

Special section

Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*)

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Abstract

Patterns of habitat use by some passerines change after the young leave the nest, and thus our understanding of habitat selection derived from counts of singing males earlier in the nesting cycle may not adequately represent the breeding habitat requirements of these species. Post-fledging changes in habitat use may have important conservation implications if the survival of fledglings is affected by characteristics of the habitat; however, there have been relatively few systematic studies of the post-fledging ecology of forest passerines and, of these, even fewer have incorporated analyses of the relationship between habitat characteristics and fledgling survival. We studied the post-fledging habitat selection and survival of ovenbirds *Seiurus aurocapilla* in northern New Hampshire, USA during two breeding seasons using radio telemetry. Habitat at sites used by radio-marked fledgling ovenbirds was characterized by fewer large trees and greater vertical structure 0–3 m above ground than ovenbird nest sites. Similarly, habitat at sites used by fledgling ovenbirds was characterized by fewer large trees and greater vertical structure than unused sites. Most (80%) of the 15 mortalities that we observed were due to predation. Nine (70%) of these occurred within the first 3 days of fledging, resulting in a significant drop in survival during this period. Fledgling survival increased significantly with increased vegetation structure. Our observations that fledgling ovenbirds are selective in their habitat use, that they select different habitat features than adult ovenbirds select for nesting and that fledgling survival is positively associated with these habitat features suggest that the use of habitat models based on counts of singing males before fledging does not adequately represent the habitat needs of this species. Conceivably, mortality during the post-fledging period could limit recruitment to levels insufficient to maintain the viability of ovenbird population even if adequate nesting habitat were available.

Introduction

Since David Lack noted that 'the mortality of the young has not been measured in any nidicolous species, but it is probably heavy' (Lack, 1954), numerous studies have been conducted on birds during this period. Studies of parids (Dhondt, 1979; Perrins, 1980; Naef-Daenzer, Widmer & Nuber, 2001), the European blackbird *Turdus merula* (McGrath, 1991), the yellow-eyed junco *Junco phaeonotus* (Sullivan, 1989) and the Florida scrub jay *Aphelocoma c. coerulescens* (Woelfenden, 1978) all indicate that mortality is indeed heavy during this period.

One aspect that is almost entirely lacking from these studies is the habitat use of fledgling birds during the period between leaving the nest and independence, and its relationship to

survival. The reason for this oversight is probably related to the fact that until relatively recently, studies of this nature had to rely on capture–recapture models of birds banded as nestlings; hence opportunities to resight juvenile birds and evaluate their habitat use were limited. This has changed with the development of lightweight radio transmitters, which have permitted a quantum leap in our understanding of the ecology of bird species during this period. To illustrate the potentially immense importance of post-fledging habitat to conservation, one need only reflect on the extreme example of marsh-nesting barn owls *Tyto alba* in the eastern United States in which offshore nesting boxes were favored because of the virtual absence of nest predation, until it was discovered upon further examination that nearly 75% of the radio-marked young were drowning soon after fledging (Bendel & Therres, 1993)!

The provision of adequate breeding habitat is important in efforts to conserve bird populations. Patterns of habitat selection by nesting adults of many bird species are relatively well understood; however, recent studies indicate that the habitat preferences of some forest birds change after the young fledge from the nest. For example, studies indicate that wood thrush fledglings move from nest sites in mature forest into stands of dense vegetation in which they stay for extended periods of time until they migrate (Anders, Faaborg & Thompson, 1998; Vega Rivera *et al.*, 1998). Moreover, fledgling survival rates are relatively low during the time period between fledging and when they reach these areas with dense vegetation, but increase dramatically thereafter (Anders *et al.*, 1997). This last point is especially important in light of studies suggesting that bird populations are particularly sensitive to mortality during the post-fledgling period (Perrins, 1980; Kurzejeski & Vangilder, 1992), suggesting that this parameter has a potentially important influence on population dynamics in at least some bird species.

