SURVIVORSHIP, HABITAT USE, AND MOVEMENTS FOR TWO SPECIES OF

MATURE FOREST BIRDS

A Dissertation

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ABSTRACT

The post-fledging period is frequently considered the least studied and

understood portion of the avian life cycle, and, as such, could arguably be described as a

"frontier" in avian ecology. Our lack of understanding about the period contrasts sharply

with the perception and recent empirical data showing that the post-fledging period has

tremendous consequences for juvenile survival and population recruitment. For

Neotropical migratory passerines, the post-fledging period begins with young fledging

from the nest and extends until the onset of fall migration and is characterized by high,

though variable, levels of mortality. One of the interesting patterns that biologists have

detected during the post-fledging period is that many species show pronounced changes

in habitat use relative to breeding season habitats. In particular, birds known to breed

exclusively in mature forest commonly shift habitats after breeding is concluded and

select habitat with dense understory vegetation, such as early-successional forest. Such

habitat shifts are presumed to enhance survival or condition, but this has not been

explicitly studied. My dissertation research used both observational and experimental

approaches to rate the importance of successional habitats to mature forest birds during

the post-fledging period. More specifically, this study aimed to (1) estimate fledgling

survivorship of Ovenbirds (*Seiurus aurocapillus*) and Worm-eating Warblers

(*Helmitheros vermivorum*), (2) identify habitat features selected by post-fledging birds,

(3) quantify the extent to which habitat use influenced survival, (4) determine which

habitat and landscape features best predicted fledgling behavior, especially as related to movements, and (5) describe the dietary trophic level of juveniles of 3 species and test the influence of diet on energetic condition.

Between 2004-2007 we radio-tagged 51 Ovenbirds and 60 Worm-eating Warblers immediately prior to fledgling from nests located in mature forests of southeast Ohio. Forested sites were located either adjacent to a regenerating clearcut or completely surrounded by additional mature forest. In addition, 85 independent juvenile Ovenbirds (ca. 4 weeks old) were radio-tagged and randomly assigned to one of three experimental treatments: 1) released in original clearcut of capture, 2) moved to and released in a different clearcut, and 3) moved to and released in a mature forest habitat. All radio-tagged birds were tracked daily, GPS (Global Positioning Systems) coordinates were collected, and habitat features were compared between actual fledgling and random locations. Known fate models in program MARK were used to estimate fledgling survival rates and evaluate the influence of understory vegetation and energetic condition on survival. For three species of forest songbirds, we examined whether fruit resources were heavily consumed during the post-fledging period using a stable isotope analyses of carbon and nitrogen.

Fledgling Ovenbirds and Worm-eating Warblers as well as independent juvenile Ovenbirds consistently selected habitats characterized by dense understory vegetation. Compared to random locations, birds not only used areas with 1.4-1.6x more understory vegetation, but use of these areas actually promoted survival. For fledgling Ovenbirds and Worm-eating Warblers and independent juvenile Ovenbirds, an individual's energetic condition at the time of radio-tagging also was positively related to survival

during the post-fledging period. Post-fledging survival rates were estimated to be 65% for fledging Ovenbirds and 67% for fledgling Worm-eating Warblers. No difference in survival was detected between independent juvenile Ovenbirds released in clearcut or mature forest habitat, and with all groups combined Ovenbirds had an 83% probability of surviving the 52 day period.

Although natal home range size for Worm-eating Warblers was nearly twice as large as those for Ovenbirds, both were substantially larger than typical breeding territories. Distances between daily locations averaged 1.5x farther for Worm-eating Warblers compared to Ovenbirds, and as fledglings aged the distance from the nest and between daily locations increased. For both species, movements of young fledglings were best explained by their energetic condition at the time of fledging. The ability of fledglings in high energetic condition to move farther distances may improve survival by facilitating the location of suitable post-fledging habitat. In contrast to young fledglings, independent juvenile Ovenbirds frequently undertook substantial movements (> 1 km in a day), and birds released into mature forest habitat were documented moving farther from their release location than those released into clearcuts.

Because others have suggested that birds may use regenerating clearcuts during the post-fledging period to gain access to abundant fruit resources, we quantified stable isotope values of retrix (grown as a nestling) and body feathers (grown after fledging) to evaluate the importance of fruit in the diet of young birds. Compared to retrices, basic plumage body feathers were more enriched in δ^{15}N and δ^{13}C values, suggesting that independent juvenile Scarlet Tanagers (*Piranga olivacea*), Wood Thrush (*Hylocichla mustelina*), and Ovenbirds primarily consumed predatory arthropods, whereas

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lepidopteran larvae were the principal food source when young were being fed by adults. We did not find evidence that diet influenced energetic condition nor did our data support the idea that mature forest birds specifically use clearcuts for fruit resources during the post-fledging period.

Although the breeding biology of most Neotropical migratory birds is well studied, information regarding the post-fledging period is generally lacking. By employing both observational and experimental approaches, this study makes a unique contribution to our understanding of post-fledging ecology by linking behavioral decisions regarding habitat use to energetic condition and survival. With respect to conservation, results suggest that dense understory vegetation is a critical feature defining suitable post-fledging habitat. Timber harvest, and clearcuts in particular, are one way to create areas with dense understory and may be necessary to maximize juvenile survival in landscapes that lack suitable post-fledging habitat. However, because clearcutting also reduces availability of breeding habitat, managing for alternate post-fledging habitats (i.e., riparian thickets, tree-fall gaps) within the mature forest may be preferable in some landscapes. In the end, conservation strategies can be greatly improved by taking into account habitat requirements during the post-fledging period.

ACKNOWLEDGMENTS

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FIELDS OF STUDY

Major Field: Natural Resources

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CHAPTER 1

POST-FLEDGING ECOLOGY OF PASSERINES:

A REVIEW OF THE LITERATURE

Abstract

The post-fledging period remains one of the least studied and understood

periods of the avian life cycle despite the potential important role it plays in juvenile

survival and recruitment into the population. In an attempt to gain a better

understanding of fledgling requirements there has recently been increased attention

devoted to the post-fledging period. In this paper, our objectives were to summarize

the current knowledge of post-fledging ecology for passerines and identify areas

where additional research is especially needed. To evaluate the current literature we

used the ISI Science Citation Index to search for publications related to post-fledging

ecology. We focused on the themes of foraging proficiency, habitat use,

survivorship, and movements during the post-fledging period. Fledgling mortality is

often very high irrespective of breeding habitat. Interestingly, only species that bred

in mature forest habitat clearly showed a shift in habitat use during the post-fledging

period. Although these birds appeared to seek out areas with dense understory

vegetation, presumably to increase their odds of survival this vulnerable period, it

remains unclear whether creating suitable post-fledging habitat is necessary.

Additional studies are necessary to examine the impact of creating post-fledging

habitat, and how fledgling survival influences source-sink dynamics. We hope this paper will stimulate research on post-fledging ecology so that knowledge regarding this period will rival that of other phases in the avian life cycle.

Introduction

Recent declines in many songbird populations (Robbins et al. 1989) have prompted numerous studies of breeding (Askins 1995; Robinson et al. 1995) and wintering ecology (Johnson et al. 2006) in an attempt to understand population demography. However, few studies have examined the post-fledging period, which is often considered the least understood portion of the avian life cycle (Anders et al. 1997; Greenwood & Harvey 1982; Vega Rivera et al. 1998). For migratory songbirds the post-fledging period has been defined as beginning with fledging and lasting until the onset of fall migration (ca. 2-3 months; Vitz and Rodewald 2006). Despite some early interest (Lack 1954) and a general recognition that the period might play an important role in population regulation, the post-fledging period has been largely ignored by ecologists and wildlife managers. Recently, though, post-fledging ecology of Neotropical migratory birds has generated increased attention among ornithologists. Initial neglect was partly a result of the difficulty associated with monitoring birds during this period as adults (Vega Rivera et al. 1999), and juveniles (King et al. 2006; Vega Rivera et al. 1998) become furtive and often seek out areas with dense vegetation. Whereas early studies relied heavily on the difficult task of following color-banded individuals (Dhondt 1979; Nolan 1978; Sullivan 1989), recent work has applied constant effort mist-netting (Marshall et al. 2003; Pagen et al.

2000; Vitz & Rodewald 2006) and radio-telemetry (Chapter 2-4, Anders et al. 1997) to the study of post-fledging ecology, and this has facilitated a more complete understanding of fledgling survivorship, habitat use, and movements for a number of species. Collectively these studies show the post-fledging period to be a unique and important phase of the avian life cycle. Nevertheless, detailed information on the post-fledging ecology of the large majority of species remains lacking.

Objectives

Newly acquired data on post-fledging ecology are beginning to challenge our current views on how best to approach songbird conservation, at least for those species breeding in mature forest habitat. In this review paper, our objective was to synthesize the state of the knowledge on the post-fledging period of passerines both to evaluate the importance of this stage in the life cycle and to provide useful information that may help guide land management decisions. More specifically, we review 1) habitat use patterns of fledglings of mature forest and early successional breeders, 2) reported rates of fledgling survival and how survival may be influenced by habitat use, and 3) fledgling movement patterns. We also suggest fruitful areas of future research on post-fledging ecology.

Methods

We used the ISI Science Citation Index Expanded between 1965-2007 to conduct a topic search on the terms "post-fledging", "postfledging", "post-breeding", "postbreeding", and "juvenile survival". After excluding unrelated articles, there

remained 204 papers contributing to our knowledge of avian ecology during the post-fledging period. Of these publications, the majority focused on either songbirds or raptors and was conducted in the United States, Canada, or Europe (Table 1.1). Few papers were published before 1985, and numbers of papers increased noticeably in the late 1980's (Figure 1.1). However, only recently have biologists begun to focus on post-fledging habitat use and survival of passerines.

Results

Fledgling Habitat Use

Habitat requirements during nesting and post-fledging are frequently thought to be similar, but changing seasonal requirements may stimulate shifts in habitat use (Marshall et al. 2003; Pagen et al. 2000; Vitz & Rodewald 2006). In particular, fledglings are not constrained by breeding requirements and can focus on survival and self-maintenance. Evidence is mounting that during the post-fledging period mature forest birds seek out habitats that are quite different than those used for breeding (Marshall et al. 2003; Vitz & Rodewald 2006). Studies utilizing radio-telemetry have documented juveniles of several mature forest species shifting away from their open understory breeding patches and using (Anders et al. 1998; Vega Rivera et al. 1998) or selecting (Chapter 2, King et al. 2006) areas with dense understory vegetation. Furthermore, understory vegetation has been reported being more dense at fledgling locations than at nest sites (Rush & Stutchbury 2008; Vega Rivera et al. 1998; Chapter 2) and random or unused locations (Chapter 2, King et al. 2006). Use of vegetatively thick areas often occurs shortly after fledging (King et al. 2006, Chapter

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2) and continues following dispersing away from the natal area (Anders et al. 1997, Chapter 3).

Several studies have reported exceptionally high capture rates of mature forest breeders in regenerating clearcuts during the post-fledging period (Marshall et al. 2003; Pagen et al. 2000; Vitz & Rodewald 2006). In Ohio, nearly all passerines that breed within the mature forest of the region were captured in regenerating clearcuts during the post-fledging period, and some forest interior specialists (i.e., Ovenbird, Worm-eating Warbler) were among the most frequent and rivaled capture rates of the most common clearcut breeders (Vitz & Rodewald 2006). A similar pattern was revealed in Missouri (Pagen et al. 2000) and West Virginia (Marshall et al. 2003). Regenerating clearcuts are specifically known to be exploited by ground foraging species (Pagen et al. 2000), family groups (Marshall et al. 2003), and juvenile birds (Vitz & Rodewald 2006). Similarly, during the post-fledging period, high numbers of juvenile Black-throated Blue Warblers (*Dendroica caerulescens*) were found within stunted montane fir forests, a habitat not used for breeding and structurally similar to regenerating clearcuts (Rimmer & McFarland 2000). Reasons for this apparently widespread use of early successional habitats by fledgling birds are largely uninvestigated and, hence, remain unclear, but some suggest that abundant food resources and dense cover promote both survival and fat accumulation for migration (Morton 1991; Vega Rivera et al. 1998; Vitz & Rodewald 2007). Alternatively, high capture rates in successional habitats during the post-fledging period might conceivably reflect a simple attraction to edge habitat, as is the case for many migrating passerines (Rodewald & Brittingham 2004). However, edge attraction does

not seem to be the driving force behind use of regenerating clearcuts as Vitz and

Rodewald (2006) documented higher capture rates of juveniles and post-breeding

adults within clearcut interiors compared to areas near the forest edge. Although

these studies collectively suggest that a shift to early successional habitat during the

post-fledging period is a general phenomenon for mature forest breeders, assuming

that use is beneficial or adaptive fails to account for cases where patterns of habitat

use (Garshelis 2000) and spatial variation in density (Van Horne 1983) are known to

be mismatched to habitat quality.

Although this apparent habitat shift may occur for mature forest birds, it

remains unclear whether juveniles of species breeding in early successional areas

undergo a similar shift in habitat during the post-fledging period. Dicksissels (*Spiza

americana*) and Eastern Meadowlarks (*Sturnella magna*) have been reported using

grassland habitats with a greater woody component and higher vegetation during the

post-fledging period compared to areas used for breeding (Wells et al. 2008).

Fledgling meadowlarks also have been documented using agricultural habitats seldom

utilized for breeding purposes (Kershner et al. 2004). Conversely, others have found

Dicksissels using similar habitats during the breeding and post-fledging periods

(Berkeley et al. 2007), and fledgling meadowlarks remaining in the same fields used

for breeding until they gained independence and left the natal area (Guzy & Ribic

2007). Similar results have been noted for two species of shrubland breeders, the

Gray Catbird (*Dumetella carolinensis*) and Yellow-breasted Chat (*Icteria virens*), and

both continued to use early successional habitats following fledging (Maxted 2001).

Because shrublands are thought to provide high quality post-fledging habitat, birds

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that breed in these habitats would not be expected to undergo a habitat shift in search of dense vegetation and abundant food resources.

Numerous studies report associations between avian habitat use and food abundance during breeding (Burke & Nol 1998) and wintering periods (Johnson & Sherry 2001; Levey 1988). In particular, habitat use can be a function of fruit abundance during migration (Martin & Karr 1986) and over-wintering periods (Levey 1988), and this same pattern may exist during the post-fledging period. Because early successional forests offer abundant fruit resources during the post-fledging period and before they are available in mature forests (Willson 1986), seasonal selection of the habitat may be promoted (Vega Rivera et al. 1998; Vitz & Rodewald 2007; White et al. 2005). Frugivory may provide an optimal foraging strategy for juveniles if limitations associated with low foraging proficiency are reduced (Stevens 1985; Desrochers 1992; Suthers et al. 2000) given that fruits are easily located and provide high energy content (McCarty et al. 2002; Parrish 2000). For example, juveniles may have trouble selecting appropriate prey items (Mueller & Berger 1970) and are least successful with complex techniques (i.e., flight-dependent foraging) that require greater skill (Breitwisch et al. 1987; Vanderwerf 1994). Thus, frugivory during the post-fledging period may be an important strategy for many species of passerines.

Abundant arthropods in regenerating clearcuts may attract birds to early successional habitat during the post-fledging period. Throughout the nesting period, arthropods are the primary food source for nearly all North American passerines and their nestlings. Indeed, arthropod abundance or biomass is known to be linked to selection of breeding territories (Burke & Nol 1998), reproductive success (Martin

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1987; Zanette et al. 2000), distribution of birds (Forsman et al. 1998), and seasonal fluctuations in avian abundance (Hutto 1985). Regenerating clearcuts may provide especially rich food resources, as arthropods were positively correlated with saplings and shrubs (Jokimäki et al. 1998) and were more abundant in regenerating clearcuts relative to adjacent mature forest habitat (Keller et al. 2003). Arthropods may prefer vegetation within regenerating forests due to leaves being more palatable (Farji-Brener 2001) and containing fewer secondary compounds (Coley 1983) compared to older plants.

