tall but < 3 cm in diameter at breast height (DBH), (2) percentage of groundcover, (3) percentage of vertical cover within 0–2 m above ground, (4) percentage of vertical cover within 2–4 m above ground, and (5) percentage of canopy cover.

Percentage of groundcover was estimated using an ocular tube. Starting at the end of a randomly chosen transect, we measured groundcover at 2.5-m intervals. At each location, we recorded whether the bare ground filled $\geq 50\%$ of the view. If the ground could be clearly seen, we recorded a "0"; if the ground was obscured, we recorded a "1." This was repeated 20 times per plot. These measurements were averaged to obtain a single estimate of groundcover for the plot. The percentage of vertical cover within the two height classes (0–2 m above ground, and 2–4 m above ground) was measured as a percentage using a 4-m-long by 1.5-m-wide cover board (consisting of 100 equally sized, alternating black-and-white squares). The cover board was extended upwards at the end of each of the transect ropes and viewed from the center of the plot, and the number of squares obscured by vegetation within each of the two height classes was recorded and used to obtain the percentage of cover for each height class. The four measurements from each plot were averaged to obtain a single estimate of vegetative cover per height class, per plot. Percentage of canopy cover was calculated using a spherical densiometer (Forestry Suppliers, Jackson, Mississippi).

We compared habitat (1) at nest sites in small and large forest fragments; (2) at nest sites versus fledgling locations; (3) at locations used by fledglings during the first six days postfledging versus thereafter; and (4) at locations used by fledglings during the first six days postfledging versus thereafter, compared by

TABLE 2. Average productivity in large and small forest fragments (mean and 95% confidence interval [CI] in parentheses; $n = 28$ nests in large forest fragments, $n = 29$ nests in small forest fragments).

Mean clutch size per nest	Cowbird parasitism (%)	Daily nest survival	Fledglings per successful nest	Daily fledgling survival	Fledglings per successful nest surviving to independence
2.83 (2.59–3.07)	29%	0.97 (0.93–0.98)	3.09 (2.59–3.59)	0.94 (0.92–0.96)	0.55 (0.24–1.05)
2.8 (2.61–2.99)	65%	0.94 (0.91–0.96)	2.25 (1.67–2.83)	0.94 (0.89–0.96)	0.34 (0.07–0.93)

forest-fragment size class. We selected these intervals because, although fledgling Hooded Warblers can fly two to three days after leaving the nest (Howlett and Stutchbury 1996), we noted a marked increase in the vagility of the young after the first week postfledging. We examined differences among frequencies in the vegetation measurements for these groups using general linear models (GLM; in SAS). The significance of the individual variables in these models was assessed using the Type III sums of squares and Tukey’s multiple-comparison tests (HSD) to assess differences in vegetation by sites. Tests for normality indicated that the distributions of data for each of the habitat variables measured were not normally distributed. Thus, we transformed the data to meet the assumptions of normality, with the number of shrubs log transformed and percentage of groundcover, percentage of vertical cover within 0–2 m above ground, percentage of vertical cover within 2–4 m above ground, and percentage of canopy cover arcsine-square-root transformed.

The distance fledglings dispersed from the nest site was calculated using the GPS waypoints obtained from the fledgling locations. We report the mean linear distance moved from the nest site rather than estimates of home range and core area because sample size did not permit these calculations. Dispersal distance was square-root transformed to meet the assumptions of normality. Statistical analysis comparing the distance moved in relation to the sex of the adult, time postfledging, and size of the forest fragment were done using general linear models GLM. Results were considered significant if $P < 0.05$.

RESULTS

Daily nest survival did not differ between large and small forest fragments ($\chi^2 = 2.71$, $df = 1$, $P = 0.1$, $n = 28$ nests in large fragments, $n = 29$ nests in small fragments; Table 2). Although clutch size per nest did not differ between large and small forest fragments (large mean = 2.80, $n = 23$; small mean = 2.83, $n = 20$; Mann-Whitney U -test, $Z = -0.36$, $P = 0.36$), we found that Hooded Warblers nesting within small forest fragments experienced greater nest parasitism by Brown-headed Cowbirds (*Molothrus ater*; 65% in small forest fragments, compared with 29% in large). Hooded Warblers nesting within large forest fragments experienced greater productivity, in terms of the number of young fledged per nest ($n = 11$ in large forest fragments, $n = 8$ in small forest fragments; Mann-Whitney U -test, $Z = -1.7$, $P = 0.04$). We obtained survival estimates for 52 fledglings from 19 families. During 2002, mean daily survival of fledglings ($n = 27$) was 0.94 (95% CI: 0.92–0.96), whereas during 2003 it was 0.85 (95% CI:

0.79–0.90, $n = 25$). There was no strong effect of fragment size on fledgling survival probabilities (Table 2).