Clearly, more information is needed on patterns of post-fledgling habitat use and its influence on fledgling survival to conserve bird populations effectively (Verner, 1992). To fill this pressing information need, we initiated a study on the post-fledgling ecology of the ovenbird *Seiurus aurocapilla* using radio telemetry. Our objectives were to (1) compare the nesting and dispersal habitats of fledgling ovenbirds, (2) compare the habitat characteristics of fledgling ovenbirds with unused habitats at both the stand and landscape level and (3) analyze the influence of habitat characteristics on the survival rates of fledgling ovenbirds.

Study area and methods

We selected the ovenbird *S. aurocapilla*, a Paruline warbler, as a study subject. The ovenbird breeds throughout much of eastern and central North America, but winters in the Antilles and Mexico as far south as northern South America. Thus, the ovenbird is a Neotropical–Nearctic migrant, a class of birds that has been the focus of substantial conservation concern in recent years (Rappole, 1995).

This study was conducted during May–July 1999 and 2000 on the USDA Forest Service Bartlett Experimental Forest in Carroll County, New Hampshire (44°04'N, 71°17'W). Elevations in the area range from 200 to 600 m above sea level. The area is characterized by warm wet summers and cold winters with deep snow. The landscape surrounding the study area is extensively forested, with only about 10% of the forest in early regeneration < 15 years old. The forest in the study area consisted of northern hardwoods dominated by sugar maple *Acer saccharum*, American beech *Fagus grandifolia* and yellow birch *Betula alleghaniensis*.

Ovenbirds typically arrive on our study sites in mid-May. Male ovenbirds sing from the lower canopy, and both males and females typically forage on the ground (Hann, 1937). Ovenbirds nest on the ground, and raise a single brood of 3–5, which typically leave the nest by mid-June to early July. Females alone build the nests and incubate; however, both

males and females care for the young in the nest and after fledging. Ovenbirds start leaving the study area in late July and August.

Nests were located by following females carrying nesting material or food, or returning to nests to incubate after bouts of foraging, or by directed searching. Fledglings were removed from the nest the day before fledging, judged on the basis of days since hatching and feather development, and fitted with 1.0 g radio transmitters (Holohil Systems Ltd, Carp, ON, Canada) using the harness design of Rappole & Tipton (1991). Radios weighed *c.* 6% of a fledgling's weight. We were unable to discern any difference in mobility or behavior between our radioed birds and the numerous unmarked fledglings we have observed in 4 years of research on ovenbirds, and radios weighing this proportion of a bird's weight do not appear to affect significantly the behavior of juvenile wood thrushes (Anders *et al.*, 1998; Vega Rivera *et al.*, 1998) or of adult hooded warblers *Wilsonia citrina* (Neudorf & Pitcher, 1997).

Fledglings were located on foot *c.* every 3 days using a 12-channel receiver and a two-element Yagi antenna. All locations were confirmed by visual contact. Radios had a battery life of *c.* 60 days and a range of 500–2000 m from the ground and 4–5 km from the air. If we were unable to locate signals from the ground, we attempted to locate them by conducting systematic searches from automobiles. Searches for birds for which signals were missing were conducted periodically for the rest of the duration of the study. In addition, during the 2000 field season we searched the surrounding area by aircraft by making concentric circles of increasing radius over the study area to a maximum radius of 5 km, and calculated that, from our elevation of *c.* 1000 m, we would have been able to detect any active transmitters within 10 km of the study site. The location of each individual was recorded using a global positioning system (GPS) system by averaging 100 readings. Readings were not base-station corrected; however, previous trials with the GPS at known locations indicated that our readings were accurate to within 20 m, well below the pixel size of the remote sensing data we used (see below).