Survival

Because fledgling birds are neither territorial nor reproductive, survival is presumably the single most important consideration driving habitat selection. Thus, habitats that allow birds to avoid predators and/or acquire sufficient nutritional resources should be two key attributes valued by fledglings. Mortality during the first few weeks following fledging can be extremely high, frequently exceeding 50% (Anders et al. 1997; Sullivan 1989), and this is likely a result of their limited mobility, conspicuousness through constant begging, lack of foraging proficiency, and inexperience at detecting and evading predators. As shown in nesting studies (Martin 1995), the primary cause of mortality for fledglings is depredation (Sullivan 1989), which is often high prior to (Anders et al. 1997) or during dispersal (Nilsson & Smith 1985; Yoder et al. 2004) but dramatically declines thereafter (Anders et al. 1997; Powell et al. 2000). Still, after fledglings gain independence mortality rates may remain elevated compared to adults (Sullivan 1989).

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Poor foraging proficiency may directly (i.e., starvation) or indirectly cause mortality in fledgling birds (Sullivan 1988). Some fledgling mortality almost certainly results from starvation, which may cause a spike in mortality once fledglings begin foraging on their own, a pattern documented in some studies (Anders et al. 1997; Sullivan 1989). Furthermore, all Yellow-eyed Juncos (*Junco phaeonotus*) lost weight after gaining independence, and those showing the most loss soon disappeared from the population suggesting starvation (Sullivan 1989). Starvation also may affect dependent fledglings as several Great-spotted Cuckoos (*Clamator glandarius*) experienced mortality due to starvation within the first week after fledging (Soler et al. 1994). In an attempt to avoid starvation young birds may spend more time foraging in order to maintain a positive energy budget (Wunderle 1991), but additional time spent foraging likely increases predation risk (Lima 1985).

While fledgling survivorship is frequently extremely low (Berkeley et al. 2007) it can be highly variable within (e.g., Wood Thrush) and among species (Appendix A) and by year (Nilsson & Smith 1985). Such variation may be influenced by the predator community, which varies among regions and habitat types. Snakes may be the primary predator in grassland systems (Thompson et al. 1999), whereas small mammals and raptors may dominate fledgling predation in forest habitat (Anders et al. 1997). Regardless of the predator community, passerine fledglings are most vulnerable to predation immediately following fledging when young birds have limited mobility and remain completely dependent on their parents. For example, mortality rates for Great (*Parus major*) and Coal Tits (*Periparus ater*) were highest during the first couple of days (5-10% daily mortality rates) with 32% of

fledglings dying during the first 4 days (Naef-Daenzer et al. 2001). However, Dhondt (1979) estimated juvenile Great Tit mortality remaining high throughout the period (13% each week), and only 22% had survived by the beginning of September. High fledgling mortality rates are not unique to breeding birds of the mature forest as similar patterns have been revealed for early successional species (Appendix A).

Despite the fact that few researchers have examined the interaction between habitat use and survival, there is some evidence that dense vegetation promotes survival. Fledgling Ovenbirds (King et al. 2006, Chapter 2) and Worm-eating Warblers (Chapter 2) had a higher probability of surviving if they used areas with increased understory vegetation. Further evidence comes from Costa Rica where White-throated Robin (*Turdus assimilis*) fledglings using agricultural habitats (i.e., pasture, coffee plantation) had a lower survival probability than those using dense tropical forest habitat, and forest habitat was used exclusively following natal dispersal (Cohen & Lindell 2004).

At least in some instances, fledgling survival appears to be influenced by nestling condition. Some studies have reported a positive relationship between nestling mass upon fledging and survival during the post-fledging period (Krementz 1989, Naef-Daenzer et al. 2001, Chapter 2; but see Anders et al. 1997; Brown & Roth 2004). However, this relationship may be most pronounced during years of resource shortage (Krementz et al. 1989; Monros et al. 2002) or late in the breeding season when food resources are reduced. Naef-Daenzer et al. (2001) concluded that an individual's condition upon fledging was not an important factor for early broods, but was critical for later broods, which experienced 5x higher mortality. The authors

suggested this pattern resulted from a combination of reduced food resources and increased predation pressure later in the season (Naef-Daenzer et al. 2001).

Another factor that may influence post-fledging survival is clutch size or the number of fledglings per brood. Experimentally enlarged clutch sizes for the Spotted Antbird (*Hylophylax naevioides*) resulted in higher rates of fledgling mortality, thereby resulting in no net increase in reproductive productivity (Styrsky et al. 2005). Because artificially increasing the clutch size did not result in higher nest predation and adults were able to fledge a higher number of young, the authors suggested that post-fledging mortality may be a leading factor contributing to clutch size evolution in tropical birds (Styrsky et al. 2005). We are not aware of any observational or experimental studies specifically designed to investigate the influence of clutch size on fledging survival for North American breeding birds. Future studies are needed to examine whether increased clutch size reduces post-fledging survival in temperate zone breeders.

Species-specific fledgling mortality may be influenced by nestling development at the timing of fledging, which varies by species and nesting guild (Remes & Martin 2002). Ground nesting species are thought to be more vulnerable to nest predation than shrub and canopy nesters, and they have adapted to high predation pressure with shorter nesting periods (Remes & Martin 2002). As a result, nestlings leave the nest earlier and at a lighter relative body mass than those employing "safer" shrub and canopy nests. Because these fledglings are initially less developed they are presumably more vulnerable to predation than species with a longer nestling phase that produce more developed chicks upon fledging. However,

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this may not always be the case as some of the highest fledgling mortality rates have been reported from species with long brooding periods (Dhondt 1979), and relatively low mortality rates are frequently documented for species with very short brooding periods (Chapter 2). Again, no studies have been designed to specifically test this hypothesis.

In contrast to the known influence of landscape composition on nesting success (Robinson et al. 1995), the relationship between landscape attributes and fledgling survival remains unclear, as both high (Chapter 2) and low (Naef-Daenzer et al. 2001) survival estimates have been reported from forested landscapes. Similar to the pattern commonly revealed for nest success, Hooded Warbler (*Wilsonia citrina*) fledgling survival was documented being low (19%) in a highly fragmented landscape and high in a forested landscape (51%, Stutchbury pers. comm.). Conversely, survival of fledgling Wood Thrush were high (75%) in a fragmented landscape, perhaps due to extensive amounts of edge habitat provided high quality post-fledging areas and improved fledgling survival (Fink 2003). Such equivocal results highlight the need for thorough studies that are explicitly designed to examine the role of landscape composition on fledgling survival and habitat use.

Most information concerning fledgling survivorship has been gathered using radio-telemetry, yet most do not evaluate possible negative effects these devices have on the study organism. In addition to survival estimates from radio-tagged birds, two studies have generated survival estimates of color-marked individuals using capture/recapture data and Cormack-Jolly-Seber models, and the results have suggested that transmitters do not substantially alter an individual's survival during

the post-fledging period (Naef-Daenzer et al. 2001) or the entire annual cycle (Powell et al. 1998). By comparing radio-tagged individuals with those only color-marked, two studies have evaluated survival using Cormack-Jolly-Seber models and have suggested that transmitters did not substantially alter an individual's survival during the post-fledging period (Naef-Daenzer et al. 2001) or the entire annual cycle (Powell et al. 1998). Furthermore, radio-transmitters do not appear to substantially influence behavior including time spent foraging (Brigham 1989), nestling provisioning rates (Neudorf & Pitcher 1997), or flying capability (Sykes et al. 1990). Following transmitter attachment captive Dicksissels were reported having increased levels of glucocorticoid (stress hormone) in their feces, though this effect appeared to be temporary as birds returned to baseline levels within 48 hours (Wells et al. 2003). Although results from these studies suggest that radio-transmitters do not greatly affect fledgling survival or behavior, caution using this method is advised as transmitters have been identified in causing parents to reject radio-tagged nestling Louisiana Waterthrush (*Seiurus motacilla*; Mattsson et al. 2006).

Movements

Fledgling mobility is important because it not only enhances their ability to escape predators, but it may facilitate the location of high quality post-fledging habitat. Fledglings of open-cup nesting passerines are thought to exhibit similar movement patterns and likely remain within 50 m of their nest during the first week following fledging (Morton 1991). Initially, fledglings attempt only short distance movements, but daily movements increase with fledgling age until they disperse away from the natal territory (Berkeley et al. 2007; White & Faaborg 2008), which

generally occurs 2-5 weeks following fledging (Morton 1991; Vega Rivera et al. 2000). Dispersal movements are reported to average only a few hundred meters in some thrush species (Cohen & Lindell 2004; White & Faaborg 2008), but over a kilometer for other species (Guzy & Ribic 2007; Kershner et al. 2004; Lang et al. 2002; Morton 1991). In fact, Eastern Meadowlarks (*Sturnella magna*) have been noted dispersing over 12 km (Kershner et al. 2004). Intraspecific dispersal distance also can vary substantially, and this may be partially attributed to females moving farther from the nest compared to males (Greenwood & Harvey 1982; Small & Rusch 1989; Tyler et al. 1990).

Several hypotheses have been proposed to explain post-fledging movements, including a gradual southward drift, intraspecific competition, and aggregation of conspecifics. The limited evidence for southward drift is found in the disappearance of birds from the breeding grounds and recoveries of banded birds south of breeding ranges before migration was thought to occur (Cherry 1985; Rappole & Ballard 1987). However, this hypothesis lacks support from radio-telemetry (Anders et al. 1998; Vega Rivera et al. 1998) or intensive banding (Nolan 1978) studies. Although movements could be explained by juvenile birds being forced into marginal habitats through intraspecific competition with dominant birds (Winker et al. 1995), both empirical and anecdotal evidence are absent for such exclusion occurring during the post-fledging period. Some evidence suggests conspecific socialization as a stimulus for post-fledging movement (Morton et al. 1991). Once fledglings disperse from their natal territory they are frequently found in loose aggregations reminiscent of mixed species flocks (Vega Rivera et al. 1998). Nolan (1978) was one of the first to

document extensive social interactions during the post-fledging period in his extensive study on Prairie Warblers (*Dendroica discolor*) and found these flocks to include both con- and interspecifics. In southern Ohio juvenile Ovenbirds and Worm-eating Warblers were frequently found traveling with several other species including Hooded Warblers, Black-and-white Warblers (*Mniotilta varia*), Red-eyed Vireos (*Vireo olivaceus*), and Wood Thrush. Such flocking behavior is commonly found outside of the breeding period (i.e., migration, winter) and is thought to be a strategy to minimize predation. However, the influence of juvenile flocking on post-fledging movements remains unclear.

Prospecting, a complex evolutionary strategy that aides breeding habitat selection, also may drive movement patterns (Cody 1985). Evidence suggests that breeding sites are selected in late summer by juvenile Field Sparrows (*Spizella pusilla*; Adams & Brewer 1981) and White-crowned Sparrows (*Zonotrichia leucophrys*; Morton 1992). In fact, young of many non-passerines are believed to prospect for breeding sites in late summer or autumn (Reed et al. 1999), which may expedite breeding activity in spring. Prospecting potentially allows for late summer evaluations of conspecific reproductive success and the opportunity to gather information regarding breeding territories, vegetation structure, and food availability (Brewer & Harrison 1975; Reed et al. 1999). Another function of prospecting may be to create a navigational map that facilitates return to the area in subsequent years (Baker 1993; Morton 1992). Although there are obvious advantages associated with prospecting, there also are possible costs. Prospecting requires extensive movements in unfamiliar areas, potentially increasing predation risk (Dufty & Belthoff 2001;

Yoder et al. 2004). This cost may outweigh the benefit of late summer prospecting

especially since many juvenile birds will not survive to breed the following summer

(Lack 1954). While prospecting may influence some post-breeding movements

(Reed et al. 1999), the extent to which it is a general phenomenon is unknown, and it

does not easily explain the use of non-breeding habitat.

Conclusion

Mortality rates during the post-fledging period may be higher than any other

portion of the life cycle for passerines, clearly establishing this period as important in

terms of juvenile recruitment and population dynamics. For forest breeding

passerines, suitable post-fledging habitat is often quite different than those used for

breeding, and some areas thought to provide high quality post-fledging habitat (e.g.,

edge habitat, regenerating clearcuts) are generally considered detrimental to breeding

birds of these same species. Clearcutting, at least temporarily, removes breeding

habitat from the landscape while increasing edge habitat that is often associated with

increased rates of nest predation and parasitism.   However, the combination of dense

cover and abundant food resources often associated with these habitats may provide

critical resources for birds during the post-fledging period, and use of areas with

dense understory vegetation have been found to promote fledgling survival. The

extent to which suitable post-fledging habitat should be created through forest harvest

is unclear, as many older forests may provide an abundance of such habitat in riparian

thickets and tree-fall gaps. To better understand the effects of timber harvest on

forest birds during the post-fledging period, future studies should examine fledgling

survival and habitat selection in forested landscapes with varying amounts of timber harvest and successional habitat. In contrast to the habitat shift found in forest breeders, specific post-fledging requirements for early successional passerines appear to be similar to those necessary for breeding. However, few studies have examined post-fledging requirements for birds breeding in early successional habitats, and additional research is necessary to verify this hypothesis. Overall, little effort has been invested in understanding the post-fledging period, compared to the extensive amount of research devoted to examining nesting patterns. The post-fledging period may be equally important as the nesting period in terms of population productivity, and we hope, that in the near future, the extent of knowledge concerning this period will rival that of nesting biology.

A)

Passerines	Ducks/Geese	Seabirds	Shorebirds	Raptors	Other	Total
76	27	36	13	47	5	204

B)

US/CA	EU	AF	PI	LA	AA	AU/NZ	ME
112	68	9	4	4	4	2	1

US/CA = United States/Canada
EU = Europe
AF = Africa
PI = Pacific Islands
LA = Latin America
AA = Antarctica
AU/NZ = Australia/New Zealand
ME = Middle East

Table 1.1. Total number of publications between 1965-2007 found using a topic

search of the post-fledging period using the ISI Citation Index A) by avian group and

B) region.
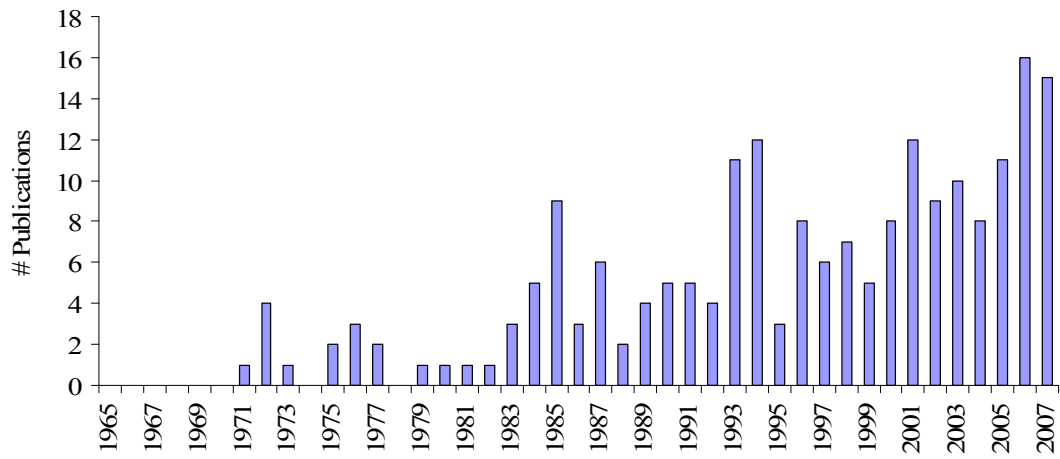
Figure 1.1.   Total number of publications by year between 1965-2007 found using a
topic search of the post-fledging period using the ISI Citation Index.

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CHAPTER 2

POST-FLEDGING SURVIVAL OF MIGRATORY FOREST SONGBIRDS: WHAT

IS THE ROLE OF HABITAT SELECTION?