A fully time-dependent model provided a better fit to our data than one where survival and resighting probabilities were constant over resighting periods (model 1; Table 3). The model based on fragment size affecting fledgling survival (model 8) had the highest AIC score. The results of the best-fitting model (model 1; Table 3) indicated that fledgling survival was lowest during the first four days postfledging but increased with fledgling age (Table 4). Collectively, only 19% of all nestlings that fledged survived the entire 28-day postfledging period.

We examined the timing of mortality among brood mates because occurrences of two brood mates dying on the same day are unlikely to be the result of independent events. We calculated the probability that two brood mates died independently on the same day as the square of daily survival probability. The fate of individual fledglings was largely independent of the fate of their brood mates (5 fledglings out of 19 families tracked). Thus, although brood mates share the same territory and sometimes the same parent as caregiver, the fate of individual nestlings appears to be largely independent.

We found that the age of the adults attending the fledglings was positively related to fledgling survival (Table 5). The model that included the age of both adults (model 1; Table 5) fit better (71% of the model weights) than models with age of either adult alone. The model that did not include adult age had a QAIC_c weight of 0 (model 4; Table 5). For the entire 28-day postfledging period, fledglings cared for by older males experienced a mean increase in survival of 24% (95% CI: 8–38%) compared with those cared for by younger males. Similarly, but of lesser effect, fledglings cared for by older females experienced a 17% (95% CI: 6–29%) increase

TABLE 3. Model selection for the effects of forest fragmentation on postfledging survival of Hooded Warblers. For clarity, only the top five models are shown.

Model	QAIC _c	ΔQAIC _c	w_i	Number of estimable parameters
(1) (φ_t , p_t)	407.07	0	0.69	26
(2) (φ_t , p_c)	409.53	2.46	0.20	14
(3) (φ_t , p_{frag})	410.81	3.74	0.11	15
(4) (φ_c , p_t)	422.98	15.91	0.00	14
(5) (φ_{frag} , p_t)	425.10	18.03	0.00	15

Model effects: frag = group effect (i.e., large vs. small forest fragments), t = time dependence, and c = constant over time.

TABLE 4. Daily survival and resighting probabilities for Hooded Warblers during the 28-day postfledging period.

Days postfledging	Mean daily survival probability	95% CI	Mean daily resighting probability	95% CI
1–2	0.72	0.61–0.82	0.96	0.88–0.99
3–4	0.69	0.55–0.83	0.71	0.55–0.85
5–6	0.88	0.74–0.98	0.75	0.59–0.88
7–8	0.91	0.79–0.99	0.70	0.54–0.85
9–10	0.94	0.85–0.99	0.71	0.55–0.85
11–12	0.93	0.83–0.99	0.78	0.62–0.90
13–14	0.88	0.74–0.97	0.80	0.63–0.92
15–16	0.90	0.77–0.98	0.69	0.51–0.85
17–18	0.89	0.76–0.98	0.79	0.61–0.92
19–20	0.93	0.83–0.99	0.89	0.76–0.98
21–22	0.90	0.78–0.98	0.89	0.76–0.98
23–24	0.93	0.83–0.99	0.94	0.83–0.99
25–26	0.94	0.83–0.99	0.94	0.83–0.99
27–28	0.94	0.83–0.99	0.94	0.83–0.99

TABLE 5. Model selection for the effects of adult age on the postfledging survival of Hooded Warblers.

Model	QAIC _c	ΔQAIC _c	w _i	Number of estimable parameters
(1) ($\varphi_{t,m,f}$, p_t)	387.55	0	0.71	26
(2) ($\varphi_{t,f}$, p_t)	390.62	3.07	0.15	26
(3) ($\varphi_{t,m}$, p_t)	390.84	3.29	0.14	26
(4) (φ_t , p_t)	407.07	19.52	0	26

Model effects: t = time dependence, m = adult male's age, and f = adult female's age.

in fledgling survival as compared with those cared for by younger females.