Large deciduous trees, deep leaf litter and open understory structure are habitat characteristics consistently associated with the distribution of nesting ovenbirds (Van Horn & Donovan, 1994; King & DeGraaf, 2000). Therefore, we measured these habitat variables on 0.04-ha circular plots at every other point where fledgling ovenbirds were located as well as at an additional point located at a random distance and direction between 25 and 100 m from the fledgling location using a modified James & Shugart (1970) technique. Basal area of deciduous trees and conifers was estimated using a 10-factor cruising prism. Litter was measured at four points located in the cardinal directions 2.5 m from each sampling point, and the average of these four measurements was used in the analyses. Vertical vegetation structure was measured as the number of vegetation contacts on a 3-m pole held vertically at 20 evenly spaced points along two 22.3-m-long perpendicular transects intersecting the center of the plot.

In addition, landscape-scale habitat variables were quantified at every third point where fledgling ovenbirds were located using a recent GIS coverage. These variables included cover type (deciduous, coniferous or mixed) and size class (early regeneration, sapling/pole and mature). To account for the fact that ovenbird fledglings did not all occupy stable home ranges, available habitat was defined separately for each location as the surrounding habitat within a circular area with a radius equal to the median daily distance moved by ovenbirds (Arthur *et al.*, 1996), which was 125 m. We defined the availability of each habitat type as the percentage of pixels of each habitat type within this radius, and calculated the resource selection function for each bird following Manley (1974).

We compared habitat at ovenbird nests with habitat occupied by fledgling ovenbirds, and habitat occupied by fledgling ovenbirds with habitat at random points, using a simultaneous test that the mean of the habitat variable at days 3, 6 and 9 are all equal to the mean at the nest or random point, respectively, using a multivariate analysis of variance (MANOVA). Afterwards, we carried out separate univariate tests for each day (3, 6 and 9) using univariate analyses of variance (ANOVA). We restricted these analyses to habitat used by fledglings during the first 9 days of fledging because too few individuals survived past this point for the repeated measures analyses, which excludes birds with missing data. However, we verified through examination of the entire data set that patterns of habitat selection did not change after 9 days. All analyses were nested by nest to account for potential non-independence of nestlings within the same nest.

We analyzed landscape scale habitat selection by calculating the resource selection probability function, which estimates the relative probability that a habitat will be selected compared with the probabilities for selection of other types, assuming all types are equally available, using maximum likelihood (Manley, McDonald & Thomas, 1993). We tested whether selectivity differed among individuals by summing the deviance values from models calculated separately for each individual and comparing this with the model constructed with data pooled over all animals using a likelihood ratio test (Arthur *et al.*, 1996). We then tested whether ovenbird habitat selection differed between years by comparing the model containing these terms with a null model assuming no selection using likelihood ratio tests. The same procedure was conducted to calculate habitat selectivity among years.

Fledgling survival was analyzed using the Kaplan–Meier product limit estimator. The resulting survival curve was divided into discrete periods with the slope of the relationship, and survival rates were calculated separately for each of the resulting intervals (White & Garrott, 1990). We compared survival among intervals using the program CONTRAST (Hines & Sauer, 1989).

We analyzed the effect of habitat on fledgling survival using logistic regression (Hosmer & Lemeshow, 1989) using a repeated measures analysis. Model significance was assessed using log-likelihood tests, and the fit of each model

was assessed using the Hosmer–Lemeshow goodness-of-fit test (Hosmer & Lemeshow, 1989). We ranked the models by their Akaike's information criterion (AIC_c) values (the AIC_c corrected for small sample size) and compared models based on the difference between the best model and other models (Δ_i) as well as their Akaike weights (Burnham & Anderson, 1998). We considered models with AIC_c values within 2 of the best model to be the best supported models given our data (Burnham & Anderson, 1998).

Results

We located 33 ovenbird nests over the 2 years of the study, and radio-marked 41 fledgling ovenbirds. Of these 41, 12 were depredated. Three additional mortalities were attributed to severe weather. Finally, four birds slipped out of their harnesses, and a fifth had a transmitter that failed. We lost radio contact with the 21 remaining birds between 10 and 38 days after fledging. We are unable to determine with certainty the fates of these birds. Some may have moved beyond the range of our receivers. Alternatively, it is possible that additional transmitter failures occurred, that transmitters were damaged during predation, or that they were taken out of range by wide-ranging predators such as hawks.