Abstract

Habitat quality on the breeding grounds has been typically evaluated by

investigating patterns in nesting success, while events that occur following fledging

have been largely ignored. However, one especially overlooked aspect of breeding

ground quality is how habitat affects post-fledging survival, which can be very low

and can greatly influence population recruitment. In this study, we estimated survival

rates, identified habitat features selected by fledglings, and then evaluated the extent

to which habitat selection and other biological factors influenced survivorship of

fledgling Ovenbirds (*Seiurus aurocapillus*) and Worm-eating Warblers (*Helmitheros*

vermivorum). From 2004-2007, we radio-tagged and recorded daily locations of 51

Ovenbirds and 60 Worm-eating Warbler fledglings in southeast Ohio, USA. We

compared vegetation structure between actual fledgling and random locations using a

chi-squared analysis. For each species separately, known fate models in program

MARK were used to generate post-fledging survival estimates and evaluate the

influence of biological covariates. Post-fledging survival rates were similar for the

two species and estimated to be 65% for Ovenbirds and 67% for Worm-eating

Warblers. Overall, fledglings of both species actively selected habitats characterized

by dense vegetation that contained 40-60% more woody stems in the understory compared to random locations. Moreover, use of dense vegetation actually promoted survival. Fledgling condition at the time of radio-tagging also was positively related to survival during the post-fledging period. Conservation strategies can be improved by taking into account fledgling habitat requirements. Although riparian thickets and tree-fall gaps within some forests may provide abundant post-fledging habitat, other forests may lack the features necessary to maximize fledgling survival. In these cases, managers should consider actively creating suitable post-fledging habitat.

Introduction

Although the breeding ecology of North American songbirds has been the focus of numerous studies, ecological information concerning other life cycle stages remains surprisingly incomplete. In fact, basic ecological parameters (i.e., survivorship, habitat use) during the post-fledging period are just beginning to be understood for some species, despite the evidence suggesting that juvenile survival rates play important roles in population ecology and demography (Anders & Marshall 2005; Yackell Adams et al. 2007). For migratory songbirds the post-fledging period generally spans 2-3 months beginning with fledging from the nest and lasting until the initiation of fall migration. Our poor understanding of post-fledging ecology results primarily from the difficulty associated with collecting data on birds during a phase when they are furtive and do not broadcast their presence through song. Nevertheless, recent technological advances have allowed for the miniaturization of radio-transmitters, thereby permitting researchers to track bird's movement, habitat

use, and survivorship. Despite increased interest and an unprecedented number of

studies on post-fledging ecology over the last 10-15 years, much research in North

America has focused on a single species, the Wood Thrush (*Hylocichla mustelina;*

Anders et al. 1997; Powell et al. 2000; Vega Rivera et al. 1998), and few data exist

for the majority of forest songbirds.

Traditionally, breeding and post-fledging habitat use was assumed to be

similar, but empirical studies show this is not necessarily the case (Anders et al. 1997;

Vega Rivera et al. 1998). Habitat needs might be expected to change across the

annual cycle given that breeding birds need to meet numerous reproductive

requirements (i.e., nest site selection, mate acquisition, courtship, nestling

provisioning), whereas non-breeding birds, including fledglings, should be primarily

focused on survival. Indeed, differences in habitat use between breeding and post-

fledging periods are well documented for Ruffed Grouse (*Bonasa umbellus*), which

frequently move their broods into areas of dense vegetation including young aspen

stands (Thompson & Dessecker 1997) and alder thickets (Rusch et al. 2000).

Similarly, there is strong evidence that Wood Thrush move from their mature forest

breeding areas into habitats with dense vegetation during the post-fledging period

(Anders et al. 1997; Powell et al. 2000; Vega Rivera et al. 1998). The extent to which

most other forest-breeding migratory birds exhibit these same patterns remains

unknown.

Several studies using mist-nets to document avian habitat use have reported

high numbers of forest breeding songbirds using early successional habitats (e.g.,

regenerating clearcut) during the post-fledging period (Marshall et al. 2003; Pagen et

al. 2000; Rappole & Ballard 1987; Vitz & Rodewald 2006). In fact, some of the
highest capture rates in early-successional habitats were species generally regarded as
forest-interior specialists (Vitz & Rodewald 2006). Although these studies suggest
that early successional forests created through forest harvesting provide suitable post-
fledging habitat for mature forest birds, they are unable to adequately address the
extent to which the habitat is being used. Furthermore, habitat use (Garshelis 2000)
or animal densities (Van Horne 1983) may not always indicate high quality habitat.
Consequently, studies examining habitat selection and survivorship are necessary to
determine what constitutes quality habitat during the post-fledging period.

Mortality during the post-fledging period has long been suspected to be high
and remain elevated even after independence due to inexperience in foraging and
evading predators (Lack 1954). The most critical period in terms of survivorship
appears to be the first 3 weeks after leaving the nest. During this time fledglings have
limited mobility, can be conspicuous to predators (i.e., begging calls), and remain
dependent on parents for food. As a result, mortality rates can be extremely high
during the post-fledging period and may frequently exceed 50% (Anders et al. 1997;
Sullivan 1989).

Researchers commonly evaluate population demography and habitat quality
by examining nesting success, but generally fail to explicitly account for post-
fledging survivorship. Despite the increasingly clear importance of post-fledging
survivorship in population demography (Anders & Marshall 2005), only one other
study has explicitly evaluated relationships between fledgling survivorship and
habitat characteristics (King et al. 2006). In this study, we estimated survival rates,

identified habitat features selected by fledglings, and then evaluated the extent to which habitat selection and other biological factors influenced survivorship of two mature-forest species, Ovenbirds (*Seiurus aurocapillus*) and Worm-eating Warblers (*Helmitheros vermivorum*).

Methods

Study sites

From 2004-2007, we studied post-fledging birds in southeast Ohio, USA (Athens and Vinton Counties) within the Ohio Hills physiographic province. The region is characterized by rolling forested hills (approximately 70% forest cover) perforated by regenerating clearcuts with non-forest land (i.e., small towns and agriculture) occurring in some valleys. Common trees within these forests included yellow-poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), red oak (*Quercus rubra*), red (*Acer rubrum*) and sugar maple (*Acer saccharum*), hickory (*Carya spp.*), and white ash (*Fraxinus americana*). Potential predators that are common on the study sites included Eastern Chipmunk (*Tamias striatus*), Gray Squirrel (*Sciurus carolinensis*), Southern Flying Squirrel (*Glaucomys volans*), weasels (*Mustela spp.*), Striped Skunk (*Mephitis mephitis*), Viginia Opossum (*Didelphis virginiana*), Raccoon (*Procyon lotor*), Red Fox (*Vulpes vulpes*), Blue Jay (*Cyanocitta cristata*), Broad-winged (*Buteo platypterus*) and Cooper's (*Accipiter cooperii*) Hawks, and Black-rat Snake (*Elaphe obsoleta*).

Ovenbirds and Worm-eating Warblers were radio-tagged at 7 sites within the Zaleski State Forest, Lake Hope State Park, and MeadWestvaco forest lands

(Appendices B, C). Each study plot was 16 ha in size, separated by $\geq$ 4 km, and was

composed of mature forest habitat (75-110 years old). Four sites were located

adjacent to a recent clearcut ($\leq$ 10 years old, < 20 ha), and 3 were completely

surrounded by additional mature forest. Approximately equal numbers of fledglings

were fitted with radio-transmitters in sites next to and away from a clearcut.

Study organisms

    We focused on Ovenbirds and Worm-eating Warblers because both are

thought to be forest-interior species (Van Horn and Donovan 1994, Hanners and

Patton 1998) and are known to frequently use regenerating clearcuts during the post-

fledging period (Vitz & Rodewald 2006). We located Ovenbird and Worm-eating

Warbler nests and monitored them every 3-5 days (every 1-2 days as fledging

approached) until they either failed or fledged young. On their fledging day, one

nestling was randomly selected from their nest (or located near the nest if the

nestlings had fledged earlier that day) and fitted with a radio-transmitter using a

figure 8 leg-loop harness constructed of a cotton/nylon blend material (Rappole &

Tipton 1991). Only one nestling per nest was fitted with a radio-transmitter because

members of the same family group may lack statistical independence (Garton et al.

2001). Each radio-tagged bird was banded with a USGS aluminum band, weighed,

and tarsus length was recorded. Ovenbirds were fitted with transmitters that were

programmed to last 6 weeks and weighed approximately 6.1% of their fledging and

4.6% of their adult mass (0.90g, BD-2, Holohil Systems Ltd.). Radios used on

Worm-eating Warblers were programmed to last 4 weeks and weighed 4.8% and

4.2% of their fledging and adult mass, respectively (0.55g, BD-2N, Holohil Systems Ltd.).

Radio-tracking

Each radio-tagged individual was located daily using the homing method, which involved approaching the bird on foot until a visual observation was documented. Birds were tracked using ATS R2000 receivers (Advanced Telemetry Systems, Inc.) and 3 element folding yagi antennas. The range of the transmitters generally was between 300-900 meters, but varied with the terrain. Once found, the bird's state was identified (whether it was alive or dead) and location recorded using a GPS (global positioning systems) unit (Magellan Meridian). An individual was reported dead if it was found intact but lifeless, the transmitter was located next to a pile of feathers, the radio was tracked to a predator, the radio was found in feces, or a radio was found with tooth or beak impressions. If an individual was not found for several days and an expired battery was not expected, an Ohio Division of Natural Resources airplane (Partenavia P68) wired for radio-telemetry was flown to traverse the study region and facilitate locating "lost" individuals.

Habitat characteristics

Although birds were tracked daily, microhabitat vegetation characteristics were measured only every other day at bird locations and paired random locations due to time constraints. Random locations were separated from actual bird locations by following a random direction for 50 m. Vegetation characteristics were evaluated within a 0.04 ha circle. The number of woody stems (< 8 cm dbh) taller than 0.5 m as well as numbers of small (8-23 cm dbh), medium (>23-38 cm dbh), and large (>38

cm dbh) trees were recorded. In addition, percent canopy cover was visually

estimated. We believe these values accurately reflected biological differences

because observers received extensive training in estimating canopy cover.

Furthermore, we were most interested with how values at random locations compared

relative to those at actual bird locations rather than absolute measures of canopy

cover. Data from all environmental variables were averaged over each individual, as

we considered the individual (rather than the daily location) as the appropriate

replicate (Garton et al. 2001). Because we also were interested whether nesting

habitat differed from post-fledging habitat, the same vegetation measurements were

collected at each nest where a nestling had been radio-tagged. For both analyses

habitat variables that did not meet the assumptions of normality were square-root

transformed in order to satisfy this requirement. We used a discriminate function

analysis to examine differences in vegetation characteristics (number of woody stems,

canopy cover, and number of small, medium, and large trees) between bird locations

and paired random locations, and the same analysis was performed between bird

locations and nest sites. Vegetation measurements at random locations were not

collected in 2004, and those individuals were dropped from the analysis involving

random locations. In addition, any individuals where post-fledging data was lacking

(i.e., experienced mortality in first 24 hours after fledging) were removed from both

analyses.

In addition to examining specific habitat variables, we evaluated selection of

particular habitats by individual fledglings by examining whether specific habitats

were used in greater proportion than would be expected given their availability.

Habitat types were classified as mature forest (> 40 years old), mid-successional forest (15-40 years old), regenerating clearcut (< 15 years post-harvest), riparian thicket, or roadside edge. Mature, mid-successional, and regenerating forest habitats, roads, and streams were identified on a digital map (using ArcView 3.2) provided by the Ohio Division of Wildlife. A 15-m wide buffer was created around all roads and streams to identify roadside edges and riparian thickets. Habitat availability was identified by the proportion of each habitat contained within an individual's natal home range, and used habitats were defined by bird locations. Natal home ranges were constructed using the Minimum Convex Polygon method with the Animal Movements extension in ArcView 3.2 (Hooge and Eichenlaub 1997). The Minimum Convex Polygon method was used over the Kernal method, because the Kernal method tends to overestimate home range size from a limited number (< 30-50) of locations (Seaman et al. 1999). A chi-square analysis was conducted to evaluate selection of available habitat types (i.e., mature forest, mid-successional forest, regenerating clearcuts, riparian thickets, and roadside edge). To minimize statistical problems associated with having low expected frequencies per habitat type, similar categories were combined (Manly et al. 2002). Mature and mid-successional forests were pooled due to their similar understory structure and classified as open forest. However, this category was primarily composed of mature forest habitat because very little mid-successional forest habitat was located within the natal home ranges. Riparian thickets, roadside edges, and regenerating clearcuts were combined into a single category as each provides dense low vegetation structure and were classified as vegetation-dense areas. In order to eliminate locations collected after an individual

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had left its natal home range, all points after a dispersal event were removed from the

home range calculation. A dispersal event was defined as an individual undergoing a

daily movement, or movements on subsequent days in the same direction, > 350 m

and did not return to the natal area. Although dispersal movements are often

substantially farther than this, we used 350 m because dispersal movements by

mature forest passerines have been documented being as short as a few hundred

meters (Anders et al. 1998). Twenty-nine Ovenbirds and 28 Worm-eating Warblers

were included in this analysis, because home ranges were only estimated for

individuals with ≥ 16 daily locations and selection could only be inferred when

habitat availability included both habitat classifications.

Fledgling survivorship

Survivorship for both species was estimated using known fate models in

program MARK (White & Burnham 1999). Known fate models are similar to the

Kaplan-Meier product-limit estimator, but are preferred because they allow for the

inclusion of covariates. We examined whether survival was time dependent within

the post-fledging period, varied by year, and used biologically meaningful covariates

to build *a priori* models that were evaluated and ranked using an AIC framework.

Individual covariates utilized in the models included time of season of fledging as

early (< 15 June) or late (≥ June 15), proximity to a clearcut (site adjacent or not),

number of nestlings from the nest and whether the nest had been parasitized by the

Brown-headed Cowbird (*Molothrus ater*), the bird's condition upon fledging, and the

average number of woody stems at post-fledging locations. Our definition of early

and late periods resulted from most first nesting attempts fledging before mid June,

whereas nestlings fledging after mid June were likely from nesting attempts following initial nest failure. Condition was evaluated using the residual from a regression of fledglings' tarsus length by body mass. A residual >0 reflects a greater mass than expected given a certain body frame size (i.e., good condition), whereas a residual <0 indicates less mass than expected for a given frame size (i.e., poor condition). Several time-dependent models within the post-fledging period were evaluated for both species. Time models for Ovenbirds included: a constant and fully time dependent daily survivorship, 4 survival periods (days 1-7, 8-14, 14-21, 22-51), 3 survival periods (days 1-7, 8-14, 14-51), and 2 survival periods (days 1-7, 8-51). These time intervals were chosen because fledgling Ovenbirds have limited flight capabilities during the first 7 days, flight ability improves substantially during the 2nd week, fledglings become competent fliers during the 3rd week, and many obtain independence during the 4th week. Within-season time models were slightly modified for Worm-eating Warblers to account for fledglings being somewhat more developed upon fledging and showing substantially improved flight by the 5th day after fledging. Worm-eating Warbler time models included: a constant and fully time dependent daily survival, 4 survival periods (days 1-5, 6-12, 12-18, 19-31), 3 survival periods (days 1-5, 6-12, 13-31), and 2 survival periods (days 1-5, 6-31). Excluding the differences in the duration of the time periods, the same covariate and time models were run for both Ovenbirds and Worm-eating Warblers. Covariates were added only to the top time model with separate models for each individual covariate and several additive models containing multiple covariates. Because an individual's condition upon fledging was presumed to be most influential during the first time period (when

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birds lacked flight abilities and are most vulnerable) we ran 2 models with the condition covariate. One time model treated condition as a covariate only during the first time period and another with condition included in each time period. The covariate included in the higher ranked model was used in the additive models. To account for our small sample size we used the corrected Akaike's Information Criterion (AIC_c) to rank models according to parsimony given a set of candidate models (Burnham & Anderson 2002). Models with a ΔAIC value within 2 of the top model were considered equally plausible given the data (Burnham & Anderson 2002).

