

Influence of forest management on pre- and post-fledging productivity of a Neotropical migratory songbird in a highly fragmented landscape

Margaret L. Eng, Bridget J. M. Stutchbury, Dawn M. Burke, and Ken A. Elliott

Abstract: Little is known about the effects of forest management on fledgling survival in birds, despite the fact that this is a key determinant of overall productivity. In 2005–2006, we compared male density, nesting success, and fledgling survival of Hooded Warblers (*Wilsonia citrina* Boddaert, 1783) among forest fragments that were reference sites ($n = 3$; not logged in >21 years) or had received either a standard selection system harvest ($n = 3$) or a heavy cut ($n = 5$) within the past 6–10 years. Density tended to be higher in logged sites than reference sites, but cumulative probability of nest survival (0.22 ± 0.02 ; 21 days) did not differ among treatments. Brown-headed Cowbird (*Molothrus ater* (Boddaert, 1783)) parasitism was significantly higher in recently logged sites, and reference sites produced significantly more Hooded Warbler young per successful nest than standard selection harvest sites. Logging treatment did not have a strong negative effect on fledgling survival, and overall, 51% (33/65) of fledglings survived until three weeks after fledging. Standard selection harvest sites had the highest Hooded Warbler density (0.2 males/ha) but also the lowest seasonal productivity (0.84 independent fledglings/female), raising the possibility of an ecological trap. The estimated number of daughters produced per female per year that are expected to survive to breeding age was lower for all treatments (reference, 0.26; selection, 0.17; heavy cut, 0.32) than the expected annual mortality probability of adult females (0.4–0.6). Forest fragments in this region appear to be population sinks, regardless of extent of partial harvest within the fragment.

Résumé : On connaît peu les effets de l'aménagement forestier sur la survie des oisillons après l'envol, bien qu'il s'agisse d'un déterminant clé de la productivité réelle. En 2005–2006, nous avons comparé la densité de mâles, le succès de nidification et la survie des oisillons après l'envol chez la paruline à capuchon (*Wilsonia citrina* Boddaert, 1783) entre des fragments de forêt témoin ($n = 3$; pas de coupe depuis >21 ans), des fragments en futaie jardinée standard ($n = 3$) et des fragments ayant subi une coupe sévère ($n = 5$) au cours des derniers 6–10 ans. La densité tendait à être plus élevée dans les sites ayant fait l'objet d'une récolte que dans les sites témoins, mais la probabilité cumulative de survie des nids ($0,22 \pm 0,02$; 21 jours) ne différait pas entre les traitements. Le parasitisme par le vacher à tête brune (*Molothrus ater* (Boddaert, 1783)) était significativement plus élevé dans les sites récoltés récemment et les sites témoins produisaient significativement plus de jeunes parulines à capuchon par nichée réussie que les sites en futaie jardinée. La récolte ligneuse n'a pas eu d'effet négatif marqué sur la survie des oisillons après l'envol et, dans l'ensemble, 51 % (33/65) des oisillons ont survécu au moins trois semaines après l'envol. Les futaies jardinées standard avaient les plus fortes densités de paruline à capuchon (0,2 mâle/ha), mais aussi la plus faible productivité saisonnière (0,84 jeune atteignant l'indépendance par femelle), ce qui soulève la possibilité d'un piège écologique. Le nombre estimé de filles produites par femelle par an pouvant atteindre l'âge reproducteur était plus faible dans tous les traitements (témoin, 0,26; futaie jardinée, 0,17; coupe sévère, 0,32) que la probabilité attendue de mortalité annuelle des femelles adultes (0,4–0,6). Les fragments de forêt de cette région semblent être des gouffres de population peu importe l'ampleur des coupes partielles dans le fragment.

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Introduction

A key issue for conservation of forest animals is the impact of forest management on abundance, productivity, and population viability (Rosenvald and Löhms 2008). In areas where agricultural development has left forest cover highly fragmented, including much of the eastern deciduous forest of North America, forest fragmentation typically increases

rates of nest predation on songbirds, increases parasitism by Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)), and for area-sensitive species, decreases breeding density (Donovan et al. 1995; Robinson et al. 1995; Burke and Nol 2000). Within large managed forests, the type and extent of forest harvest can influence species richness and density (Norton and Hannon 1997; Chambers et al. 1999; Simon et al. 2000; Weakland et al. 2002; Vitz and Rodewald 2006),

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food availability (Duguay et al. 2001; Smith et al. 2006), male pairing success (Burke and Nol 1998), and nest success (Poulin et al. 2010). Individual species respond differently to forest management alternatives, with mature forest species typically declining dramatically in abundance after clearcut logging, whereas gap specialists and aerial foragers often increase in response to partial harvest or tree cutting that leaves mature trees such as the selection system (Robinson and Robinson 1999; Rodewald and Yahner 2001; Holmes et al. 2004; Tozer et al. 2010). Selection system cutting that removes trees as scattered individuals (single-tree selection) or in small groups (group selection) at relatively short intervals can maintain late successional species within managed stands (reviewed in Vanderwel et al. 2007).