The information we have on the identity of predators is circumstantial; however, the eastern chipmunk *Tamias striatus* and accipiters, such as the northern goshawk *Accipiter gentilis*, are probably important predators (Yakel Adams, Skagen & Adams, 2001). Nearly half of the dead fledglings we recovered were buried in chipmunk burrows, and chipmunks are known to be important nest predators. Similarly, accipiters are known to depredate nests, and we have video footage of a goshawk killing a fledgling hermit thrush *Catharus guttatus*. Furthermore, the remains of several birds were found plucked on elevated perches, a behavior typical of accipiters.

We measured stand-level habitat variables at 288 points: 33 points at ovenbird nests and 33 corresponding random points, as well as 111 points where 31 of the radio-marked ovenbirds were relocated and 111 corresponding random points. Ovenbird fledglings were subject to substantial predation; hence fewer and fewer young were located as time progressed. Thus, the habitat analyses were conducted on a subset of 17 fledglings from 14 nests that were tracked for at least 9 days post-fledging.

Differences in habitat between nest sites and sites occupied by fledglings were clearly evident. Ovenbirds nested in areas characterized by more large trees ($F_{(3,5)} = 6.64$, $P = 0.03$) and lower understory structure ($F_{(3,5)} = 66.2$, $P < 0.001$) than sites occupied by fledglings (Fig. 1). Similarly, there were pronounced differences between points occupied by fledglings and corresponding random points. Fledglings occupied areas characterized by fewer large trees ($F_{(3,5)} = 14.0$, $P = 0.007$) and greater understory structure ($F_{(3,5)} = 22.6$, $P = 0.003$) than corresponding random points (Fig. 1). These same patterns were also evident in visual

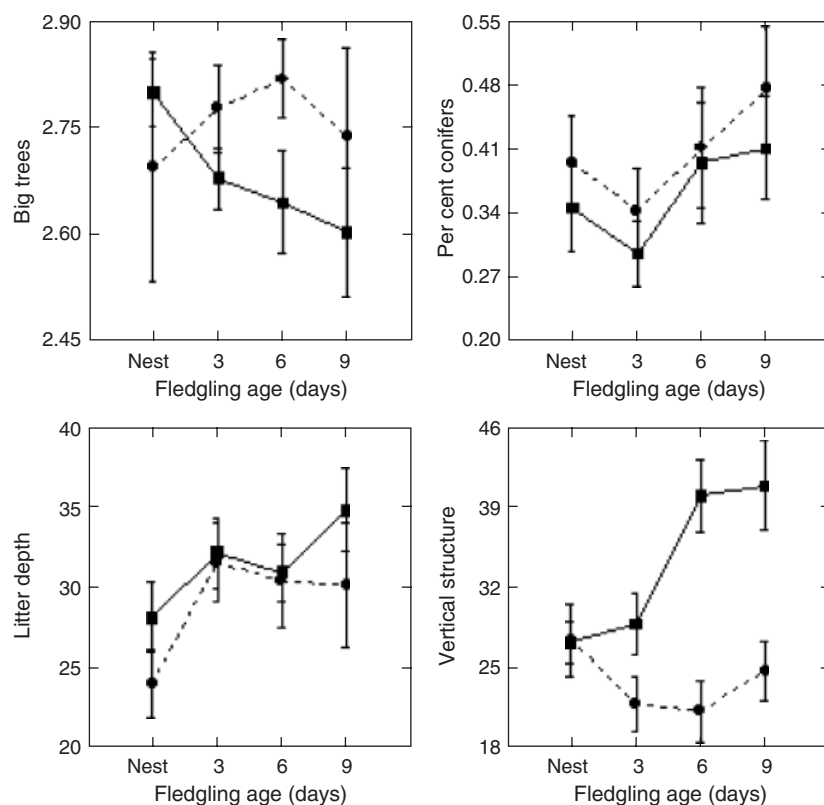


Figure 1 Mean and standard errors of habitat variables compared between locations occupied by fledgling ovenbirds *Seiurus aurocapilla* (squares) and corresponding random locations (circles) for ovenbird fledglings on the Bartlett Experimental Forest, New Hampshire.

inspection of the entire 38-day data set, although very few birds survived past 9 days for statistical comparison.