Results

During the 4-year study we found and monitored 134 Ovenbird and 103 Worm-eating Warbler nests. Sample sizes increased each year with 35, 44, and 55 Ovenbird nests and 15, 36, and 52 Worm-eating Warbler nests being monitored in 2004, 2005, and 2006, respectively. From these nests 12, 20, and 20 Ovenbirds and 4, 23, and 23 Worm-eating Warblers were radio-tagged in successive years between 2004-2006 (Table 2.1). Because a number of the BD-2N radios prematurely failed in 2006, 10 replacement radios were used on Worm-eating Warblers in 2007. Twenty-eight Ovenbirds and 31 Worm-eating Warblers were radio-tagged at mature-forest sites adjacent to clearcuts, while 24 Ovenbirds and 29 Worm-eating Warblers were radio-tagged at mature-forest sites surrounded only by mature forest. For surviving individuals the period that we were able to detect radio signals varied between 26-51 days for Ovenbirds and 3-31 days for Worm-eating Warblers. Numerous signals were lost between 3-4 weeks likely a result of dispersal away from the natal territory

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and out of range of our equipment. Others were located following dispersal, and the eventual loss of their signals was likely due to long distance movements or transmitter battery expiration.

Upon fledging Ovenbirds were flightless and Worm-eating Warblers exhibited limited flight capabilities making them vulnerable to predation. The primary cause of fledgling mortality was predation, although a few individuals may have died from starvation. Within a few days of fledging two Ovenbirds were discovered buried just beneath the ground surface. Such caching behavior is characteristic of the Eastern Chipmunk, an important predator in eastern North America (Reitsma et al. 1990). This was most prevalent in 2006 a year when chipmunks were especially common, likely a result of high over-winter survival due to an abundant hard mast crop the previous fall (Vitz pers obs). One radio was found in skunk scat, two were tracked to black rat snakes, and several other radios were found amongst plucked feathers suggesting hawk predation. Although the majority of predation occurred during the first 3 weeks after fledging, one transmitter was found in a snake 6 weeks after the Ovenbird fledged, and another Ovenbird was killed by a domestic cat (*Felis catus*) after dispersing away from the natal area. Overall, the primary predators of fledglings were probably sciurids and snakes prior to the development of strong flight capabilities, and hawks after fledglings gained flight proficiency (Appendix D; Appendix E).

Habitat

We found evidence of microhabitat differences among areas used by fledglings and those used for nesting or random locations. Post-fledging habitat

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differed from nesting habitat for both Ovenbirds (Wilks' Lambda $F_{5,92} = 19.19$, P < 0.001) and Worm-eating Warblers (Wilks' Lambda $F_{5,112} = 30.97$, P < 0.001). For Ovenbirds the average number of woody stems was 1.8x higher ($F_{1,96} = 6.38$, P = < 0.001; Fig. 2.1) and canopy cover was 14% less ($F_{1,96} = 6.38$, P = < 0.001; Fig.2.2) at fledgling locations compared to nest sites. For Worm-eating Warblers fledgling locations were characterized by 2.2x more woody stems ($F_{1,116} = 108.24$, P = < 0.001; Fig. 2.1) and 16% less canopy cover ($F_{1,116} = 48.35$, P = < 0.001; Fig. 2.2) than nest sites. Similarly, we detected significant differences in habitat characteristics between fledgling and paired random locations for Ovenbirds (Wilks' Lambda $F_{1,74} = 4.35$, P = 0.002) and Worm-eating Warblers (Wilks' Lambda $F_{5,106} = 10.02$, P < 0.001). In this case, the average number of woody stems was 40% higher ($F_{1,74} = 12.50$, P = 0.001; Fig. 2.1) and canopy cover was 8% lower ($F_{1,74} = 6.35$, P = 0.014; Fig. 2.2) at Ovenbird locations compared to random locations. For Worm-eating Warblers, actual compared to random locations had 60% more woody stems ($F_{1,110} = 12.50$, P < 0.001; Fig. 2.1) and 8% less canopy cover ($F_{1,110} = 12.50$, P = 0.008; Fig 2.2).

At the macrohabitat scale all individuals demonstrating habitat selection (i.e., that used a particular habitat more than expected given its availability) used the vegetation dense habitats more than expected, though approximately half of Ovenbirds (14 of 26 birds) and Worm-eating Warblers (14 of 28) showed no sign of preferences for any particular habitat. Although clearcuts were considered to be a vegetation-dense habitat, this habitat type was not available to all fledglings. For Worm-eating Warblers clearcuts were only available to 11 fledglings, and 6 of these were detected using them. For Ovenbirds clearcuts were identified as being available

to 8 individuals. Although all of these Ovenbirds were documented in regenerating clearcuts, half of them were only located once within this habitat type. In contrast, 86% (25/29) of Ovenbird and 93% (26/28) of Worm-eating Warbler fledglings were documented using riparian or roadside edge habitat. In addition to substantial use of riparian and edge habitat, fledglings frequently utilized dense vegetation within tree-fall gaps or even within the branches of recently fallen trees (Vitz pers. obs.).

Survivorship

Overall mortality was similar for the two species and was documented for 17 of the 53 radio-tagged Ovenbirds and 14 of the 60 radio-tagged Worm-eating Warblers. We focused on survival estimates for the highest ranked time model (Table 2.2, daily survival estimated for 3 time periods) rather than higher ranked alternative models incorporating covariates to facilitate comparisons with previous studies that commonly used Kaplan-Meier estimates (but see tables 2.2-2.5 for survival estimates from all models). Survival probability of fledgling Ovenbirds was 65% through the first 51 days after fledging. Daily survival was lowest during the first week (0.967 ± 0.10 SE), increased slightly during the second week (0.985 ± 0.007 SE), and sharply increased after the second week (0.998 ± 0.002 SE) following fledging (Fig. 2.3). For Worm-eating Warblers the top time model in program MARK was the model estimating daily survival for two time periods (Table 2.3). This model identified a 67% probability of surviving the 31 day period following fledging. Daily survival was lowest during the first 5 days (0.976 ± 0.009 SE) and increased but remained constant for the remainder of the period (0.990 ± 0.004 SE, Fig. 2.3).

The most important covariates in our Ovenbird models were the number of woody stems and the bird's energetic condition. The top model for Ovenbirds identified in program MARK included 3 time periods for survival and covariates for the number of woody stems and the bird's condition at fledging applied only to the first time period (Table 2.4). A closely ranked alternative model included these same parameters with the addition of a time of season covariate that identified early and late fledging individuals. In fact, individuals that fledged before 15 June (early) had a 69% (95% CI = 0.331-0.781) probability of survival, whereas those fledging on or after that date (late) had a survival rate of 57% (95% CI = 0.513 -0.827). For Ovenbirds the covariates identifying the number of nestlings, whether the nest was parasitized, and the nest's proximity to a clearcut did not greatly affect fledgling survivorship. The overall weight of evidence for models with woody stems as a covariate was 0.606 for Ovenbirds, as surviving individuals used habitats with 15% more woody stems (Fig. 2.4). Models containing energetic condition had a 0.738 weight of evidence for Ovenbirds and this variable was positively related to survival (Fig. 2.5).

The two most important covariates for Worm-eating Warblers also were woody stems and energetic condition. The top model identified for Worm-eating Warblers included 2 time periods for survival and covariates for the number of woody stems and the bird's condition applied to both time periods (Table 2.5). This model was nearly 1.5x more likely than the second best model, which was identical to the top model but included the number of nestlings as an additional covariate. For Worm-eating Warblers the covariates included in models with ΔAIC values <2 were

number of nestlings, brood parasitism, proximity to a clearcut, and time of season. An increased number of nestlings per nest, brood parasitism, closer proximity to a clearcut, and nestlings from early nests resulted in slightly lower post-fledging survivorship. Although the pattern between time of season and survival differed between Worm-eating Warblers and Ovenbirds, only 7 Worm-eating Warblers (compared to 18 Ovenbirds) were radio-tagged after 14 June. The overall weight of evidence for models with woody stems as a covariate was 0.631 for Worm-eating Warblers, as surviving individuals used habitats with 19% more woody stems (Fig. 2.4). Models containing energetic condition had a weight of evidence of 0.823 for Worm-eating Warblers as energetic condition was positively related to survival (Fig. 2.5).

Discussion

This study represents the first examination of post-fledging ecology for Worm-eating Warblers and only the second for Ovenbirds. Fledgling survival was similar for Ovenbirds (65%) and Worm-eating Warblers (67%) in southern Ohio. Similar to other studies, mortality rates were highest immediately after fledging and decreased as the birds gained flight capabilities (Anders et al. 1997; Berkeley et al. 2007; King et al. 2006; Naef-Daenzer et al. 2001; Sullivan 1989). In contrast to some (Anders et al. 1997; Sullivan 1989) but not other studies (Kershner et al. 2004), we failed to detect an increase in mortality once fledglings began foraging on their own.

Our data provide strong evidence that two species, whose breeding requirements are associated with large blocks of mature forest (Van Horn and

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Donovan 1994; Hanners and Patton 1998), select post-fledging habitats that differ

structurally from those used for breeding. This habitat shift from mature to early-

successional forest is widely regarded as a strategy to minimize predation by

facilitating access to protective cover to fledglings (Vega Rivera et al. 1998). We

found that during the post-fledging period Ovenbirds and Worm-eating Warblers used

areas with a higher density of woody stems than either paired random or nesting

locations, a result consistent with reports from other forest-breeding species (Anders

et al. 1998; King et al. 2006; Rush & Stutchbury 2008; Vega Rivera et al. 1998;

White et al. 2005). Some species may use early successional habitat during the post-

fledging period to gain access to the temporarily abundant fruit resources (Vega

Rivera et al. 1999; Vitz & Rodewald 2007; White et al. 2005).

This study is one of the first to examine the extent to which habitat use

influences fledgling survival. We documented that the probability of fledgling

survival for two mature forest breeders was positively associated with the number of

woody stems and an open canopy. In fact, surviving individuals of both species used

areas with approximately 20% more woody stems than non-surviving individuals.

Our results support those of King et al. (2006) who reported a positive relationship

between low vegetation structure and fledgling survival. Similarly, Hooded Warbler

fledglings in heavily cut areas with dense understory vegetation had a higher

survivorship (85%) than either those from less intensive cuts (37%) or in the absence

of forest harvest (51%, Stutchbury pers. comm.). These results reveal that dense

understory vegetation selected for by fledgling birds promote their survival, and

providing such habitat within a forested landscape may improve juvenile survivorship and increase recruitment into the population.

Numerous other variables also may help to explain variation in fledgling survival. We found that a bird's condition upon fledging and their survival probability were positively related for both Ovenbirds and Worm-eating Warblers. This finding is consistent with some (Dhondt 1979; Green & Cockburn 2001; Magrath 1991; Soler et al. 1994), but not all studies (Anders et al. 1997; Brown & Roth 2004). In fact, evidence exists that reduced nestling mass may increase lifetime reproduction, as heavier nestling Eurasian Blackbirds (*Turdus merula*) had an increased likelihood of breeding in the study region compared to lighter nestlings (Magrath 1991). Relationships between nestling mass and fledgling survival may be most prominent when food resources are low, which may explain the lack of consensus between studies (Krementz et al. 1989). We found some evidence that Ovenbirds fledging earlier in the season survived at a higher rate than those fledging later in the season when fewer arthropods may be available. Although Monros et al. (2002) found no relationship between fledgling mass and hatching date, they reported that mortality rates were up to 5x higher for later fledging individuals, but this trend may vary annually. Following a nest failure, a successful renesting attempt may incur substantial fitness consequences from higher post-fledging mortality (Naef-Daenzer et al. 2001) and reduced clutch size (Rowe et al. 1994). In addition to fledging time, fledgling survival may increase if parental care is provided by older adults (Rush & Stutchbury 2008), but it is less clear if the sex of the attending parent influences survival (Wheelwright et al. 2003). It has been suggested that parasitism by the

Brown-headed Cowbird reduces fledgling survival (Hoover and Reetz 2006). We did not find substantial evidence for increased fledgling mortality from brood parasitism by the Brown-headed Cowbird, but no study to date (including this one) has been specifically designed to test this. There also may be a trade off between fledgling survival and clutch size, although strong support for such a relationship has not been found in North America. However, in the Tropics the positive relationship between the number of fledglings and their mortality rate may drive the evolution for small clutch sizes in tropical birds (Styrsky et al. 2005).

Although biologists frequently consider fledgling survival to be constant across species, this may not be biologically appropriate as it fluctuates dramatically across species (Anders & Marshall 2005; Appendix 1). Such variation in post-fledging survival within and among species may be partly driven by landscape effects. Nesting success is often depressed in agricultural (Hoover et al. 1995) and urban (Phillips et al. 2005) landscapes, and even may be low in forested regions with certain land uses (Rodewald & Yahner 2001). Expecting a similar pattern for fledgling survival seems reasonable, particularly because the association between landscape and nesting success is thought to be driven by the increased abundance of predators (Hoover et al. 1995). Although we did not find substantial differences between fledgling survival from sites adjacent to clearcuts compared to those surrounded by mature forest, we note that all sites were located within a forested region. Fledgling survival for only a few species has been examined in both contiguous and fragmented landscapes. Hooded Warblers have been reported having substantially higher fledgling survival (51%) in a forested landscape in Ontario

(Stutchbury pers. comm.) compared to an agricultural landscape (19%) in Pennsylvania (Rush & Stutchbury 2008). However, within this agricultural matrix, forest patch size did not affect post-fledging survival suggesting that landscape composition rather than patch size characteristics may better predict habitat quality for fledglings of forest songbirds. In contrast, Wood Thrush fledglings have been documented having an extremely high survival rate (77%) in fragmented forests in Missouri, possibly a result of the extensive edge habitat in the region (Fink 2003). Unfortunately, the effects of landscape on fledgling survival of forest birds are not well understood because few studies have been conducted in heavily fragmented landscapes.

Conclusions

We achieved our objectives of identifying habitat selection, survivorship, and the influence of habitat on survival for fledgling Ovenbirds and Worm-eating Warblers. Because our results suggest that habitat characteristics may promote fledgling survival, there may be opportunities to reduce predation rates during the post-fledging period through habitat management. The dense woody vegetation and open canopy structure that was positively associated with survival can, for example, be created through silvicultural techniques, some of which may simultaneously provide breeding habitat for many early successional species. At the same time, though, managers should be cautious given that certain silvicultural practices, such as clearcutting, can reduce the amount of available breeding habitat for forest birds. For example, our study area in southern Ohio appears to contain abundant post-fledging habitat within the forested landscapes. Creating early successional habitat through

forestry practices may especially benefit forest bird populations in regions with heavy

herbivore browse (e.g. deer) where the forest interior lacks areas of dense vegetation

in the understory. Future studies should examine fledgling survival in landscapes

with differing forest management strategies in order to better understand how large-

scale forest planning can improve our ability to conserve bird populations. In

addition, more studies are needed to simultaneously examine nesting and post-

fledging mortality to gain insight into source/sink dynamics and how they vary

regionally.

	CC	WH	WT	RE	KH	WL	LH	Total
Ovenbird 2004	3	0	3	4	2	0	0	12
Ovenbird 2005	2	1	2	6	2	5	2	20
Ovenbird 2006	5	1	1	0	5	5	3	20
Worm-eating Warbler 2004	1	0	0	0	1	2	0	4
Worm-eating Warbler 2005	4	5	1	3	4	3	3	23
Worm-eating Warbler 2006	5	2	3	0	4	5	4	23
Worm-eating Warbler 2007	7	0	0	0	0	0	3	10

Table 2.1. The number of radio-tagged Ovenbirds and Worm-eating Warblers by site in southern Ohio, 2004-2007. Sites adjacent to a clearcut included CC, WH, WT, and RE. Sites surrounded by additional mature forest included KH, WL, and LH.

Model	AIC$_c$	ΔAIC$_c$	AIC$_c$ weight	k	Deviance	ϕ	SE	95% CI
ϕ t3	172.37	0.00	0.47	3	166.36	0.651	0.070	0.505-0.774
ϕ t4	172.94	0.56	0.35	4	164.91	0.642	0.073	0.490-0.770
ϕ t2	175.15	2.78	0.12	2	171.14	0.622	0.075	0.469-0.755
ϕ t trend	176.28	3.90	0.07	2	172.27	0.659	0.068	0.516-0.778
ϕ	186.89	14.53	0.00	1	184.89	0.547	0.080	0.391-0.695
ϕ t daily	246.75	74.37	0.00	51	140.94	0.643	0.073	0.490-0.771

Table 2.2. Results from Ovenbird (n = 51) time models using Akaike's Information

Criterion corrected for small sample sizes (AIC$_c$) generated from known fate models

in program MARK. The parameters in these models include time models with 2-4

periods (t2, t3, t4) with unique survival estimates, a constant survival (ϕ), daily

survival estimates (daily), and a model specifying a daily trend in survival (trend).