Many studies have experimentally examined the short- and long-term effects of selection system cutting on forest birds (e.g., Annand and Thompson 1997; Robinson and Robinson 1999; Harrison et al. 2005; Campbell et al. 2007; Vanderwel et al. 2007; Mahon et al. 2008), and most rely on species abundance to assess the impacts of forestry management because it is logistically difficult to find and monitor large numbers of nests to obtain productivity measures. Ideally, the assessment of postharvest habitat quality should also be based on nesting success and the production of independent juveniles as these demographic measures are critical for assessing population stability. For Brown Creepers (*Certhia americana* Bonaparte, 1838), an old forest specialist whose density is highly sensitive to partial harvest, seasonal reproductive success was lower in plots with single-tree selection harvesting than in control plots (Poulin et al. 2010). In the Ovenbird (*Seiurus aurocapilla* (Linnaeus, 1766)), a closed forest canopy species, density and productivity were both significantly higher in untreated forest plots than partially cut ones (Pérot and Villard 2009). However, nest survival across a variety of forest types and passerine species often does not vary significantly with level of tree retention (Tittler and Hannon 2000; Stuart-Smith and Hayes 2003) or between reference sites and different partial cut and clearcut treatments (King and DeGraaf 2000; Duguay et al. 2001; Bourque and Villard 2001; Gram et al. 2003).

The postfledging period, after the young leave the nest and before independence from parents, can be one of the most vulnerable life stages but is understudied in forest management research owing to the difficulty of quantifying fledgling survival. Several radio-tracking studies of forest songbirds have found that only half of fledglings, or fewer, survive to independence from their parents (Anders et al. 1997; King et al. 2006; Rush and Stutchbury 2008). Fledglings may experience high predation risk in disturbed landscapes (Rush and Stutchbury 2008) or require different habitat for survival and growth than that used for nesting (Anders et al. 1998; Cohen and Lindell 2004; King et al. 2006). In a managed boreal coniferous forest, radio-tagged fledgling Blackpoll Warblers (*Dendroica striata* (J. R. Forster, 1772)), but not Yellow-rumped Warblers (*Dendroica coronata* (Linnaeus, 1766)), were more likely to be observed in patches surrounded by high amounts of clearcut land (Mitchell et al. 2010). The only study of which we are aware that has examined fledgling survival in different forest treatments found that Rose-breasted Grosbeak (*Pheucticus ludovicianus* (Linnaeus, 1766)) fledgling survival did not differ significantly among

forest fragments that had been managed by single-tree selection, diameter-limit harvest, or reference sites (Moore et al. 2010).

Our objective was to assess how partial harvesting in a fragmented landscape in southern Ontario influenced the productivity of a Neotropical migratory songbird, the Hooded Warbler (*Wilsonia citrina* Boddaert, 1783). The Hooded Warbler breeds in deciduous forests of eastern North America and is a gap specialist, nesting in the understory of forest gaps and, less often, along forest edges (Evans Ogden and Stutchbury 1994). Hooded Warblers are federally listed as threatened in Canada because of their small population size and restricted distribution in southern Ontario, at the northern limit of their range (James 2000). Hooded Warblers are a model species for examining the effects of forest management on gap specialists, in part because their frequent and distinctive songs make the species easily detectable. Over time, canopy gaps created by partial harvests become densely vegetated, increasing the availability of habitat for Hooded Warblers (Robinson and Robinson 1999). For instance, Wallengord et al. (2007) found that Hooded Warblers were not present in uncut sites within large even-aged stands in Missouri, but within four years of cutting, density increased four- to five-fold in both clearcut areas and the 100 m buffer zones adjacent to clearcuts. Similarly, Heltzel and Leberg (2006) found that Hooded Warblers were uncommon in reference sites (>30 years after harvest) in Louisiana, but abundance doubled in sites with older partial harvests (12–18 years after harvest).

In this study, we examined two previously unexplored aspects of the effects of forest management on this gap specialist. First, unlike the studies above in which logging treatments were embedded within large forest tracts, our study took place in a highly fragmented landscape where regional forest cover averages less than 20%. The effect of forest management alternatives on a species may vary across landscapes due to differences in species abundance, predator communities, and area effects that result from fragmentation (Thompson et al. 1995; Vanderwel et al. 2007). Second, our study quantified how both nest survival and fledgling survival in Hooded Warblers varies among forest management treatments. An earlier study on Hooded Warblers in Pennsylvania found that although 38% of nests escaped predation, only 19% of fledglings subsequently survived to independence (Rush and Stutchbury 2008). We compared Hooded Warbler density, nesting success, and fledgling survival in forest fragments that had not been recently logged (reference sites), had been heavily cut (more than one-third of basal area (BA) removed, usually focused on the largest trees), or cut to a standard single-tree selection system prescription.

Methods

Study species and area

This study was conducted in collaboration with the Ontario Ministry of Natural Resources (OMNR) as part of a long-term study examining the effects of partial harvest methods in forest fragments in the Carolinian forest zone of Canada (Holmes et al. 2004; Smith et al. 2006; Moore et al. 2010). The landscape in this area is largely agricultural, with an average forest cover of approximately 17% (OMNR 2006),

and the majority of the remaining suitable hardwood forest is highly fragmented and privately owned. Forest fragments were chosen based on suitable logging history and the known presence of Hooded Warblers, which was established through preliminary surveys. We surveyed nine study sites in 2005 and added two sites in 2006; sites were spread across Norfolk, Elgin, and Middlesex counties in the deciduous forest region of southern Ontario (Fig. 1). The number of sites that we could monitor was limited by the restricted distribution of Hooded Warblers in the region, the number of forest fragments to which we had access, and the time-intensive monitoring needed to quantify fledgling survival. Fragments in which we monitored Hooded Warblers were 1–20 km apart and clustered into two different regions, and fragments size averaged 141 ha (range 47–260 ha). Forest cover within a 10 km radius of the forest fragments occupied by Hooded Warblers ranged from 17% to 32%. To verify that spatial autocorrelation of nest and fledgling survival was not a concern, we calculated Moran's I using ROOKCASE (Sawada 1999). We found no evidence of spatial autocorrelation of nest survival ($I = -0.0006$, $p = 0.63$) or fledgling survival ($I = -0.1236$, $p = 0.92$).