Our landscape-scale analyses indicated that ovenbirds were selective in their use of different cover types ($\chi^2_{(3)} = 56.9$, $P < 0.001$) and forest age classes ($\chi^2_{(3)} = 36.7$, $P < 0.001$; Fig. 2). Mature hardwood and mixed hardwood softwood forest was most preferred (selection indices 0.467 and 0.418, respectively), whereas the preference for conifer forest and regenerating forests was much lower (0.115). Pole-sapling stands and non-forest habitats were not used at all.

Three time periods were defined by examining a survivorship curve calculated using the Kaplan–Meier product limit estimator (Fig. 3): 0–3, > 3–10 and > 10–38 days. There also appeared to be a break in survivorship around 28 days, and originally we included a fourth time period, 28–38 days; however, there were very few birds present on the study area after 28 days, and the survivals between 10–28 and 28–34 were nearly identical, suggesting that this drop in survivorship represents noise in the data because of the small sample size. There was a substantial drop in survivorship during the time period directly after fledging ($\chi^2_{(2)} = 14.7$, $P = 0.001$), and survival during the period between fledging and 3 days old (0.894) was significantly lower than the period > 3–10 (0.987) or > 10–38 (0.995; $P > 0.05$). Survival did not differ between > 3–10 and > 10–38 days ($\chi^2_{(1)} = 0.00$, $P = 1.00$).

Logistic regression analyses indicated that fledgling survival was positively significantly related to vegetation structure ($\chi^2_{(1)} = 7.32$, $P = 0.007$; Table 1). None of the other variables

were supported, as indicated by the fact that the Δ_i value for the second model was > 2 (Burnham & Anderson, 1998). Sites where live fledglings were located had significantly greater vegetation structure than sites where dead fledglings were located ($P < 0.05$; Fig. 4). There were no significant differences in any of the other habitat variables.

Discussion

Our observation that a significant shift in habitat selection occurs between the nesting period and the post-fledging period in the ovenbird is consistent with the results of other recent studies of habitat use by fledgling birds. Juvenile wood thrushes in Missouri (Anders *et al.*, 1998) and Virginia (Vega Rivera *et al.*, 1998) dispersed to sites with more open canopy, more pines, and more shrubs and saplings than nest sites. Similarly, habitat occupied by juvenile Botteri's sparrows was taller and denser than habitat at nest sites (Jones & Bock, 2005). Pagen, Thompson & Burhans (2000), Marshall *et al.* (2003) and Vitz & Rodewald (2006) have all reported that regenerating clearcuts were occupied during the post-fledging period by forest birds that do not nest in early seral habitats, including ovenbirds. These results suggest that current bird–habitat relationships based on associations between singing birds and habitat parameters may provide an incomplete understanding of the habitat requirements of bird species that, like the ovenbird, alter their habitat use after nesting is complete and singing largely ceases. Ovenbird habitat is generally characterized in the literature as