Model	AIC_c	ΔAIC_c	AIC_c weight	k	Deviance	ϕ	SE	95% CI
ϕ_{t2}	147.777	0.000	0.349	2	143.765	0.674	0.076	0.512-0.803
ϕ	148.238	0.461	0.277	1	146.234	0.635	0.077	0.475-0.769
ϕ_{t3}	149.078	1.301	0.182	3	143.053	0.655	0.083	0.480-0.796
$\phi_{t\,trend}$	149.831	2.054	0.125	2	145.819	0.668	0.086	0.485-0.811
ϕ_{t4}	151.077	3.300	0.067	4	143.035	0.649	0.094	0.452-0.806
$\phi_{t\,daily}$	186.340	38.562	0.000	31	122.206	0.651	0.093	0.455-0.807

Table 2.3. Results from Worm-eating Warbler (n = 60) time models using Akaike's

Information Criterion corrected for small sample sizes (AIC_c) generated from known

fate models in program MARK. The parameters in these models include time models

with 2-4 periods (t2, t3, t4) with unique survival estimates, a constant survival

(ϕ), daily survival estimates (daily), and a model specifying a daily trend in survival

(trend).

Model	AIC_c	ΔAIC_c	AIC_c weight	k	Deviance	ϕ	SE	95% CI
$\phi_{t3+stem+cond1}$	168.822	0.000	0.274	5	158.780	0.689	0.074	0.530-0.813
$\phi_{t3+stem+cond1+sea}$	169.335	0.514	0.212	6	157.277	0.693	0.074	0.533-0.818
$\phi_{t3+cond1}$	170.694	1.872	0.107	4	162.666	0.669	0.072	0.517-0.793
$\phi_{t3+stem}$	171.493	2.671	0.072	4	163.465	0.664	0.072	0.513-0.788
$\phi_{t3+cond1+sea}$	171.793	2.972	0.062	5	161.752	0.672	0.072	0.518-0.796
$\phi_{t3+cond}$	172.292	3.470	0.048	4	164.264	0.660	0.071	0.511-0.783
ϕ_{t3}	172.374	3.552	0.046	3	166.357	0.651	0.070	0.505-0.774
$\phi_{t3+stem+cut}$	172.821	3.999	0.037	5	162.780	0.668	0.072	0.515-0.792
ϕ_{t3+sea}	173.678	4.856	0.024	4	165.650	0.653	0.071	0.505-0.776
$\phi_{t3+stem+cond1+sea+para+nestl+cut}$	173.735	4.913	0.023	9	155.610	0.706	0.075	0.541-0.830
$\phi_{t3+cond1+para+nestl}$	173.903	5.081	0.022	6	161.845	0.672	0.072	0.518-0.796
$\phi_{t3+para}$	174.022	5.200	0.020	4	165.994	0.653	0.071	0.505-0.776
ϕ_{t3+cut}	174.140	5.319	0.019	4	166.113	0.653	0.070	0.505-0.776
$\phi_{t3+nestl}$	174.366	5.544	0.017	4	166.338	0.651	0.070	0.504-0.774
ϕ_{t3*yr}	174.485	5.663	0.016	7	160.407	.	.	.

Table 2.4. Results from Ovenbird (n = 51) survival models using Akaike's Information Criterion for small sample sizes (AIC_c) generated from known fate models in program MARK. The parameters in these models include 3 time periods (t3), number of woody stems (stem), energetic condition applied only to the first time period (cond1), energetic condition applied to each time period (cond), time of season of fledging (sea), proximity to a clearcut (cut), number of nestlings (nestl), whether the nest was parasitized (para), and year (yr).

Model	AIC_c	ΔAIC_c	AIC_c weight	k	Deviance	ϕ	SE	95% CI
$\phi_{t3+stem+cond}$	142.078	0.000	0.331	4	134.037	0.688	0.081	0.513-0.822
$\phi_{t3+stem+cond+sea}$	143.045	0.967	0.204	5	132.983	0.703	0.081	0.525-0.835
$\phi_{t3+cond}$	144.061	1.983	0.123	3	138.036	0.699	0.078	0.528-0.828
$\phi_{t3+cond+sea}$	145.088	3.009	0.073	4	137.046	0.709	0.078	0.536-0.837
$\phi_{t3+stem}$	145.221	3.142	0.069	3	139.196	0.680	0.080	0.509-0.814
$\phi_{t3+cond+para+nestl}$	145.324	3.246	0.065	5	135.261	0.719	0.080	0.540-0.847
$\phi_{t3+cond1}$	146.898	4.820	0.030	3	140.873	0.686	0.077	0.520-0.815
$\phi_{t3+stem+cut}$	147.064	4.985	0.027	4	139.022	0.678	0.080	0.507-0.812
$\phi_{t3+full}$	147.490	5.412	0.022	8	131.339	0.717	0.082	0.533-0.849
ϕ_{t3}	147.777	5.699	0.019	2	143.765	0.674	0.076	0.512-0.803
ϕ_{t3+cut}	148.750	6.671	0.012	3	142.724	0.675	0.077	0.510-0.805
$\phi_{t3+nestl}$	149.233	7.154	0.009	3	143.208	0.681	0.076	0.517-0.809
$\phi_{t3+para}$	149.407	7.329	0.008	3	143.382	0.673	0.076	0.510-0.802
ϕ_{t3+sea}	149.559	7.481	0.008	3	143.534	0.678	0.076	0.515-0.807
ϕ_{t3*yr}	157.039	14.961	0.000	8	140.888	.	.	.

Table 2.5. Results from Worm-eating Warbler (n = 60) survival models using Akaike's Information Criterion corrected for small sample sizes (AIC_c) generated from known fate models in program MARK. The parameters in these models include 3 time periods (t3), number of woody stems (stem), energetic condition applied only to the first time period (cond1), energetic condition applied to each time period (cond), time of season of fledging (sea), proximity to a clearcut (cut), number of nestlings (nestl), whether the nest was parasitized (para), and year (yr).
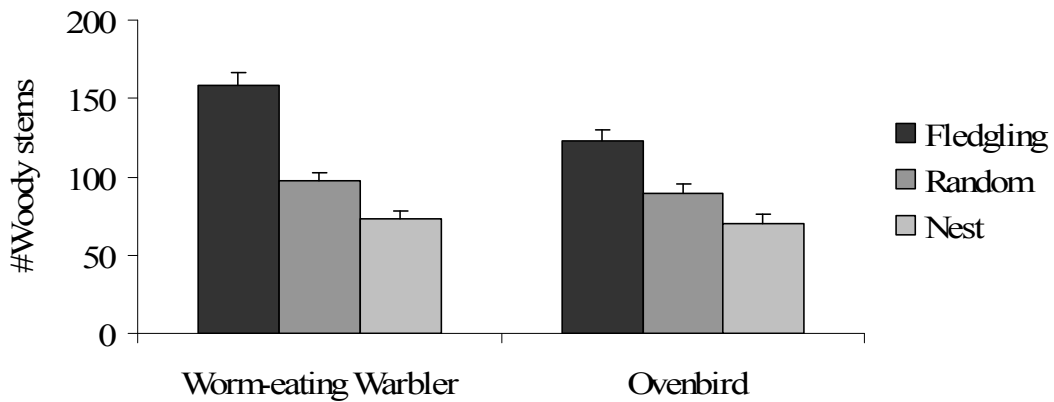
Figure 2.1. The mean number (+ SE bars) of woody stems at fledgling (n = 56), random (n = 56), and nest locations (n = 59) for Worm-eating Warblers and fledgling (n = 38). random (n = 38), and nest (n = 49) locations for Ovenbirds in southern Ohio.
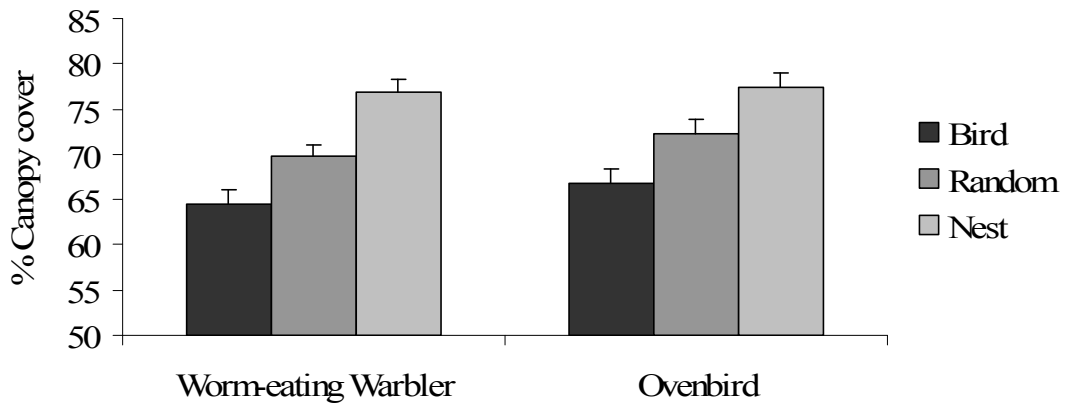
Figure 2.2. The mean percent canopy cover (+ SE bars) at fledgling (n = 56), random (n = 56), and nest locations (n = 59) for Worm-eating Warblers and fledgling (n = 38). random (n = 38), and nest (n = 49) locations for Ovenbirds in southern Ohio.
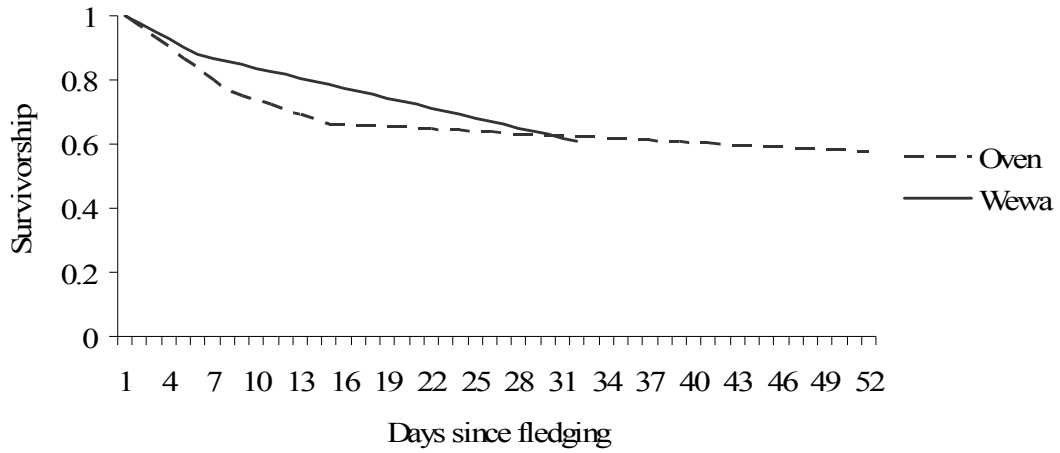
Figure 2.3. Cumulative survivorship using estimates from the top ranked time model for Ovenbirds (n = 51) and Worm-eating Warblers (n = 60) in southeast Ohio.
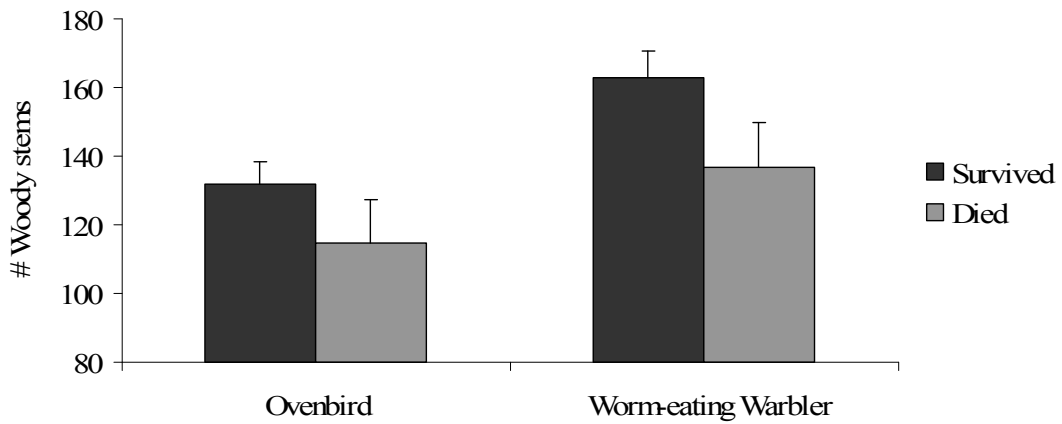
Figure 2.4. The mean number (+ SE bars) of woody stems at Ovenbird locations of individuals that survived (n = 34) and died (n = 16) and at Worm-eating Warbler locations of individuals that survived (n = 46) and died (n = 13) during the post-fledging period in southern Ohio.
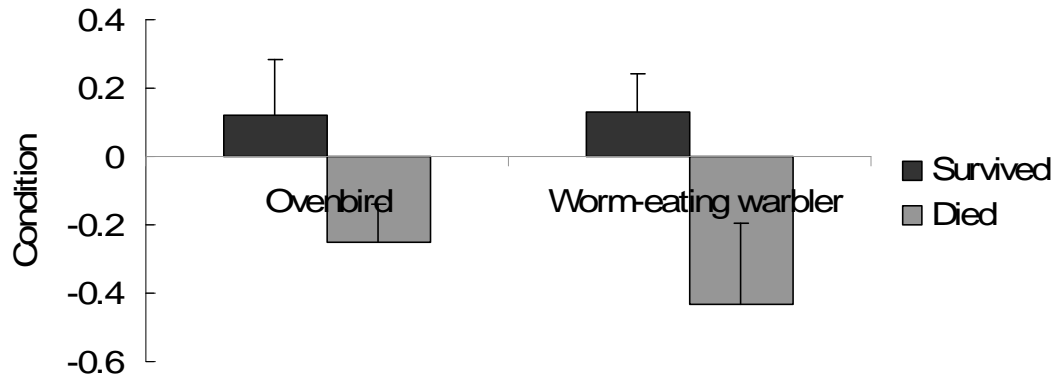
Figure 2.5. The mean energetic condition (+ SE bars) upon fledging for Ovenbirds that survived (n = 34) and died (n = 17) and for Worm-eating Warblers that survived (n = 46) and died (n = 14) during the post-fledging period in southern Ohio.

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CHAPTER 3

SURVIVAL AND MOVEMENT PATTERNS FOR A JUVENILE SONGBIRD:
AN EXPERIMENTAL APPROACH

Abstract

What is known about independent juvenile songbirds during the post-fledging

period comes from a few observational studies. One of the most commonly described

patterns is a pronounced shift in habitat use from mature-forest to successional

habitats displayed by many species. The objectives of this study were to

experimentally test the extent to which access to and use of regenerating clearcuts

influenced habitat use, survival, and movements of independent juvenile Ovenbirds

(*Seiurus aurocapilla*). Between 2004-2006 we radio-tagged 85 Ovenbirds that were

captured using passively managed mist-nets in regenerating clearcuts. Radio-tagged

Ovenbirds were placed into three experimental groups 1) released in original clearcut

of capture, 2) moved to and released in a different clearcut, and 3) moved to and

released in a mature forest habitat. Survival patterns were evaluated using known fate

models in program MARK. We did not detect evidence of a difference in survival

among the three experimental groups. Using the top time model (constant survival

across the 52 day period) with all data combined survival throughout the period was

83%. Compared to random locations, actual juvenile locations were characterized by

denser understory vegetation, a habitat attribute that, along with the energetic

condition at time of capture, promoted survival. Interestingly, Ovenbirds released

into mature forest habitat traveled farther from their release location after both 7 and

14 days compared to birds released into both clearcut treatments. We found no

evidence that Ovenbirds preferentially moved in either a northern or southern

direction. As a whole, these results suggest that dense understory vegetation may be

a critical habitat feature defining suitable post-fledging habitat. Although such

habitat is found in regenerating clearcuts, alternative suitable habitat (i.e., riparian

thicket, tree-fall gap) is frequently provided within the mature forest.