We found that the age of adult Hooded Warblers varied with forest-fragment size. During the two years of the study, we captured and aged 108 adult Hooded Warblers. Of males captured within large forest fragments ($n = 44$), 77% were aged as ASY, compared with 55% of the males captured within small forest fragments ($\chi^2 = 19.56$, $P < 0.01$). This age skew was also found among the females, with 65% aged as ASY in the large forest fragments ($n = 26$), and 44% ASY ($n = 18$) in the small forest fragments ($\chi^2 = 12.71$, $P < 0.01$).

For each of the regression tests, we found significant differences in the distributions of several habitat variables. Comparison of the structure of vegetation associated with nest sites in small and large forest fragments revealed that the vertical cover of vegetation 0–2 m ($F = 9.55$, $df = 1$ and 20, $P < 0.01$) and 2–4 m ($F = 4.48$, $df = 1$ and 20, $P < 0.05$) above ground was greater at nest locations in small forest fragments (non-transformed mean [\pm SE] = 0.88 ± 0.04 and 0.69 ± 0.09 , respectively) than in large (non-transformed mean = 0.66 ± 0.06 and 0.50 ± 0.06 , respectively), whereas the vertical cover of vegetation 2–4 m above ground ($F = 4.83$, $df = 5$ and 122, $P < 0.03$) was greater at locations used by fledglings (non-transformed mean = 0.700 ± 0.264) compared with nest sites (non-transformed mean = 0.58 ± 0.27). Also,

during their first six days postfledging, juvenile Hooded Warblers used locations with significantly more shrubs ($F = 13.13$, $df = 5$ and 122, $P < 0.01$; non-transformed mean = 25.84 ± 29.75) compared with locations used by fledglings during days 7 to 28 postfledging (non-transformed mean = 9.68 ± 9.73). However, during days 7 to 28 postfledging, fledglings in small forest fragments used locations with a greater proportion of cover within 0–2 m ($F = 18.28$, $df = 1$ and 93, $P < 0.01$; non-transformed mean = 0.88 ± 0.02) and 2–4 m above ground ($F = 13.20$, $df = 1$ and 93, $P < 0.01$; non-transformed mean = 0.77 ± 0.05) than those in large forest fragments (non-transformed mean = 0.74 ± 0.04 and 0.59 ± 0.03 , respectively).

We found that the distance fledglings moved from the nest site did not differ with forest-fragment size ($F = 0.82$, $df = 1$ and 152, $P = 0.37$). The farthest a fledgling traveled from the nest site was 144 m, and no family group moved outside of a forest fragment. As expected, the movements of fledglings increased as they became older. During the first six days postfledging, the distance moved from the nest (mean = 37.04 m) was significantly less than during the period 7–15 days postfledging (mean = 70 m, $F = 7.49$, $df = 1$ and 152, $P = 0.01$). Although this distance was significantly related to the sex of the attending adult (females: mean = 55.71 m; males: mean = 49.6 m; $F = 9.62$, $df = 2$ and 151, $P < 0.01$), there was no interaction between time postfledging and the sex of that adult ($F = 0.78$, $df = 2$ and 151, $P = 0.38$).

DISCUSSION

We found that the postfledging survival of Hooded Warblers did not differ between large (155–231 ha) and small (5–29 ha) forest fragments but that Hooded Warblers experienced high mortality during the 28-day postfledging period. Only 19% of fledglings survived to independence. Like King et al. (2006), we found that most mortality occurred within the first few days postfledging and that fledgling survival was positively related to the age of the attending adults.

The most likely explanation for fledgling survival being similar in large and small fragments is that predation risk is similar. However, we cannot definitively identify predator communities that affected nest success and fledgling survival. Small mammals are known to actively prey upon Hooded Warbler eggs and nestlings (McShea 2000), and several studies have suggested that some species of small mammals may not exhibit area sensitivity (Andr n 1994, Nupp and Swihart 2000, Chalfoun et al. 2002). Additionally, the significant annual variation in the postfledging survival of Hooded Warblers could reflect fluctuations in small-mammal populations (Schmidt and Ostfeld 2003). The absence of a fragment-size effect on nest and fledgling predation may occur because predators are abundant in both our small and large fragments (e.g., Donovan et al. 1997). Additionally, edge effects for nest predators vary between landscape and predator types (Lahti 2001), making it difficult to predict the circumstances in which fragmentation will affect fledgling survival.