Study sites were categorized into one of three categories based on intensity of harvest as compared with Provincial single-tree selection silvicultural system guidelines (OMNR 2000): (i) reference sites ($n = 3$) that had not been harvested for at least 45, 40, and 22 years; (ii) standard cut sites ($n = 3$) that were assessed to have stand structures or records indicating that they had been cut according to OMNR guidelines for single-tree selection (OMNR 2000); and (iii) heavy cut sites ($n = 5$) that had more than the guideline of one-third of the BA removed, with three sites having been cut to diameter-limit regulations (e.g., all largest trees removed), one site cut to a shelterwood, and the final site representing a heavy single-tree selection cut (36% BA removed). Standard cut and heavy cut sites were logged between 1989 and 2001, and average time since harvest was 6–10 years.

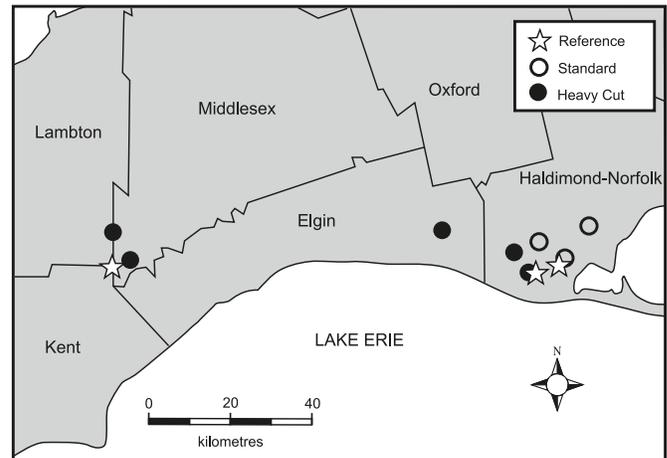
Density

We surveyed each fragment for the presence of Hooded Warblers every 2–4 days, starting in the first week of May and continuing until early August. In this region, Hooded Warblers occur at low density within forest fragments, but males sing frequently, allowing for rapid detection. The density of Hooded Warblers was determined using spot mapping of singing males in each fragment (e.g., Melles et al. 2009). Territorial males were identified throughout the breeding season, and the territory location was plotted on a map of each site. Density was calculated as the number of males detected divided by the search area size (number of males per hectare). An average of 120 h was spent in each site per season conducting spot-mapping observations in conjunction with nest searching and fledgling observations.

Nest and fledgling monitoring

Nesting productivity is potentially high as females can produce multiple broods per summer. Young fledge 8 to 10 days after hatching but are dependent on parents for another 3–4 weeks (Evans Ogden and Stutchbury 1994). We searched all male territories for nests from mid-May to early August, and located nests were monitored every three days until com-

Fig. 1. Location of forest fragments in southwestern Ontario occupied by Hooded Warblers that were reference sites ($n = 3$) and those that had received a standard selection system harvest ($n = 3$) or a heavy cut harvest ($n = 5$).



pletion. The number of eggs and (or) nestlings, Brown-headed Cowbird parasitism, parental activity, time of visit, and the date were recorded for each nest visit. Nests that fledged at least one Hooded Warbler young were considered successful. Adults were captured with mist nets, and young were banded at the nest on day 6 of the nestling stage with one U.S. Geological Survey aluminum band and a unique combination of three color bands.

Productivity

Nest productivity estimates were based on cumulative nest survival rates, number of young fledged per successful nest, and number of nesting attempts per season (Anders et al. 1997). We assumed a maximum of two successful broods per season and up to two re-nesting attempts, which is typical of this species at the northern extreme of its breeding range. Cumulative nest survival rates were taken from our nest survival analysis. The average number of young fledged per successful nest was calculated for each treatment based on nest-monitoring data. We calculated average season-long nest productivity per female using the probability of different nest fates (e.g., successful on first and second nest, failed on first and second nest, successful on final nest).

Fledgling survival

Although fledgling Hooded Warblers and parents are highly vocal, making it possible to monitor family groups after fledging (Evans Ogden and Stutchbury 1997), we used radiotelemetry of parents (2005; Rush and Stutchbury 2008) and fledglings (2006) to more accurately estimate fledgling survival. In 2005, we radio-tracked only male parents because female Hooded Warblers often double brood, leaving the male to care for the brood (Evans Ogden and Stutchbury 1997). Radio transmitters were attached with the figure-eight leg loop harness (Rappole and Tipton 1991). We fit the males with 0.51 g transmitters (model BD-2N, Holohil Systems, Carp, Ontario, Canada), which have a range of detection of about 500 m in a forested landscape. We located radio-tagged males every three days with receivers (model TRX-1000S, Wildlife Materials, Carbondale, Illinois, USA)

Table 1. Mean (\pm standard error (SE)) of habitat characteristics of forest fragments with different logging treatments in southern Ontario.