Introduction

Ecologists now recognize that the post-fledging period, which begins with

fledging and extends until the initiation of fall migration, is important to consider

when evaluating adult productivity and population viability (Anders & Marshall

2005). In fact, the post-fledging stage of the annual life cycle may represent the

period of greatest mortality rates, which frequently exceed 50% during the first few

weeks after leaving the nest (Anders et al. 1997; Berkeley et al. 2007). This high

mortality is generally attributed to the fact that juveniles have limited mobility and

are inexperienced at foraging and evading predators (Anders et al. 1997; Naef-

Daenzer et al. 2001). The vulnerability experienced by birds during the post-fledging

period may be responsible for a widely documented post-breeding habitat shift, where

mature forest birds shift to using successional habitats characterized by an open

understory into areas with dense vegetation in the understory (Anders et al. 1997;

Vega Rivera et al. 1998), including regenerating clearcuts (Marshall et al. 2003;

Pagen et al. 2000; Vitz & Rodewald 2006). Indeed, nearly all mature forest breeding

birds in southern Ohio were captured in shrubby regenerating clearcuts, with over 70% of birds being juveniles (Vitz & Rodewald 2006). Using areas with dense vegetation may be an adaptive response to mitigate high risk of predation faced by juvenile birds (King et al. 2006, Chapter 2), but to our knowledge no studies have explicitly examined if use of successional habitats promotes survival of juvenile birds. Furthermore, no studies to date have evaluated the extent to which habitat use influences survival for independent juveniles.

Movements and habitat use of independent juvenile birds during the post-fledging period may be guided by a number of factors. Independent juveniles may concentrate their activities in areas with high food abundance and thick cover to minimize risk of starvation and predation. During the post-fledging period juveniles must acquire enough resources to complete their first pre-basic molt and store fat reserves for migration (Murphy & King 1992). Other activities during this period may include prospecting for future breeding locations (Reed et al. 1999), and the development of a search image of the area to facilitate return in subsequent years (Baker 1993).

Over the last decade, an increasing amount of attention and number of publications have been devoted to post-fledging ecology (Chapter 1). Although these data have been critical for identifying patterns of survivorship and habitat use, nearly all of these employed an observational approach, limiting their ability to evaluate causal relationships (Garton et al. 2001). Experimental manipulations are seldom incorporated in radio-telemetry studies and are virtually absent from post-fledging research (Garton et al. 2001). The single manipulative post-fledging study of which

we are aware has prompted new insights on life history evolution, particularly

regarding clutch size evolution in tropical birds (Styrsky et al. 2005).

Objectives

We studied habitat use, survivorship, and movement ecology for independent

juvenile Ovenbirds (*Seiurus aurocapilla*). Specifically, we (1) experimentally tested

if access to regenerating clearcuts was associated with higher survival rates of

independent juvenile Ovenbirds, (2) identified habitat features selected by juveniles,

(3) assessed the ways in which habitat influenced movement behavior, and (4)

evaluated if movements were consistent with premigratory movements to the south.

Methods

Study sites

This study was conducted between 2004-2006 in southeast Ohio in Athens

and Vinton Counties. Study sites were located in the Zaleski State Forest, Lake Hope

State Park, and MeadWestvaco forest lands. The area is located within the Ohio Hills

physiographic region and is characterized by a mixed-mesophytic forest. These

forests have regenerated from large scale clearcutting in the early 1900's and are

currently perforated by small regenerating clearcuts (typically between 4-20 ha) with

non-forest land (i.e., small towns and agriculture) occurring in some valleys.

Independent juvenile Ovenbirds were captured in regenerating hardwood

clearcuts (4-10 years post harvest) using 7-9 passively managed mist-nets (12 m long,

2.6 m high, 30 mm mesh) between 27 June – 3 August. Mist-nets were opened 0.5

hour before sunrise, checked every 30 minutes, and closed 4.5 hours later when nets became exposed to direct sunlight and capture rates greatly decreased. In 2004, birds were captured in six clearcuts ranging in size from 4-16 ha and were spatially separated by a minimum of 4 km. However, only four of these sites were utilized in 2005 and three in 2006 (Table 3.1). Once captured, individuals were identified as juveniles using criteria based on plumage characteristics and skull ossification (Pyle 1997). Each bird was banded with a USGS numbered aluminum band and fitted with a radio-transmitter (0.90g, BD-2, Holohil Systems Ltd.) using the leg-loop harness technique (Rappole & Tipton 1991). To minimize any negative effects, transmitters weighed < 5% of the Ovenbirds' body mass, and the leg loops were composed of an elastic cotton/nylon blend that fit the bird from day 1 while allowing for growth due to pre-migratory fattening. Basic morphological measurements (i.e., wing and tarsus length) and mass were recorded for all radio-tagged birds. Initially, radios used on these birds were designed to last for six weeks. However, in 2004 a number of radio-tagged Ovenbirds frequently went undetected limiting the amount of data collected. In an attempt to minimize such data loss, transmitter signals were amplified at the expense of the battery life. As a result, transmitters used in 2005 and 2006 were intended to function for 4 weeks following activation.

Each radio-tagged individual was randomly assigned to one of three treatment groups. Birds assigned to treatment 1 were released in the original clearcut of capture. Treatment 2 birds were transported to a different regenerating clearcut, and birds assigned to treatment 3 were released into mature forest habitat (> 400m from a clearcut). To minimize bias associated with holding and transporting birds, all birds

were held for comparable periods and transported in a vehicle for a similar distance and time (with birds from treatment 1 simply returned to their original location).

Radio-tracking

Birds were tracked using ATS R2000 receivers and 3 element folding, aluminum yagi antennas (Advanced Telemetry Systems). The transmitters' signals could be detected by the receivers between 400-1100 meters, but varied with the birds topographic (on a ridge or in a valley) and foraging (i.e., on the ground or in a tree) location. If an individual was not found for several days and an expired battery was not suspected, an airplane (Partenavia P68), owned by the Ohio Division of Natural Resources, wired for radio-telemetry, was used to traverse the study region and facilitate their location.

Habitat use

Radio-tagged Ovenbirds were located daily using the homing method, which involved approaching the bird on foot until a visual observation was confirmed. Once located, GPS (global positioning systems) coordinates were recorded (Magellan Meridian), the habitat type was identified (i.e., early successional, mid successional, mature forest), and data on micro habitat characteristics (i.e., number of saplings, canopy cover) were recorded within a 0.04 ha circle at bird locations and paired random locations. Random locations were identified by walking 50 m at a random direction from actual bird locations. Data collected included a tally of the number of woody stems (< 8 cm dbh and taller than 0.5 m) and the number of small (8-23 cm dbh), medium (>23-38 cm dbh), and large (>38 cm dbh) trees. In addition, percent canopy cover was visually estimated. We believe this estimate accurately reflects

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biological differences due to the extensive training we provided crews and in light of

our primary interest being relative differences in canopy cover between actual and

random locations. Data from all environmental variables were averaged over each

individual, as we considered the individual as the appropriate replicate (Garton et al.

2001). Habitat differences between actual and random locations were examined

using multiple variables in a discriminant function analysis. If a significant

difference was found, we used general linear models to examine variables separately

(SAS Institute 1990). To meet the assumption of normality several variables were

transformed. Normality was achieved for all variables except the percent of canopy

cover which approached normality.

Survivorship

Independent juvenile Ovenbird survival was estimated using known fate

models in program MARK (White & Burnham 1999). These models are similar to

the Kaplan-Meier product-limit estimator, but are advantageous because they allow

for the evaluation of biological covariates and the comparison of alternative models

(White & Burnham 1999). We examined whether survival during the post-fledging

period was time dependent, varied by year, and used biologically meaningful

covariates to build, evaluate, and rank *a priori* models using Akaike's Information

Criterion (AIC). To evaluate time dependent survival we combined data for the three

treatments. To examine whether survival varied within a season we evaluated early

(days 1-26) and late (days 27-52) periods separately. Yearly variation was evaluated

by treating data from each year as separate groups in program MARK. The top time

model was used as the base model to evaluate survival for the three release treatments

and include biological covariates. To increase our ability to test for relationships between clearcuts and survival, we also ran models after combining data from the 2 clearcut groups. Individual covariates incorporated into this analysis included the average number of woody stems at individual bird locations and the bird's energetic condition at the time of radio-tagging. Energetic condition was determined by the residual from a regression of the first axis of a principal components analysis (PCA) containing structural characteristics (tarsus and wing cord) and mass (Green 2001). To account for small sample sizes we used the corrected Akaike's Information Criterion (AIC_c) to rank candidate models according to parsimony (Burnham & Anderson 2002). Models with a ΔAIC_c value within 2 of the top model were considered equally plausible given the data (Burnham & Anderson 2002).

Movements

To evaluate movement patterns, all Ovenbird locations were downloaded into ArcView 3.2. We used the Animal Movement extension (Hooge and Eichenlaub 1997) to calculate successive distances between daily locations, as well as the distance between daily locations and capture and release locations. We examined patterns among treatments in the distance between release locations and actual locations after 7, 14, and 21 days using general linear models (SAS Institute 1990). These increments were chosen because they reflect movements over the course of the study period. All data met the assumption of normality.

We examined whether birds demonstrated a southward drift during the post-fledging period (Baker 1993). Because translocating birds may influence their movements, for this analysis we only used individuals that were released into the

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original clearcut of capture. For each individual we calculated the direction of movement (0-360 degrees) between the first and last documented locations. Because we were interested in whether juveniles moved in a southerly direction, individuals were removed (one bird) from this analysis if they demonstrated a strong movement to the east or west (if the movement was within 20° of 90° or 270° it was removed). In addition, birds that moved less than 500 m were removed (4 birds) from the analysis because they did not demonstrate a substantial movement. Movements of the other individuals (n = 22) were identified as either in a northern or southern direction. Specifying an equal probability to move north or south, a chi square analysis was performed to evaluate if juvenile Ovenbirds were more inclined to move in a particular direction.

Results

Between 2004-2006 we radio-tagged 85 independent juvenile Ovenbirds. Of these, 28 Ovenbirds were captured in 2004, 33 in 2005, and 24 in 2006. Twenty-eight Ovenbirds were released in the original clearcut of capture, 29 were moved to a different clearcut, and 28 were transported to a mature forest habitat > 400 m from any type of forest harvest (Table 3.2; Appendix F). Ovenbirds were captured between 2 July and 3 August with the latest bird being tracked until 23 August. Translocated birds were moved 4.8 – 18.4 km from their capture origin. On average individuals released in a different clearcut were moved 8.12 km ($\pm$ 0.71 SE), and those released in mature forest habitat were transported 8.61 km ($\pm$ 0.39 SE). Following release, individuals were tracked between 0-43 days. Because large daily

movements were common, many individuals were not detected every day. Although a few birds remained in the region for the duration of their transmitter lifespan, many radio signals went undetected before their projected expiration, likely a result of individuals leaving the study region.

Independent juvenile Ovenbirds were similar to adults in both size and plumage and had developed strong flight capabilities making them less vulnerable to predation than newly fledged juveniles. In total, mortality was confirmed for five individuals. Of these, two were included in the mature forest treatment, and three were released in the same clearcut of capture. Predation appeared to be the cause of mortality in all but one case. Although we were not able to witness any predation events, available evidence (i.e., beak impressions on the radios, plucked feathers) suggested that 4 mortalities were from raptors. Forest hawks breeding in the area included Broad-winged (*Buteo platypterus*), Cooper's (*Accipiter cooperii*), and Sharp-shinned hawks (*Accipiter striatus*). The final mortality appeared to be cause by a collision with a vehicle as the bird was found intact on the side of a state highway (Appendix F).

Survival models

The top time model incorporated a constant rate of survival within and between seasons. The model specifying a constant between year survival and separate early and late season survival estimate had an ΔAIC_c value less than two and can be considered plausible given the data (Table 3.3, Burnham and Anderson 2002). Using the top time model, daily survival rate of independent juvenile Ovenbirds was estimated to be 0.996 (SE = 0.002), which resulted in 83% of individuals surviving

the 52 day period (Table 3.3, Figure 3.1). When examining the three treatments separately the highest mean ($\pm$ SE) survival probability was associated with birds moved to a clearcut (0.897 $\pm$ 0.097), followed by those released in the original clearcut (0.820 $\pm$ 0.115) and, showing the lowest survival rates were birds released into mature forest habitat (0.777 $\pm$ 0.138). The top time model was emphasized over higher ranked models incorporating covariates, because it is more easily compared to previous studies that commonly used Kaplan-Meier estimates; however, survival estimates were derived for all models (Table 3.3). The top time model was used as a base for building models containing biological covariates.

The top overall model included the covariate for the average number of woody stems at locations for each Ovenbird. However, the models including both average number of woody stems and birds' energetic condition at the time of radio-tagging, as well as the model only containing energetic condition also were highly ranked (Table 3.4). Models containing woody stems had a 0.632 weight of evidence, and surviving juvenile Ovenbirds used areas with 1.5x as many woody stems and demonstrated a higher mean (SE) energetic condition (0.030 $\pm$ 0.085) than those that did not survive (-0.478 $\pm$ 0.368; Table 3.5). The most basic model with no covariates and a constant survivorship within and between seasons also had an AIC value under two. Neither the top time model nor models containing covariates provided evidence that survival differed among the three treatments. In addition, no difference was found in survival between birds released at clearcut sites and those released into mature forest when the two clearcut treatments were combined into a single category. In fact, all models that generated separate survival estimates using either two or three

treatments had AIC values greater than two and thus, garnered less support from the data (Table 3.4).

Habitat

We found that habitat used by independent juvenile Ovenbirds differed from habitat at paired random locations (Wilks' Lambda $F_{5,106} = 3.75$, $P < 0.004$). Specifically, there were significantly more (1.4x more) woody stems at actual compared to random locations ($F_{1,110} = 10.52$, $P = 0.002$; Figure 3.2). However, no difference was detected between used and random locations in percent canopy cover ($F_{1,110} = 0.99$, $P = 0.322$) and the numbers of small ($F_{1,110} = 0.100$, $P = 0.754$), medium ($F_{1,110} = 0.34$, $P = 0.560$), and large trees ($F_{1,110} = 1.25$, $P = 0.266$).

Movements

Independent juvenile Ovenbirds showed substantial variation in the overall distance they moved away from the release location. For each experimental treatment, Ovenbirds gradually moved farther from the release location during the first four weeks following release. Over the entire period, Ovenbirds translocated to mature forest habitat consistently moved the greatest distances, those moved to a different clearcut showed intermediate movements, and the shortest distances were revealed for birds released in the original clearcut of capture. In fact, we found a significant difference among the 3 treatments in the distance they had moved from the release location after both 7 ($F_{2,51} = 3.34$, $P = 0.043$) and 14 days ($F_{2,40} = 8.79$, $P = 0.001$) following release (Figure 3.3). A post-hoc analysis revealed that birds relocated to mature forest moved significantly father than those released in their original clearcut treatments after both 7 ($F_{1,33} = 6.92$, $P = 0.013$) and 14 days ($F_{1,28} =$

19.34, P < 0.001). Although a significant difference was not detected 21 days ($F_{2,30}$ = 1.56, P = 0.226) following release, the same trend persisted.

The mean distances between capture and release locations for Ovenbirds released in mature forest habitat and those moved to a clearcut were 8611 m (SE = 387 m) and 8117 m (SE = 705 m), respectively. Although few radio-tagged Ovenbirds returned to the vicinity of their capture location, several individuals did return and settle in those areas. This was most clearly exemplified by an individual in 2004 that was translocated nearly 18.5 km to the south. This individual remained in the vicinity of its release site for 3 days, was located midway between its release and capture locations, and was found 6 days later approximately 1 km from the original capture location where it remained for 7 days before disappearing altogether.