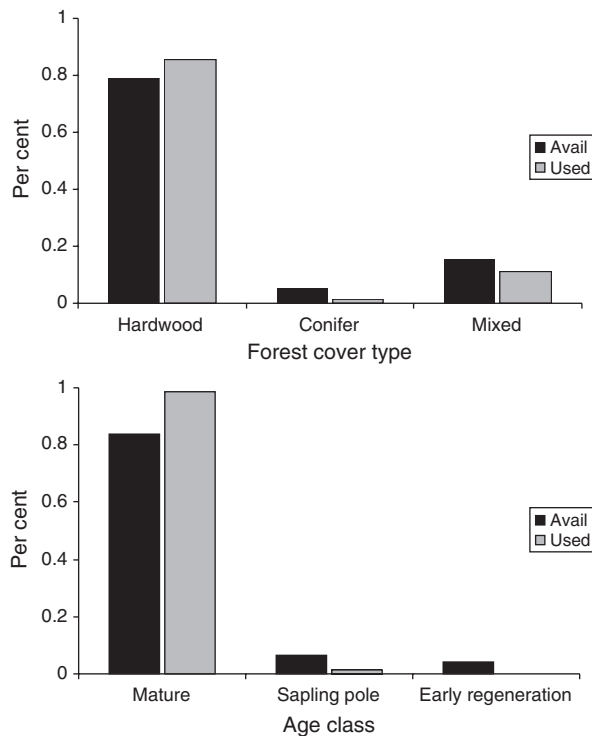


Figure 2 Proportion of habitat on the study area consisting of forest of different cover type and age class compared with the proportion of locations of ovenbirds *Seiurus aurocapilla* during the post-fledgling period on the Bartlett Experimental Forest, New Hampshire.

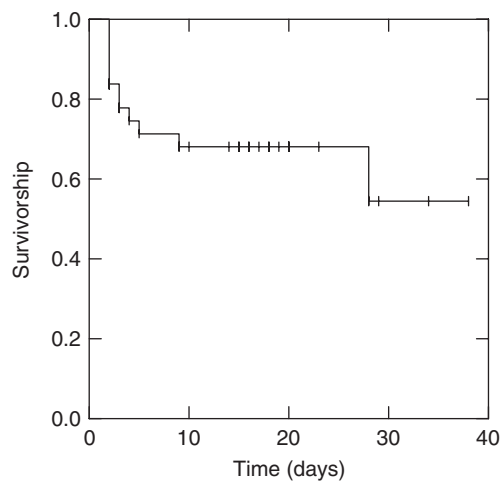


Figure 3 Survivorship function for ovenbird *Seiurus aurocapilla* fledglings on the Bartlett Experimental Forest, New Hampshire, calculated using the Kaplan–Meier product limit estimator.

forest consisting of large deciduous trees with an open understory (Van Horn & Donovan, 1994; Flaspohler, Temple & Rosenfield, 2000; King & DeGraaf, 2000); however, the habitat preferred by fledgling ovenbirds is very different,

Table 1 Results of logistic regressions of survival of 33 ovenbird *Seiurus aurocapilla* fledglings in relation to habitat characteristics, 1999 and 2000

Model	$\chi^2_{(1)}$	<i>P</i>	AIC _c	Δ_i	<i>W_i</i>
$Y = 0.1445 + 0.1056$ (structure)	7.32	0.007	49.6	0.00	0.619
$Y = 0.9400 + 0.0557$ (litter depth)	2.15	0.14	53.5	2.33	0.193
$Y = 2.4646 + 1.0651$ (conifers)	0.40	0.52	59.5	2.68	0.162
$Y = 2.2117 + 0.2354$ (big trees)	0.12	0.73	60.0	7.44	0.015

AIC_c, Akaike's information criterion.

characterized by fewer large trees than nest sites and a denser understory.

Our results indicate that fledgling ovenbirds use habitat non-randomly, selecting habitat with a dense understory of shrubs and saplings relative to random points. These locations were mostly dense areas of regeneration of canopy species such as beech and hemlock, but also included patches of hobblebush *Viburnum alnifolium* as well as dead material from blowdowns or ice damage and, in areas with sparse canopy, brambles (*Rubus* spp.). Anders *et al.* (1998) reported that juvenile wood thrushes used habitats with dense understory such as early successional and high-graded forest, riparian areas and forest-field edges in a proportion significantly greater than random. Similarly, Vega Rivera *et al.* (1998) found that juvenile wood thrushes used habitats with dense understory extensively (> 70% of all radio locations) such as early-successional forest and forest damaged by gypsy moths. In contrast to these studies, the dense habitats used by fledgling ovenbirds seldom included early regeneration forest, as illustrated by the very low selection index for regenerating habitats at the landscape scale.