Habitat variable	Heavy cut (<i>n</i> = 5)		Standard cut (<i>n</i> = 3)		Reference site (<i>n</i> = 3)		<i>F</i>	<i>p</i> value
	Mean	SE	Mean	SE	Mean	SE		
Fragment size (ha)	108.1	28.9	127.7	43.4	208.9	33.7	2.27	0.16
Canopy cover (%)	53.5a	4.1	64.8b	3.5	72.2b	4.3	6.23	0.0027
BA (m ² /ha)	21.1a	1.2	23.9ab	1.2	28.5b	1.2	8.9	0.0003
Sapling cover (%)	23.2a	2.8	19.6a	2.4	8.5b	0.9	8.09	0.0005
Shrub–seedling cover (%)	14.5	2.4	19.4	2.5	18.8	3.2	0.69	0.50
Regeneration cover (%)	14.4	2.0	18.2	2.4	11.5	2.3	2.08	0.13
No. of shrubs <2.5 cm DBH	49.9	5.2	65.8	5.6	55.1	4.9	2.09	0.12
Average distance to closest tree (m)	5.2	0.3	5.2	0.2	4.8	0.2	0.74	0.48
Distance to edge (m)	140.8a	12.7	183.9b	12.9	175.0a,b	14.5	3.17	0.046
Distance to gap (m)	5.17a	0.8	6.2a	0.9	9.6b	1.3	4.8	0.01

Note: *p* values are given for nested ANOVAs, and letters indicate a significant difference between treatments using Tukey's post-hoc test. BA, basal area; DBH, diameter at breast height.

with hand-held three-element Yagi antennae. We observed the family group for 2 h or until each fledged young (located by conspicuous begging calls) was identified by color bands. If no young were encountered, two additional 1 h observation periods were conducted on the following two days to reconfirm that all missing fledglings were still absent (and presumed dead) and not being fed elsewhere by the female. We determined the fate of 38 fledglings, and each fledged young from a family was treated as an individual observation. To validate our assumption that each fledged young could be treated as statistically independent, we used a chi-square goodness-of-fit test to evaluate if the distribution of mortalities was random among broods, according to methods described in Schwartz et al. (2006).

In 2006, we fit nestlings with 0.42 g transmitters (model LB-2N, Holohil, Carp, Ontario, Canada) that had been modified by reducing power output for longer battery life (three weeks) and by cutting the length of the antenna in half (7 cm) to minimize interference with fledgling movement. The transmitter was attached to one randomly selected nestling (brood size ranged from one to five nestlings). The range of detection was approximately 300 m in wooded areas, which was much greater than the average distance that fledglings moved between observation periods (68.2 ± 3.6 m, mean \pm SD). Tagged fledglings (*n* = 27) were tracked every two days to determine their fate. The mobility of tagged young appeared comparable with that of the untagged young from the same brood. Young were considered dead if their remains or a damaged transmitter was recovered or if the radio signal was absent and the dependent young could not be found with the family group (e.g., being fed by parents). Lost signals were most likely due to predators removing the fledgling along with the radio transmitter from the site.

Habitat sampling

To characterize habitat structure of logging treatments, we measured vegetation at 10–20 random plots within each site. Plots were chosen by randomly selecting a point on a 100 m \times 100 m grid placed over the entire search area of the site and from that point going in a random direction and distance (<100 m). Logged sites had less canopy cover and BA but more sapling cover compared with reference sites (Table 1). We also measured habitat at nest sites and at

fledgling locations. For each family group, fledgling resightings were broken up into three age classes (1–5, 6–10, and 11+ days after fledging), and vegetation was measured at one randomly chosen resighting location per age class.

Vegetation surveys were done according to established OMNR protocol using 5 m radius plots (e.g., Smith et al. 2006). For all vegetation plots, we measured number of deciduous shrubs < 2.5 cm DBH (diameter at breast height), percentage cover of shrubs or seedlings (woody stems < 0.5 m high), regeneration (woody stems 0.5–1.3 m high), saplings (woody stems > 1.3 m high and < 2.49 cm DBH), small trees (> 1.3 m high and < 10 cm DBH), and canopy (>10 m high), average distance to closest tree (based on measurements from each of the four cardinal directions), distance to closest edge, BA, distance to closest canopy gap, and size of the closest canopy gap. At nest sites, we also measured nest height and nest concealment. To calculate nest concealment, the percentage of the nest concealed was visually estimated at nest height level from the four cardinal directions, as well as from above the nest, and the average of all five estimates was taken. We used a factor 2 m wedge prism for timber cruising to calculate BA, and at each plot, the prism was used to determine which trees were “in” and the number was multiplied by 2 to determine the BA of that point. To calculate canopy gap size, we measured longest diameter and the widest point perpendicular to the length, and then used the formula for an ellipse (area = π ·length·width/4; Runkle 1981).

Survival analysis

Daily nest and fledgling survival rates were estimated using the nest survival model in program MARK (White and Burnham 1999). The nest survival model is used for modeling known-fate data and requires information on when the individual was first observed (i.e., when the nest was found or the date of fledging), when the individual was last observed alive, and whether the individual survived or died. We were interested primarily in how logging treatment affects nest and fledgling survival. For nest survival analysis, we also examined other variables likely to influence survival including nest age, the presence or absence of Brown-headed Cowbirds in the nest, date of start of incubation, year, site size, and vegetation characteristics near the nest that could affect exposure to predators (nest height, understory cover, average dis-

Table 2. Model selection results from program MARK for nest survival of Hooded Warblers.

Model	<i>K</i>	AIC _c	ΔAIC _c	<i>w_i</i>
Age + BHCO	3	571.81	0.00	0.187
Age	2	572.19	0.38	0.154
Age + BHCO + date	4	573.74	1.93	0.071
Age + BHCO + fragment size	4	573.76	1.95	0.070
Age + BHCO + year	4	573.81	2.00	0.069
Age + date	3	574.85	2.26	0.060
Age + fragment size	3	574.14	2.33	0.058
Age + year	3	574.17	2.36	0.057
Age + treatment + BHCO	5	575.62	3.81	0.027
Age + BHCO + date + fragment size	5	575.68	3.87	0.027
Age + BHCO + date + year	5	575.75	3.94	0.026
Age + year + BHCO + fragment size	5	575.76	3.96	0.025
Age + date + year	4	576.03	4.22	0.022
Constant survival	1	576.42	4.61	0.018
BHCO	2	576.51	4.70	0.017
BHCO + date	3	576.84	5.03	0.015
Vegetation + age	7	577.22	5.42	0.012
Treatment + age + year + BHCO	6	577.62	5.81	0.010