To examine directional post-fledging movements and evaluate the hypothesis that birds generally drift south during the post-fledging period, we incorporated data from 22 birds in the control (original clearcut) treatment. We did not find any evidence that independent juvenile Ovenbirds showed a preference to move either south or north [χ^2 (1, n = 22) 0.727, p = 0.394]. Overall, 13 and 9 independent juvenile Ovenbirds were documented moving in a northerly and southerly direction, respectively.

Discussion

Habitat and survival

This is the first study to examine survival rates of independent juveniles and to experimentally test relationships between habitat use and survival rates. Results

from our experiment do not support the idea that access to large patches of early-successional habitat promotes survival of independent juvenile birds. As such, we found similar survival rates (78-90% over 52 days) for independent juvenile Ovenbirds irrespective of release habitat.

Although elevated mortality rates have been reported for fledglings immediately after they leave the nest (Berkeley et al. 2007; Naef-Daenzer et al. 2001) and once they begin foraging on their own (Anders et al. 1997; Sullivan 1989), we found relatively low rates of mortality for independent juvenile Ovenbirds. Similarly, Wood Thrush (*Hylocichla mustelina*) and Eastern Meadowlarks (*Sturnella magna*) are known to suffer little to no mortality following natal dispersal (Anders et al. 1997; Kershner et al. 2004). Independent juveniles are full grown and are skilled fliers, which presumably should make them less vulnerable to predation than younger fledglings. Conversely, some have suggested that following independence juvenile birds suffer high mortality rates (Nilsson & Smith 1985), possibly a result of extensive wandering (Morton 1992). Indeed, this pattern was revealed for Great Tits (*Parus major*) with high mortality reported for several months after fledging (Dhondt 1979). Similarly, Yellow-eyed Juncos (*Junco phaeonotus*) were reported having a 53% mortality rate between reaching independence and the end of the summer with the majority of mortality occurring during the first two weeks following independence (Sullivan 1989). Collectively, these high mortality rates by independent juveniles may be explained by an increase in mortality associated with dispersal (Dufty & Belthoff 2001; Yoder et al. 2004; but see Small et al. 1993), and

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following dispersal they may continue to lack the experience necessary to survive
(Powell et al. 2000).

Independent juveniles lack extensive experience in foraging and detecting and
evading predators and probably encounter higher mortality rates than adults (Lack
1954; Sullivan 1989). Starvation may be most acute as juveniles gain independence.
During this transition, all juvenile Yellow-eyed Juncos initially lost mass, and those
with the highest proportion of weight loss disappeared from the population and
probably died of starvation (Sullivan 1989). Although we did not find evidence that
starvation directly caused mortality, long foraging bouts necessary to maintain a
positive energy budget may increase predation risk (Wunderle 1991). One such
example of inexperience increasing predation risk includes an observation of an
independent juvenile Ovenbird repeatedly and precariously dive-bombing a black-rat
snake (*Elaphe obsolete*), despite the fact that this individual would seem to have little
to gain from such an activity. We found evidence that the primary predators for
independent juvenile Ovenbirds were raptors, which was similar to results reported
for Wood Thrush fledglings (Anders et al. 1997). In Europe, breeding Sparrowhawks
(*Accipiter nisus*) primarily prey on songbird fledglings, and they switch prey species
to match fledgling availability (Newton & Marquiss 1982). Still, other sources of
mortality for fledglings may be quite common. For example, one individual was
found dead on the side of a state highway and appeared to be the victim of a collision
with a vehicle. On a related project, one Ovenbird that had gained independence and
dispersed away from its natal territory was depredated by a black-rat snake and
another was depredated by a domestic cat (*Felis silvestris*). Elevated mortality rates

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for juvenile birds have been found to extend through the winter (Johnson et al. 2006), and may be exacerbated by their subordinate status and the floater strategy employed by many juvenile birds (Rappole et al. 1989).

Although we did not find evidence for treatment effects, our data clearly show that habitat structure affected survival rates. Not only did independent juvenile Ovenbirds use areas with significantly more woody stems than random locations, but that use promoted survival. Surviving individuals used habitat with 1.5x more woody stems than birds that did not survive the period. To our knowledge the only other study to examine links between habitat use and survival found that the use of dense understory vegetation increased survival for fledgling Ovenbirds (King et al. 2006). More often reported is that fledglings frequently use habitat with more dense vegetation than their nesting habitat (Vega Rivera et al. 1998; Wells et al. 2007). Cases failing to show this pattern (e.g., fledgling Eastern Meadowlarks, *Sturnella magna*; Guzy & Ribic 2007) are the exception and may be due to the fact that nesting habitats already provide dense vegetation (e.g., as for shrub-successional breeders), giving little incentive to move.

Our results show that independent juvenile Ovenbirds of higher energetic condition had greater probability of survival.   This is consistent with studies of nestlings that have demonstrated higher survival for individuals with a higher energetic condition or body mass (Green & Cockburn 2001; Magrath 1991; Naef-Daenzer et al. 2001; but see Anders et al. 1997). Individuals demonstrating a high energetic condition are likely using high quality post-fledging habitat, which may accelerate the molting and premigratory fattening process. This may allow juveniles

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to initiate migration earlier, permitting them to reach their wintering ground more rapidly. An early arrival on the winter grounds should increase their probability of securing a high quality territory, promoting over-winter survival (Rappole et al. 1989). Such carry-over effects have been documented from wintering to breeding grounds (Marra et al. 1998), and a similar phenomenon may exist linking post-fledging and wintering areas.

Movements

A number of competing hypotheses have been suggested to explain extensive movements by juvenile birds during the post-fledging period. One explanation is a form of dispersal known as prospecting, which is a complex evolutionary strategy that aides breeding habitat selection (Cody 1985). For example, the end of the breeding season may be the most appropriate time to prospect, and indeed, evidence suggests that breeding sites are selected in late summer by juvenile Field Sparrows (*Spizella pusilla*; Adams & Brewer 1981) and White-crowned Sparrows (*Zonotrichia leucophrys*; Morton 1992) as well as several other passerines (reviewed in Reed et al. 1999). Although prospecting may expedite breeding activity in spring, the costs of prospecting for a juvenile Neotropical migratory bird may outweigh the benefits as movements in unfamiliar areas are thought to increase predation risk (Dufty & Belthoff 2001; Yoder et al. 2004), and many juveniles will not survive to breed the following summer (Lack 1954). In the end, while biologists recognize that prospecting may influence some post-breeding movements (Reed et al. 1999), the phenomenon does not easily explain the use of non-breeding habitat.

Another function of extensive movements may be to create a navigational map that facilitates return to the area in subsequent years (Baker 1993; Morton 1992). Some movements may be driven by the search to locate appropriate staging areas where birds can molt and gain fat in preparation for migration. Juveniles may undergo extensive movements to locate pre-migratory flocks. Participation in flocks may be important for juvenile birds as they offer added protection from predation through group mobbing, and vigilance sharing can permit individuals to spend more time foraging (Caraco 1979). In fact, we frequently found radio-tagged Ovenbirds with groups of conspecifics as well as other species (Vitz pers. obs.), a pattern commonly reported from other studies (Nolan 1978; Vega Rivera et al. 1998).

Our work does not support the suggestion that extensive movements during the post-fledging period represent a gradual movement to the south. Rappole and Ballard (1987) had suggested southerly movements after capturing several species in late summer that were thought to be 100 km south of their breeding range, and none of the individuals showed any evidence of being in a migratory state (Rappole & Ballard 1987). However, similar to our results, Vega Rivera et al. (1998) failed to support this hypothesis. Although we did not find any evidence for a southward drift for birds that remained in the study region, the possibility exists that the majority of individuals that went permanently "missing" had left the area, gradually moving south.

Management Implications

Our data show that irrespective of access to regenerating clearcuts independent juvenile Ovenbirds have high survival rates (83%) over the 52-day period that we studied them. Rather than relying exclusively on large successional patches of habitat, birds also selected dense vegetation within mature forests and frequently used riparian thickets, roadside edges, and tree-fall gaps. The extensive movements demonstrated by independent juvenile Ovenbirds suggests that habitat features at the landscape scale should be seriously considered when addressing requirements for juvenile birds. Overall, the results from this study suggest that even-aged forest management, such as clearcutting, is not necessary to create appropriate post-fledging habitat for independent juvenile Ovenbirds, and other forest breeding songbirds likely follow a similar pattern. Instead, managers should manage for uneven-aged forests that contain the structural heterogeneity typical of old forests.

Site	Latitude	Longitude	2004	2005	2006
CCC	39º17'N	82º20'W	13	12	13
Webb Hollow	39º18'N	82º24'W	0	11	3
Will Tract	39º15'N	82º24'W	3	6	8
Kick Gate	39º12'N	82º22'W	5	4	0
Connaut	39º23'N	82º17'W	6	0	0
REMA1	39º09'N	82º23'W	1	0	0

Table 3.1. The number of independent juvenile Ovenbirds captured and radio-tagged at each site between 2004-2006 in southeast Ohio.

Year	Original Clearcut	Different Clearcut	Mature forest
2004	7	11	10
2005	13	10	10
2006	8	8	8

Table 3.2. The number of independent juvenile Ovenbirds released in each habitat

group between 2004-2006 in southeast Ohio.

Model/Year	AIC_c	ΔAIC_c	AIC_c weight	k	Deviance	ϕ	SE	95% CI
ϕ	68.475	0	0.618	1	33.280	0.832	0.068	0.656-0.928
ϕ_{per}	70.389	1.914	0.237	2	33.188	0.825	0.075	0.630-0.929
ϕ_{year}	72.178	3.703	0.097	3	32.969	0.889	0.105	0.500-0.985
2005						0.807	0.123	0.472-0.951
2006						0.810	0.121	0.478-0.952
$\phi_{year*per}$	73.615	5.140	0.047	6	28.363	0.872	0.120	0.455-0.982
2005						0.708	0.203	0.262-0.943
2006						0.841	0.103	0.540-0.960

Table 3.3. Time models for independent juvenile Ovenbird (n = 85) using known fate models in program MARK. The parameters in these models include a constant daily survival over a 52 day period (ϕ), early (days 1-26) and late (days 27-52) season periods (per), year effects (ϕ_{year}), and a year*season interaction ($\phi_{year*per}$).

Model/Treatment	AIC_c	ΔAIC_c	AIC_c weight	k	Deviance	ϕ	SE	95% CI
ϕ_{+stem}	66.626	0	0.220	2	62.617	0.900	0.068	0.670-0.975
$\phi_{+stem+cond}$	67.035	0.410	0.180	3	61.018	0.910	0.066	0.675-0.980
ϕ_{+cond}	67.466	0.840	0.145	2	63.457	0.867	0.070	0.664- 0.955
ϕ	68.475	1.849	0.087	1	66.472	0.832	0.068	0.656-0.928
$\phi_{2g+stem/clearcut}$	68.632	2.006	0.081	3	62.615	0.901	0.071	0.656-0.977
Mature forest	.	.	.	.	.	0.896	0.099	0.519-0.986
$\phi_{2g+stem+cond/clearcut}$	69.043	2.417	0.066	4	61.015	0.912	0.068	0.664-0.982
Mature forest	.	.	.	.	.	0.907	0.094	0.523-0.989
$\phi_{2g+cond/clearcut}$	69.310	2.684	0.058	3	63.293	0.881	0.073	0.653-0.967
Mature forest	.	.	.	.	.	0.831	0.124	0.464-0.966
$\phi_{3g+stem/original}$	69.672	3.046	0.048	4	61.643	0.850	0.112	0.503-0.970
Clearcut-moved	.	.	.	.	.	0.953	0.057	0.626-0.996
Mature forest	.	.	.	.	.	0.914	0.091	0.524-0.990

continued

Table 3.4. Survival estimates for independent juvenile Ovenbirds (n = 85) using known fate models in program MARK. The parameters in these models include constant daily survival over a 52 day period (ϕ), number of woody stems (stem), energetic condition upon capture (cond), survival estimated for 2 groups based on release habitat (clearcut or mature forest; 2g), and survival estimated for the 3 treatment release groups (original clearcut, moved clearcut, mature forest; 3g). Models incorporating separate treatment groups report separate survival estimates by treatment.

Table 3.4 (continued).

$\phi_{3g+stem+cond/clearcut}$	70.203	3.577	0.037	5	60.161	0.865	0.110	0.503-0.976
Clearcut-moved	.	.	.	.	.	0.953	0.055	0.646-0.996
Mature forest	.	.	.	.	.	0.916	0.090	0.527-0.991
$\phi_{2g/clearcut}$	70.212	3.59	0.037	2	66.203	0.856	0.077	0.637-0.953
Mature forest	.	.	.	.	.	0.777	0.138	0.421-0.944
$\phi_{3g+cond/clearcut}$	70.852	4.227	0.027	4	62.824	0.837	0.114	0.500-0.963
Clearcut-moved	.	.	.	.	.	0.924	0.077	0.587-0.991
Mature forest	.	.	.	.	.	0.833	0.123	0.468-0.966
$\phi_{3g/clearcut}$	71.965	5.339	0.015	3	65.948	0.820	0.115	0.498-0.955
Clearcut-moved	.	.	.	.	.	0.897	0.097	0.525-0.986
Mature forest	.	.	.	.	.	0.777	0.138	0.421-0.944

Fate	Woody Stems	SE	Condition	SE
Survived	181.700	9.331	0.030	0.085
Died	121.235	36.394	-0.478	0.368

Table 3.5. Mean and standard error for the number of woody stems at daily locations and energetic condition of independent juvenile Ovenbirds that survived (n = 80) and died (n = 5) in southeast Ohio.
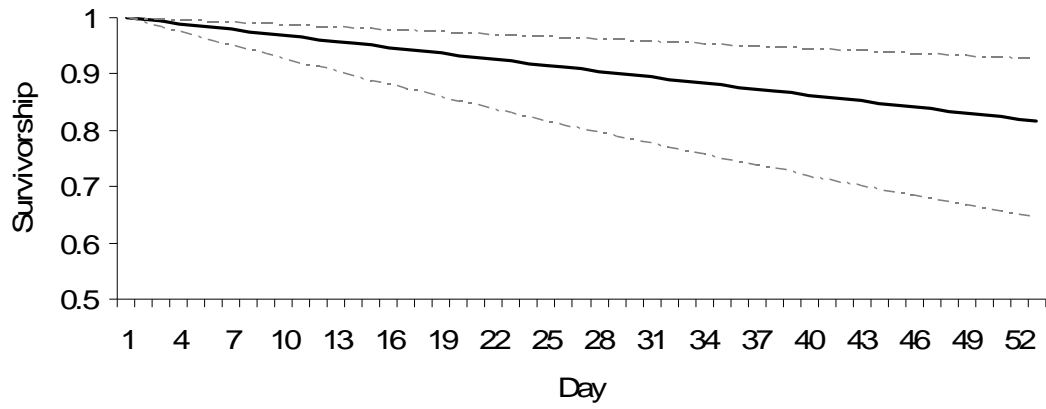
Figure 3.1. Cumulative survivorship with 95% confidence interval using estimates

from the top ranked time model (with no covariates) for independent juvenile

Ovenbirds (n =85) in southeast Ohio.
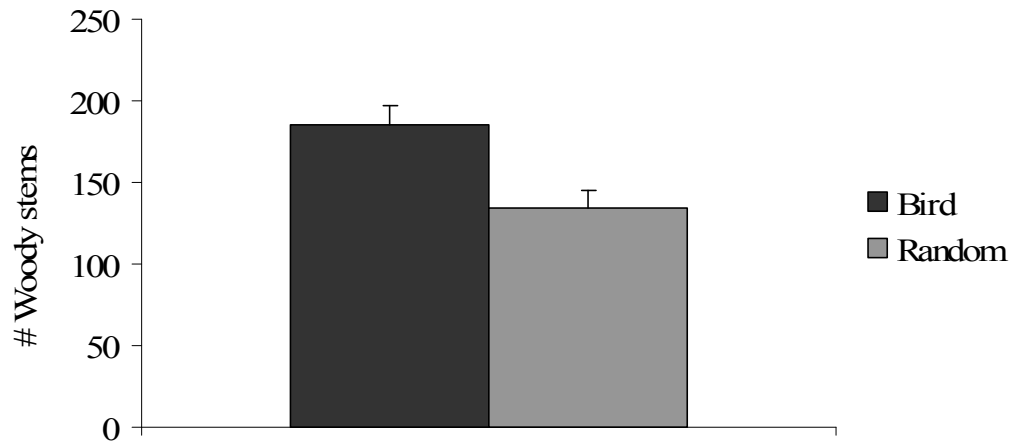
Figure 3.2. The mean number of woody stems (with standard error bars) at actual bird and random locations for independent juvenile Ovenbirds (n = 112) during the post-fledging period in southeastern Ohio.
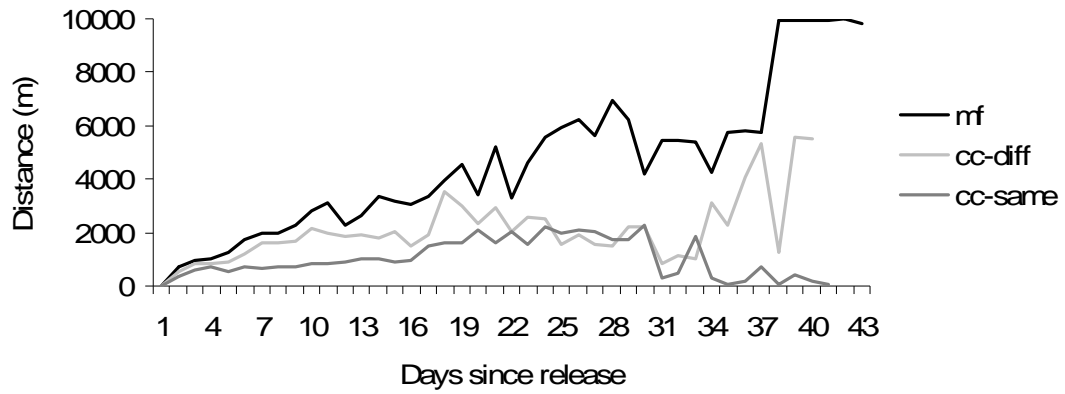
Figure 3.3. The mean distance moved from the release location for independent

juvenile Ovenbirds for each of the three treatment groups (mf = mature forest, cc-diff

= moved to a different clearcut, cc-same = released in original clearcut of capture).