Our finding that fledgling survival was significantly positively related to habitat structure is consistent with the results of other studies. Anders *et al.* (1998) suggested that juvenile wood thrushes likely selected habitat with greater structure than random sites because dense vegetation might mitigate the risk of predation. Similarly, Cohen & Lindell (2004) suggested that lower survival of fledgling white-throated robins *Turdus assimilis* in coffee relative to pasture was due to less complex vegetation structure in coffee. Watts (1990) reported that wintering sparrows were subject to higher predation from raptors in areas where screening cover had been experimentally reduced by mowing. Finally, Suhonen (1993) found that tits shifted their habitat use in response to increased predation risk from owls.

Food availability is also thought to potentially influence habitat selection by fledgling birds (Morton, 1991; Anders *et al.*, 1998). We do not have information about food resources; however, studies indicate that ovenbird prey abundance decreases with increased shrub density, and ovenbird fledglings in our study use areas with higher shrub density (Smith & Shugart, 1987). Thus, it is unlikely that the association between ovenbird fledglings and high structure was the result of preference for areas with greater prey abundance. Furthermore, we did not observe any association between ovenbird fledglings and leaf litter depth, which is associated

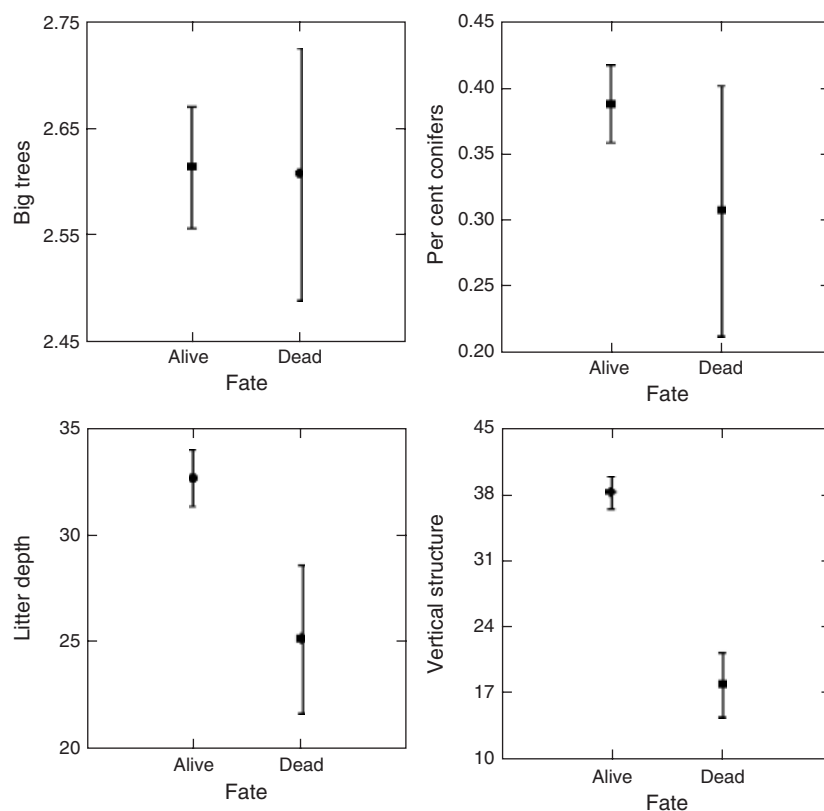


Figure 4 Mean and standard errors of habitat variables compared between locations of alive and dead ovenbird *Seiurus aurocapilla* fledglings on the Bartlett Experimental Forest, New Hampshire.

with increased abundance of ovenbird prey (Burke & Nol, 1998). Sullivan (1989) observed that predation was the primary source of mortality of yellow-eyed Junco fledglings until they achieved independence from their parents, and thereafter starvation assumed more importance as a cause of mortality. The patterns of habitat selection revealed in our statistical analyses were consistent over the entire 38-day period, however, which indicates that there was no dramatic change in selection for habitat characteristics associated with safety from predators or food abundance over this time period.