Note: *K*, number of estimable parameters in the model; AIC_c, Akaike's information criterion corrected for small sample sizes; ΔAIC_c, difference in AIC_c value from that of the best model; *w_i*, Akaike weight indicating relative support for the model. A total of 30 a priori models incorporated treatment (standard cut, heavy cut, or reference site), fragment size (size of forest fragment), vegetation (nest height, understory cover, average distance to closest tree, distance to edge, and size of closest gap), age of nest, date (start date of incubation), year, brood size (total number of fledglings in the brood), and BHCO, presence or absence of a Brown-headed Cowbird in the nest. Only model results with Akaike *w_i* ≥ 0.01 are shown here.

tance to closest tree, distance to edge, and size of closest gap). For fledgling survival, in addition to logging treatment, we considered the effect of fledge date, year, and site size.

To compare the a priori candidate models, we used Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). We calculated normalized Akaike weights (*w_i*) for each model and model averaged all substantially supported models (ΔAIC_c ≤ 2; Burnham and Anderson 2002) to quantify parameter estimates and unconditional standard errors. Parameter estimates with 95% confidence excluding zero were considered to be influential. We also calculated the odds ratio (OR) and relative importance (Σ*w_i*) for each parameter.

Daily survival rates were calculated by back-transforming the model-averaged logit equation. We calculated the cumulative nest survival and cumulative three-week postfledgling survival from the model-averaged product (based on a 21-day nest period and a 21-day fledgling period). We present cumulative survival rates for average case scenarios.

Habitat analysis

To determine which, if any, habitat variables best discriminate between nesting and fledgling habitat, we used logistic regression (PROC LOGISTIC). Odds ratios were examined for each habitat variable to identify the probability of a nest site versus a fledgling location given the habitat characteristics. We ran preliminary univariate tests to identify habitat variables with *p* values ≤ 0.25 to include in further multivariate analysis. We also tested for multicollinearity and found that no variables exceeded *r* ≥ 0.7. We assessed the goodness of-fit test, and in all cases, the data fit the model well. We developed a set of 20 a priori models using combinations of the variables of interest and conducted model selection and

model averaging using AIC_c following the same strategy used for survival analysis. Statistical analysis was performed using SAS 9.1 (SAS Institute Inc. 2002).

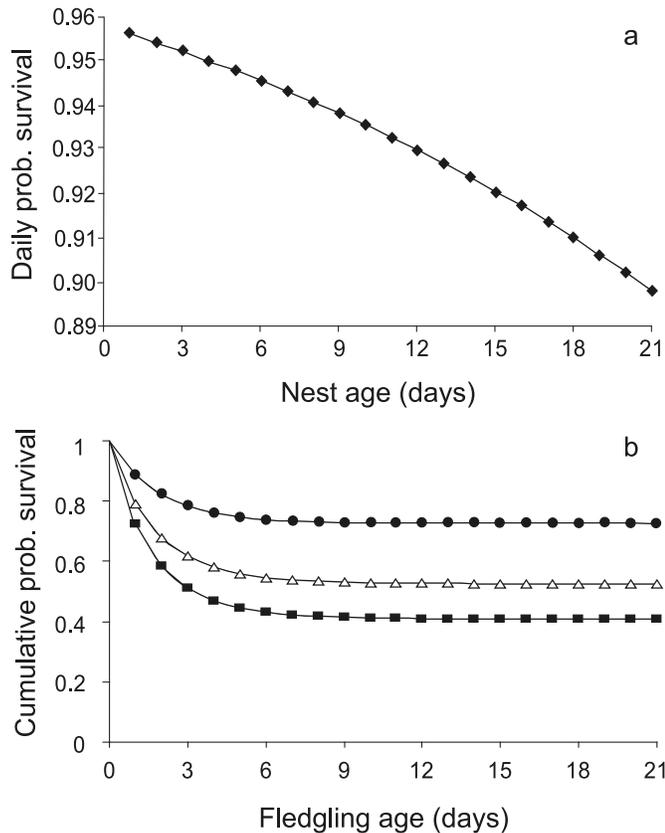
Results

Density and nest survival

Density of male Hooded Warblers did not differ between years ($F_{[1,19]} = 0.31, p = 0.584$), so data for both years were combined. Density was higher in standard cut (0.20 ± 0.01 males/ha) than in heavy cut (0.15 ± 0.02) or reference sites (0.11 ± 0.02), but the difference was not significant ($F_{[2,8]} = 2.08, p = 0.187$).

We determined the fate of 157 Hooded Warbler nests that were monitored for a total of 1716 exposure days across a 100-day interval (20 May – 27 August). Overall, 56 nests (36%) survived, and the primary cause of nest failure was predation (81% of 101 failed nests) followed by Brown-headed Cowbird parasitism (16%) and nest abandonment (3%). The proportion of nests that failed was not significantly influenced by logging treatment (heavy cut, 36/53; standard cut, 30/50; reference, 35/54; $\chi^2_2 = 1.21, p = 0.547$). Nest survival was best explained by models that incorporated the effects of nest age (Table 2; model averaged $\beta_{\text{age}} = -0.045$, 95% CI = $-0.080, -0.010$; OR = 0.956, 95% CI = 0.923, 0.990), and all of the strongly supported models (ΔAIC_c ≤ 2) included nest age (Fig. 2a). The model-averaged cumulative 21-day nest survival probability was 0.22 ± 0.02 . Three of the four top models also included Brown-headed Cowbird parasitism (model averaged $\beta_{\text{BHCO}} = -0.329$, 95% CI = $-0.744, 0.087$; OR = 0.720, 95% CI = 0.475, 1.091). Logging treatment and nest vegetation were not a component of any well-supported survival models (Table 2).