The number of young fledged per nest—and, consequently, the number of fledglings that survived to independence—was significantly higher in large fragments (Table 2), largely because of lower cowbird parasitism. Daily nest survival was also lower in small fragments (0.94 vs 0.97), though the difference was

not statistically significant. In the only other study of forest-fragmentation effects on fledgling survival, fledgling Rufous Treecreepers (*Climacteris rufa*) in southwestern Australia also did not have higher survival in an unfragmented landscape, even though overall productivity was higher (Luck 2003). Further work is needed to determine how food supply and predation risk interact to affect fledgling survival in forest fragments, and why negative effects of fragmentation on nesting success do not carry over to the fledgling stage. For instance, nests, which are stationary, are likely to be subject to different predators than fledglings, which are mobile; thus, different habitat characteristics should be selected for protection from these different groups of predators.

Several studies that have estimated the survival of fledgling songbirds have equipped the fledglings with radiotransmitters (Anders et al. 1997), whereas we equipped the adults with transmitters and then followed them to identify the color-banded young. Both of these techniques may hold certain methodological biases: placing the radiotransmitters on the young may inadvertently decrease fledgling survival, particularly for newly fledged young of small species such as Hooded Warblers. Placing the transmitters on the adults eliminates this concern, though it may ultimately lead to missed observations of some of the fledglings, especially when they are young, despite intense observations of fledgling feeding. Although resighting was relatively low (0.74) from 2 to 14 days—when young tend to hide (Table 4), making it difficult to see color bands—the overall average daily resighting probability for the four-week period was 84%. This difference in resighting probabilities over the 28-day postfledging period indicates that fledglings should be observed for the full four-week period to obtain accurate estimates of survival.

Anders and Marshall (2005) called for field-based estimates of fledgling survival for Neotropical migrants, because the few existing studies suggested that the typical estimates used in population modeling are, in fact, overestimates. Particularly for forest birds, direct estimates of fledgling survival are scarce (Anders et al. 1997). For both years combined, we found that fledgling survival of Hooded Warblers was only 0.19 for the four-week postfledging period. This estimate is much lower than (1) the year-round estimate of juvenile survival of 0.31 (Temple and Cary 1988) or an estimate based on 50% of adult survival (0.24; Martin et al. 1995) and (2) that reported for two studies of the Wood Thrush where fledgling survival was only 0.42 for an 8-week postfledging period (Anders et al. 1997) and 0.75 for a 14-week period (Powell et al. 2000). We believe that varying estimates of fledgling survival may stem from differences in geographic location, time, and habitat type associated (Krementz et al. 1989, Anders et al. 1997, Vega Rivera et al. 1998). In the present study, we found that fledgling Hooded Warblers in small forest fragments may benefit from the ability to locate vegetation that affords greater cover and possible protection from differing levels of predation pressure.

The high fledgling mortality that we found suggests that typical estimates of fledgling survival are too high and may overestimate the ability of forest fragments to sustain populations of forest songbirds. Holmes et al. (1989) gave survival estimates for two species of warbler on the wintering grounds as 0.68. To estimate annual survival for juvenile Hooded Warblers, we multiplied this estimate by the postfledging survival estimate determined for our study (0.19) to arrive at an estimate of 0.13

(after Anders et al. 1997), which we consider conservative, given that it does not include mortality during migration. We found that large fragments produced an average of 1.54 female fledglings per nest; thus, assuming one successful nesting attempt per year (Evans Ogden and Stutchbury 1996), large forest fragments would appear to be source habitats. However, with our estimate of fledgling survival, females in large fragments can expect to produce only 0.2 recruits per breeding season, and a female would have to live five years to replace herself. Clearly, this extremely low recruitment is not enough to offset annual female mortality, which is likely ≥ 0.50 , judging from typical values for other Neotropical migrants (e.g., Sillett et al. 2000). The situation is even worse for females nesting in small fragments, which are the predominant habitat even in our study site, which has substantial forest cover (40%).

Our finding of substantial annual variation in fledgling survival cautions against extrapolating the results of short-term studies in assessing the stability of songbird populations over longer periods and across large geographic areas (e.g., James et al. 1996). To implement functional conservation practices, it is essential that (1) postfledging survival is quantified for each species over multiple years and study sites and (2) the resulting estimates are then used in calculating the stability of populations (Jones et al. 2004, Anders and Marshall 2005).

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