A third potential explanation for the preference of ovenbird fledglings for habitat with dense structure might be that dense habitat structure provides a better thermal environment for fledglings. For example, DeWoskin (1980) reported that the thermal cover provided by dense shrubs could reduce the metabolic rate of foraging white-crowned sparrows *Zonotrichia leucophrys* by up to 20%. If the association of ovenbird fledglings with dense habitat was the result of thermal considerations, however, we might expect this association to diminish as fledglings grew and their ability to thermoregulate increased. In contrast, the association between fledglings and dense structure became more apparent between day 3 and day 6, indicating that the selectivity by fledglings for habitat with dense structure did not decrease over time, contrary to this prediction. Further research involving habitat and food manipulation and detailed microclimatological measurements would be helpful in discriminating between these alternative hypotheses.

Previous studies indicate that bird populations are strongly influenced by variations in fledgling survival rate (Perrins, 1980; Kurzejeski & Vangilder, 1992), suggesting that viability of populations of ovenbirds and other bird species associated with high vegetation structure during the post-fledgling phase of the life cycle may be significantly affected by the availability of dense habitat. We examined this by calculating the finite rate of increase (Pulliam, 1988) using values for adult survival conventionally used in the literature (0.62; Donovan *et al.*, 1995), values of ovenbird fecundity from our study sites (1.2 females per pair; King & DeGraaf, 2002), and values of fledgling survival calculated for birds that occupied habitats characterized by understory density less than the median (0.13) versus habitats with understory greater than the median (0.48). We calculated these survival rates as the product of our observed survival rate 0–38 days (for low and high structure habitats separately) and 0.70, the probability of an adult surviving 270 days to return to breed, given the conventionally used annual survival rate of 0.62. What we found is that habitats with high structure are sources ($\lambda = 1.19$) and habitats with low structure are sinks ($\lambda = 0.78$).

Our observation that fledgling survival as lowest directly after fledgling is consistent with other recent studies of juvenile passerines (Cohen & Lindell, 2004; Kershner, Walk & Warner, 2004). This pattern has been attributed to increased vulnerability to predation of newly fledged young, who typically have very limited mobility. Our observation

that fledgling survival is positively related to habitat structure suggests that the vulnerability of fledglings due to limited mobility might be compounded by the exposure of fledglings to predation as they move from nest sites with open habitat structure to more protected habitat.

Our observations that fledgling ovenbirds are selective in their habitat use, and that they select different habitat features than adult ovenbirds select for nesting, indicate that studies based on surveys of singing males before fledging do not adequately represent the habitat needs of this species. Furthermore, the positive relationship between fledgling survival and habitat structure that we report, and its potential to affect population viability suggest that the availability of quality habitat for rearing young out of the nest could limit ovenbird populations even if adequate nesting habitat were available. These findings may have important implications for the effective conservation of forest birds. For example, forest-dwelling Neotropical migrants, such as the ovenbird, are species of special management concern in many areas, including on National Forests, which are managed using silviculture. Because ovenbirds sing most during the nest-building stage, a silvicultural prescription based on counts of singing males might emphasize habitat characteristics associated with nest sites, that is open understory and large trees (Van Horn & Donovan, 1994). Although these habitat conditions do provide suitable nesting habitat, our findings that fledgling ovenbirds favor dense understory suggest that the conditions created by this management regime would not provide adequate habitat for this potentially critical phase of the reproductive cycle. We recommend that post-fledging habitat use and its potential influence on population viability should be considered in future studies and conservation programs dealing with Neotropical migrants as well as other passerines.

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