Fig. 2. (a) Model-averaged daily probability (prob.) survival versus nest age for Hooded Warblers and (b) cumulative probability of fledgling survival in heavy cut (circles) and standard cut (squares) treatments and reference sites (triangles).



The proportion of nests parasitized by Brown-headed Cowbirds was significantly higher in heavy cut and standard cut sites (49% and 42%, respectively) than in reference sites (24%; $\chi^2_2 = 7.14$, $p = 0.028$). Although 75% (44/59) of parasitized nests fledged at least one Hooded Warbler, Brown-headed Cowbirds significantly decreased the average number of warbler young that fledged from successful nests (unparasitized, 3.19; parasitized, 1.73; $t_{[54]} = 5.41$, $p < 0.0001$). As a result, logging treatment had a significant effect on number of young fledged per successful nest ($F_{[2,46]} = 5.85$, $p = 0.005$), with reference sites producing more Hooded Warbler young/successful nest than standard cut sites (Tukey $p = 0.004$; standard cut = 2.53 ± 0.26 , $n = 35$; heavy cut = 2.76 ± 0.28 , $n = 36$; reference = 3.10 ± 0.23 ; $n = 30$). Season-long nest productivity, given observed probabilities of nest failure and double brooding, was 2.06 young fledged per female in standard cuts, 2.22 in heavy cuts, and 2.44 in reference sites.

Fledgling survival and habitat selection

We determined the fate of 65 fledglings for 668 exposure days over a 69-day interval (15 June – 22 August). Just over half ($33/65 = 51\%$) of tracked fledglings survived to the end of the tracking period (21 days after fledging). Overall, fledgling mortality was 29% in heavy cuts ($n = 21$), 63% in standard cuts ($n = 19$), and 56% in reference sites ($n = 25$). Mortality appeared to have been caused by predation, with

no evidence of starvation or of radio transmitter harness entanglement. Parents typically split the brood upon fledging (Evans Ogden and Stutchbury 1997), and young from the same brood were often in separate locations. In 2005 when family groups were monitored, survival of individual fledglings within a brood was independent ($\chi^2_{10} = 6.921$, $p = 0.733$), and it was uncommon for all of the young within a nest to have the same fate. There were no instances in which all of the young within a brood died on the same day, which would have suggested a single predation event.

All fledgling deaths occurred within the first six days after fledging, and the most important predictor of fledgling survival was age ($\Sigma w_i = 1.0$; Fig. 2b); there was nearly no support for models that did not include age as a predictor (Table 3). Models with logging treatment had moderate support ($\Sigma w_i = 0.67$), and the cumulative probability of survival was higher (0.73; Fig. 2b) in heavy cut sites compared with reference (0.53) and standard cut (0.41) sites, although the difference was not significant because the 95% confidence intervals overlap zero ($\beta_{\text{heavy cut}} = 0.733$, 95% CI = -0.613 to 2.079 ; OR = 2.082, 95% CI = 0.542, 7.999; $\beta_{\text{standard cut}} = -0.360$, 95% CI = -1.410 to 0.689 ; OR = 0.697, 95% CI = 0.244, 1.992). The model-averaged 3-week post-fledging cumulative survival was 0.57. Models including fragment size had relatively low support ($\Sigma w_i = 0.39$). There was no significant year effect, which would be expected if radio-tracking negatively affects fledgling survival. Season-long productivity of independent fledglings, given estimated nestling production and survival probability of fledglings, ranged from 0.84 to 1.62 fledglings/female across sites (Table 4).

We compared fledgling habitat with the nest site habitat to evaluate habitat use by fledglings. Regeneration and sapling cover, as well as distance to closest tree, were important for distinguishing nesting from fledgling habitat (Table 5). After leaving the nest, fledglings tended to move away from areas with shorter regeneration cover (nest sites = $43.50\% \pm 2.17\%$ regeneration cover, fledgling sites = $33.69\% \pm 2.31\%$ regeneration cover; OR = 0.767, 95% CI = 0.660, 0.891) and into areas with more sapling cover (nest sites = $17.79\% \pm 1.09\%$ sapling cover, fledgling sites = $26.27\% \pm 1.80\%$ sapling cover). For each 10% increase in sapling cover, fledglings were 1.57 times more likely to be found than a nest (95% CI = 1.283, 1.925). Fledglings were also found in sites where the trees were more spaced out than at nest sites (average distance to closest tree for nest sites = 5.14 ± 0.14 m, for fledgling sites = 6.03 ± 0.22 m; OR = 1.269, 95% CI = 1.079, 1.492).

Discussion

Most studies of the effects of partial harvest on bird populations have found a strong effect on abundance or density for many species (reviewed in Vanderwel et al. 2007). In this study, Hooded Warbler density was almost twice as high in standard cut sites (0.20 males/ha) than in reference sites (0.11/ha), but the difference was not significant owing to low statistical power. Hooded Warblers are a gap specialist, which explains the relatively high density in partially harvested forest fragments with artificially created gaps (Gram et al. 2003). Male density in our logged sites was comparable

Table 3. Model selection results (for models with Akaike $w_i \geq 0.01$) from program MARK for fledgling survival of Hooded Warblers.

Model	K	AIC _c	Δ AIC _c	w_i
Age + treatment	4	144.57	0.00	0.28
Age + fragment size	3	145.21	0.64	0.21
Age + treatment + fragment size	5	145.71	1.14	0.16
Age	2	146.31	1.74	0.12
Age + treatment + date	5	145.59	2.02	0.10
Age + treatment + year	5	146.60	2.03	0.10
Global model (age + treatment + date + year + fragment size)	7	149.71	5.14	0.02

Note: K , number of estimable parameters in the model; AIC_c, Akaike’s information criterion corrected for small sample sizes; Δ AIC_c, difference in AIC_c value from that of the best model; w_i , Akaike weight indicating relative support for the model. A total of 13 a priori models were run that included fledgling survival probability, treatment (standard cut, heavy cut, or reference site), fragment size (size of forest fragment), age, date (date of fledging), and year.

Table 4. Productivity measures (mean \pm standard error) for Hooded Warblers breeding in forest fragments in southern Ontario that received heavy or standard cuts or were not recently logged (reference site).

Variable	Heavy cut	Standard cut	Reference site
Density (no. of males/ha)	0.15 \pm 0.02	0.20 \pm 0.01	0.11 \pm 0.02
Nest survival probability (three weeks) ^a	0.22	0.22	0.22
No. of young fledged per successful nest	2.76 \pm 0.28	2.53 \pm 0.26	3.10 \pm 0.23
Estimated no. of young fledged per female per breeding season ^b	2.22	2.06	2.44
Postfledging survival probability (three weeks) ^c	0.73	0.41	0.53
Estimated no. of independent fledglings per female per breeding season	1.62	0.84	1.28

^aEstimated from program MARK (Table 2).

^bEstimated from probability of different nest fates and number of fledged nestlings produced per successful nest.

^cEstimated from program MARK (Table 3).

Table 5. Mean (\pm standard error) of habitat characteristics for nest and fledgling locations, and statistical comparison to evaluate habitat use by fledglings.

Habitat variable	Nest sites	Fledgling sites	Nest vs. fledgling habitat		
			β	OR	Σw_i
Shrub–seedling cover (%)	35.3 \pm 2.0	25.2 \pm 2.0	-0.007 (-0.022, 0.009)	0.937 (0.801, 1.096)	0.275
Regeneration cover (%)	43.5 \pm 2.2	33.7 \pm 2.3	-0.027 (-0.042, -0.012)*	0.767 (0.66, 0.891)	1
Sapling cover (%)	17.8 \pm 1.1	26.3 \pm 1.8	0.045 (0.025, 0.065)*	1.572 (1.283, 1.925)	1
Small tree cover (%)	12.4 \pm 0.9	17.7 \pm 1.3	0.024 (-0.001, 0.050)	1.277 (0.992, 1.643)	0.674
Canopy cover (%)	52.4 \pm 1.9	45.3 \pm 2.5	-0.009 (-0.023, 0.005)	0.915 (0.796, 1.051)	0.421
Average distance to closest tree (m)	5.1 \pm 0.1	6.0 \pm 0.2	0.238 (0.076, 0.400)*	1.269 (1.079, 1.492)	0.991
No. of shrubs < 2.5 cm DBH	97.9 \pm 7.4	89.3 \pm 6.9	—	—	—
BA (m ² /ha)	22.3 \pm 0.6	20.8 \pm 0.8	—	—	0.176
Distance to edge (m)	157.6 \pm 6.8	171.2 \pm 7.4	—	—	—
Distance to gap (m)	3.1 \pm 0.4	2.6 \pm 0.3	—	—	—
Gap size (m ²)	334.1 \pm 33.4	413.9 \pm 33.6	0.0003 (-0.001, 0.001)	1.014 (0.975, 1.055)	0.144

Note: Model averaged β estimates (95% CI) for habitat variables included in models with Δ AIC_c \leq 2. Asterisks indicate model parameters with 95% confidence interval limits that do not include zero and were considered to be influential, and dashes indicate variables that were not included in any of the supported models (Δ AIC_c \leq 2). The odds ratio (95% CI) is the ratio of the odds of an event occurring in one group (nest site location) to the odds of it occurring in another group (fledgling location). Odds ratios are with respect to an increase of 10% in vegetation cover, 1 m in distance to closest tree, and 50 m² gap size. The relative importance (Σw_i) is the total weight of all models that contain the habitat variable. OR, odds ratio; BA, basal area; DBH, diameter at breast height.

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with that found in large managed forests in Missouri after cutting (12–14 males/100 ha; Wallendorf et al. 2007). Our reference sites had a higher male density compared with other studies, likely because our sites were forest fragments rather than unmanaged sites within a large contiguous forest. Our study took place 6–10 years after harvest, and it is not known how long after harvest high warbler density would persist (Robinson and Robinson 1999).

Old-forest and closed-canopy specialists have both low density and low reproductive success in partial harvest sites (Pérot and Villard 2009; Poulin et al. 2010), but many species experience little impact on nesting success (e.g., Rodewald and Yahner 2001; Gram et al. 2003). In our study, the cumulative nest survival probability (0.22) was lower than in other Hooded Warbler populations (0.32–0.47; Moorman et al. 2002; Rush and Stutchbury 2008). The proportion of Hooded Warbler nests that failed was similar for reference and logged sites (60%–68%), and nest survival models that included logging treatment had little support. Forest fragmentation and small fragment size increases Brown-headed Cowbird densities, and nest parasitism on songbirds and can have a big impact on productivity for many host species (Robinson et al. 1995; Howell et al. 2007). Parasitism rate by Brown-headed Cowbirds in logged sites was approximately double that in reference sites, and nest survival models that included brood parasitism had relatively high support (Table 2). Productivity measured as the number of young fledged per female ranged from 2.06 to 2.44 across sites and was significantly higher in reference sites than in recently logged sites. Although density of this gap specialist was highest in logged sites, these sites apparently offer no benefit in terms of reduced predation risk or increased fledgling production in successful nests. Instead, there is a cost to productivity as a result of high Brown-headed Cowbird parasitism. Similarly, small fragment size in northern Pennsylvania lowered nest productivity of Hooded Warblers via higher Brown-headed Cowbird parasitism rather than higher nest predation (Rush and Stutchbury 2008). In a forested landscape in South Carolina, female Hooded Warblers nesting near clearcut edges versus group selection edges had similar nest predation rates but experienced a higher risk of Brown-headed Cowbird parasitism, reduced clutch size, and fewer fledglings per successful nest (Moorman et al. 2002). These studies suggest that productivity of gap specialists in managed forests may be influenced more by Brown-headed Cowbird responses to habitat disturbance than by predator responses.

Several studies of forest songbirds have shown that fledgling movements (Vitz and Rodewald 2006; Mitchell et al. 2010) and survival (King et al. 2006) are associated with dense understory and regenerating clearcuts, likely as a result of greater cover from predators and increased food supply. We found that heavy cut sites tended to have higher fledgling survival (Fig. 2) compared with reference sites, and that productivity of independent Hooded Warbler young was 26% greater. However, standard cut sites tended to have lower fledgling survival probability than reference sites even though there was more cover. These differences were not statistically significant, and although difficult to achieve in fledgling survival studies, larger samples sizes and more years of study would be necessary to confirm these patterns. Given that standard cut sites had the highest density but low-

est per-capita production of nestlings and independent fledglings (Table 4), our results suggest that Hooded Warblers could experience an ecological trap in response to partial harvest (e.g., Gates and Gysel 1978; Weldon and Haddad 2005). Testing for an ecological trap would require demonstrating that the standard selection sites are population sinks but are preferred during habitat selection and have earlier male arrival dates, earlier first egg dates, and a greater proportion of older birds (Weldon and Haddad 2005).

In a stable population, recruitment (fecundity \times annual juvenile survival) equals adult mortality (Pulliam 1988), and on average, a breeding female will replace herself in her lifetime with a daughter that survives to breed. Hooded Warbler populations in southwestern Ontario forest fragments do not appear to be producing young at replacement levels, regardless of logging treatment. Productivity ranged from 0.42 to 0.81 independent female fledglings per female per season across treatments (Table 4; assuming equal sex ratio in fledglings). Empirical estimates of annual juvenile survival are rare for songbirds (Gardali et al. 2003), but estimates of annual adult survival rates typically range from 0.4 to 0.6 in forest-breeding Neotropical migrant passerines (e.g., Desante et al. 1995; see also Moore et al. 2010). Juvenile survival during migration and on the wintering grounds is likely lower for juveniles than adults due to competition for winter territories (Stutchbury 1994). Assuming that annual juvenile survival is similar to the lower value (0.4) for adult survival, female Hooded Warblers in this landscape produced 0.17–0.32 recruiting daughters per year across treatments, which is lower than the expected annual mortality of adult females (0.4–0.6) and suggests that forest fragments in this region are population sinks.

Fledgling survival probability to independence was 0.51 in this study, intermediate to other studies of forest songbird species (0.40–0.62; Anders et al. 1997; King et al. 2006; Schmidt et al. 2008; Moore et al. 2010). Survival probability of fledglings in our study was lowest the first five days out of the nest and then remained high the next two weeks. Higher mortality during the first week after fledging has been consistently documented in other studies of juvenile passerines (Anders et al. 1997; King et al. 2006; Rush and Stutchbury 2008; Moore et al. 2010). The increase in fledgling survival probability with age was likely the result of their increased mobility, which increases their ability to escape from predators. Unlike nestlings, fledglings are not in a fixed location and parents may use habitats for feeding fledglings that reduce detection by predators (King et al. 2006; Mitchell et al. 2010; Moore et al. 2010). In our study, fledglings were located in areas with heavier sapling cover but less regeneration cover compared with nest sites, which likely results from the placement of nests low (<1m) in the understory, whereas fledglings seeking cover are not restricted to this strata.

Conclusions

We found that predation on Hooded Warbler nests and fledglings was high regardless of silvicultural practices within the forest fragment, likely because of low regional forest cover. Nest and fledgling survival probability depends on the types and abundance of predators (Schmidt et al. 2008),

and these predators are common in forests fragmented by agriculture (Keyser 2002; Rodewald and Yahner 2001). A clear forest management recommendation for Hooded Warblers remains elusive for this region because (i) nest and fledgling survival did not differ significantly across treatments and (ii) standard cut sites tended to have the highest density but also the lowest nest productivity due to Brown-headed Cowbird parasitism. It is possible that partial harvesting creates an ecological trap by attracting both Hooded Warblers and Brown-headed Cowbirds, but this requires demonstrating that Hooded Warblers preferentially select recently logged sites over reference sites during habitat settlement.

A complication for forest management decisions is that forest-breeding species respond differently to a particular harvest method and a species' response can vary across different landscapes (Gram et al. 2003; Holmes and Pitt 2007; Mitchell et al. 2010). In the same study area, nest monitoring and radio-tracking of Rose-breasted Grosbeaks also found that logging treatment did not predict nest survival (Smith et al. 2006) or fledgling survival (Moore et al. 2010). Although predation on Hooded Warblers and Rose-breasted Grosbeaks was not strongly affected by logging treatment, there are other forest birds that are more sensitive to partial harvest (Bourque and Villard 2001; Pérot and Villard 2009; Poulin et al. 2010). One would expect fledgling survival in species associated with old forest (e.g., Brown Creeper) or closed-canopy forest (e.g., Ovenbird) to be negatively impacted by partial harvesting, exacerbating the negative effects on density and nesting success already documented.

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