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CHAPTER 4

SONGBIRD POST-FLEDGING MOVEMENTS ON AND BEYOND
THE NATAL HOME RANGE

ABSTRACT

Post-fledging movement patterns have been documented for a number of

species, but the purpose of such movements remains unclear. Our objectives were to

investigate the relationship between fledgling age and movements, calculate natal

home range size, determine the distance moved when dispersing away from the natal

area, and to rank the importance of biological covariates on movements shortly after

fledging for Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers

(*Helmitheros vermivorum*). Between 2004-2007 we radio-tagged, and tracked daily,

51 Ovenbirds and 60 Worm-eating Warblers in southeast Ohio. For each radio-

tagged bird we calculated the distance between daily locations and their nest,

successive distances between daily locations, mean dispersal distance away from the

natal area, number of days before dispersing, and the natal home range (MCP) size

for those with $\geq$ 16 daily locations. We used Akaike's Information Criterion (AIC_c)

to build and rank alternative models representing potential mechanisms driving

movements two days following fledging. Natal home range size of Worm-eating

Warblers (10.36 ha $\pm$ 1.50 SE) was nearly twice as large as those for Ovenbirds (5.02

ha $\pm$ 0.56 SE). Fledgling age was positively correlated with the distance moved from

the nest and the distance between daily locations. For both species the mean distance

between fledgling daily locations two days after leaving the nest was best explained

by their energetic condition at the time of fledging. If increased fledgling mobility

facilitates the location of suitable post-fledging habitat, then healthy nestlings may

have improved post-fledging survival. We suggest that area-sensitivity in songbirds

may be partially driven by large natal home ranges and relatively long dispersal

distances away from the natal area. Consequently, conservation strategies should

consider juvenile behavior when developing reserve design and especially when

determining minimum patch size and habitat connectivity.

INTRODUCTION

Post-fledging ecology remains somewhat of a mystery for the majority of

songbirds (Anders & Marshall 2005), and the little that is understood frequently

relates to habitat use (Vega Rivera et al. 1998; Vitz & Rodewald 2006) and survival

(Anders et al. 1997). In a few cases, fledgling survival has been documented to be

positively related to understory vegetation structure (Chapter 2; King et al. 2006), and

the ability of fledglings to move away from their nest location in order to locate

suitable post-fledging habitat may be critical for their survival. However, studies

seldom report patterns of pre-dispersal fledgling movements, and almost nothing is

known about the factors that drive movement behavior. Because fledglings typically

disperse from natal territories following independence, an understanding of

movement ecology may be critical for reserve design and other conservation efforts.

In this study, we focused on natal dispersal, which represents a unidirectional movement from the natal area to the first breeding location (Salewski & Bruderer 2007). Ecologists have suggested that increased production of the stress hormone corticosterone is the proximate mechanism prompting dispersal and may be responsible for triggering facultative movements away from areas with deteriorating environmental conditions, thereby promoting survival (Dufty & Belthoff 2001; Wingfield & Ramenofsky 1997). Indeed, experimentally increased levels of corticosterone were found to stimulate natal dispersal in Willow Tits (*Poecile montanus* Silverin 1997).

Dispersal behavior is considered one of the remaining frontiers in avian ecology and plays a central role in population distribution and dynamics (Walters 2000). Because dispersal affects population connectivity and gene flow, movement behavior is necessary to gauge a species' sensitivity to habitat fragmentation and isolation (Walters 2000). Although movements away from the natal home range during the post-fledging period represent only a portion of natal dispersal, these movements may strongly influence settlement of future breeding sites if prospecting occurs during this period. In fact, it is widely thought that birds prospect during the post-fledging period and support for this has been found in a number of species (reviewed in Reed et al. 1999).

Objectives

We evaluated and compared movement patterns during the post-fledging period for two forest-interior species, the Ovenbird (*Seiurus aurocapilla*) and Worm-eating Warbler (*Helmitheros vermivorum*). Specifically, our objectives for both

species were to 1) quantify movements within and beyond the natal home range, 2) calculate natal home range size, 3) determine fledgling age at dispersal, and 4) model the influence of biological variables on fledgling movements.

METHODS

Study Area

This study was conducted in southeast Ohio within the Ohio Hills physiographic region. For a description of the study area see chapter 2. Ovenbirds and Worm-eating Warblers were radio-tagged at 7 mature forest sites (75-110 years old; Appendices B, C) that were 16 ha in size with location markers every 50 m. Although all sites were located within the same contiguous forest, study plots were separated by at least 4 km.

Radio-tracking

At all sites, Ovenbird and Worm-eating Warbler nests were found and monitored every 3-5 days (1-2 days as fledging approached) until their fate (failed or successful) was determined. On their projected fledging day, a radio-transmitter was affixed to a single randomly selected nestling in each nest (or located near the nest if the nestlings had fledged earlier that day). Only one nestling per nest was radio-tagged as members of the same family group may lack independence (Garton et al. 2001). Transmitters were attached using a leg-loop harness constructed of an elastic cotton/nylon blend material (Rappole & Tipton 1991). All birds were banded with a USGS aluminum band, weighed, and tarsus length was recorded. Wing cord was not measured because the secondary and primary feathers were only partially grown at

the time of fledging. Transmitters used on Ovenbirds contained a battery programmed to last 6 weeks and weighed approximately 6.1% of fledging and 4.6% of adult mass (0.90 g, BD-2, Holohil Systems Ltd.). Smaller transmitters were used on Worm-eating Warblers with batteries programmed to function for 4 weeks and weighed 4.8% and 4.2% of fledging and adult mass, respectively (0.55 g, BD-2N, Holohil Systems Ltd.).

Radio-tagged birds were tracked once each day using the homing method, which involved locating the bird on foot until a visual identification of the bird was obtained (White & Garrott 1990). To locate birds we used R2000 receivers and custom tuned (4 MHz range) folding, aluminum yagi antennas (3 element) manufactured by Advanced Telemetry Systems. There was substantial variation in the range that transmitters could be detected (300-900 m), and this was primarily a result of topography. Once found, each bird location was recorded in Universal Transverse Mercator (UTM) coordinates using a 12 parallel channel GPS receiver (Magellan Meridian).

Natal Home Range

Average successive distance between daily locations was calculated for both species. In addition, we documented the distance between each fledgling location and their nest site. We used the Minimum Convex Polygon (MCP) method to estimate natal home range size for all fledgling Ovenbirds and Worm-eating Warblers with $\geq$ 16 locations because Worm-eating Warblers began dispersing around that age. We used the MCP method over the 95% Kernal estimator because the Kernal requires a minimum of 30-50 locations to produce reliable results, and this method tends to

overestimate home range size with small samples (Seaman et al. 1999). Locations recorded following dispersal away from the natal territory were removed from the natal home range analysis. A dispersal event was identified if an individual underwent a daily movement or successive movements in the same direction > 350 m and did not return to the natal area. We identified fledgling age at the time of dispersal and recorded the distance between the center of the natal home range and the area settled after dispersal. All spatial analysis performed for fledgling Ovenbirds and Worm-eating Warblers was accomplished using the Animal Movements extension within ArcView 3.2 (Hooge and Eichenlaub 1997). We used a general linear model (Proc Glm) to examine interspecific differences in natal home range size between Ovenbird and Worm-eating Warbler fledglings. Prior to analysis data for the natal home range size were normalized using a square-root transformation.

Movements

　　We evaluated the extent to which a variety of biological variables, including energetic condition, site level nest success, understory vegetation at the nest site, and the number of fledglings in the brood, explained movement patterns shortly after fledging. The distance fledglings moved from the nest after two days of fledging was used as the response variable because young are most vulnerable immediately following fledging, and their ability to move during this period may be critical for survival. Due to high mortality rates for newly fledged birds (Naef-Daenzer et al. 2001), there should be strong evolutionary pressure to immediately locate protective cover; however, once appropriate habitat is found motivation to move may decrease. First, energetic condition of captured individuals was determined by calculating a

residual value from a linear regression of tarsus length on body mass. This measure of energetic condition is preferred over a simple mass value because it accounts for the structural size of the individual (Green 2001). A residual with a positive value reflected an above average condition, whereas a negative value represented a below average energetic condition. Next, we evaluated if site level predation risk influenced fledgling movements. We identified risk of predation as the daily survival rate (DSR) for nests of all open-cup nesting birds. Site level DSR was calculated using the nest survival model in program MARK. We treated site level DSR as a categorical variable with each site characterized by low (< 0.960) or high (> 0.960) nest survival. Because nest success showed annual variation, a separate DSR was generated for each site by year and ranged between 0.915–0.975 (unpub. data). Site-level nest success should reflect the risk of predation for a fledgling because fledgling movements frequently traversed the majority of the site, and many predators (e.g., Blue Jay, Eastern Chipmunk) are known to depredate both nests and young fledglings. Third, vegetation structure around each nest was included as a variable, because if the area around a nest was characterized by a dense understory fledglings may have little incentive to move away. Understory vegetation structure was measured every 2 m along two perpendicular 20 m transects with the center at the nest location. At each point, understory vegetation structure was quantified by recording the number of woody stems touching a telescoping pole between 0.5-3.0 m in 0.5 m increments. The final variable was the number of nestlings in the brood at the time of fledging. This may influence movements because adults feeding a higher number of fledglings may be more constrained in their movements. For Ovenbirds

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and Worm-eating Warblers, the only continuous variable not following a normal distribution was understory vegetation structure, thus, a 4th root transformation was used to meet the assumption of normality.

An Akaike Information Criterion (AIC) framework was used in this analysis because it allowed for the ranking and evaluation of competing explanatory models. Models were ranked based on AIC$_c$ values, which incorporate a bias correction term for small sample sizes (Burnham & Anderson 2002). Separately by species, we built individual models for each variable in addition to a null model with no explanatory variables. We used generalized linear models (Proc Genmod, SAS), specifying a normal distribution and an identity link function, to obtain a log-likelihood value. Using this information, AIC$_c$ values were calculated in Excel.

RESULTS

We radio-tagged a total of 52 Ovenbirds with 12, 20, and 20 fledglings being tracked in 2004, 2005, and 2006, respectively. Sixty Worm-eating Warblers were radio-tagged with 4, 23, 23, and 10 individuals being tracked in successive years between 2004-2007. In 2006, 14 transmitters used on Worm-eating Warblers failed prematurely ($\leq$ 11 days), with 9 of those lasting no longer than a week. As a result, 10 replacement transmitters were used in 2007. Ovenbirds were tracked for a maximum of 51 days, and Worm-eating Warblers were tracked for a maximum of 31 days.

Movements

We found that as fledglings of both species aged, they gradually moved away from their nest location. Overall, Worm-eating Warblers were located farther from their nest compared to Ovenbird fledglings of the same age (Figure 4.1). By Day 6, Worm-eating Warblers were nearly 1.5x farther from the nest compared to Ovenbird fledglings, and by day 11 this increased to nearly twice as far from the nest, a relationship that remained through the 4th week (Figure 4.1). A similar pattern was found when examining the successive distance between daily locations. By 3 days after fledging, the distance between daily points was over 1.5x greater for Worm-eating Warblers compared to Ovenbirds, and this pattern was maintained through nearly the entire period for which we had data (Figure 4.2). Of individuals for which a dispersal event was documented, the average time between fledging and dispersing was 21.8 days (SE = 2.22) for Worm-eating Warblers (n = 5) and 29.20 days (SE = 0.63) for Ovenbirds (n = 23). In addition, the mean distance between the center of natal home range and the dispersal area was 1141 m (SE = 245 m) for Worm-eating Warblers and 1314 m (SE = 174 m) for Ovenbirds.

We calculated natal home ranges for 37 Ovenbirds and 36 Worm-eating Warblers. Home range size did not vary by year for Worm-eating Warblers ($F_{3,32}$ = 0.95, P = 0.427), but did for Ovenbirds ($F_{2,34}$ = 6.40, P = 0.004). Because Ovenbirds showed the same tendency to have smaller home ranges than Worm-eating Warblers across each year, we combined yearly data for each species. The mean (SE) natal home range size estimated for Worm-eating Warblers was 10.36 ha ($\pm$ 1.50) and significantly larger and more than twice the mean size of 5.02 ha ($\pm$ 0.56) for Ovenbirds ($F_{1,71}$ = 12.72, P < 0.001; Figure 4.3). This pattern existed despite the fact

that natal home ranges constructed for Worm-eating Warblers averaged fewer numbers of daily locations (22.50, SE = 0.69) than those generated for Ovenbirds (30.97, SE = 0.97).

Distance moved by fledglings two days after leaving the nest was positively related to and best explained by energetic condition at the time of fledging (Figure 4.4). In fact, for both species, the top model and the only one with an AIC value <2 included energetic condition (Table 4.1). For Ovenbirds, this model was considered 7x more plausible than the second best model and had a weight of evidence of 0.739. For Worm-eating Warblers the model containing energetic condition was ranked over 5x more plausible than the second best model with a weight of evidence of 0.727. For both species, other models received little support. (Table 4.1; Burnham & Anderson 2002).

DISCUSSION

Biological Predictors

This study is the first to explicitly examine biological factors that influence fledgling movements shortly after birds leave the nest, during the time when they are most vulnerable to predation. We found that immediately following fledging, distances moved between daily locations for Ovenbirds and Worm-eating Warblers were best explained by their energetic condition at the time of fledging, and fledglings in better energetic condition tended to move a greater distance (Figure 4.4). Enhanced movement ability may facilitate the location of suitable post-fledging habitat and potentially reduce their risk of predation. Energetic condition also has

been found to be positively related to survival in some (Chapter 2; Krementz et al. 1989; Naef-Daenzer et al. 2001), but not other studies (Anders et al. 1997; Brown & Roth 2004; Sullivan 1989). A fledgling's condition may be most important during periods of environmental stress (Krementz et al. 1989) or when long movements are required to access suitable post-fledging habitat. In contrast to our results, Dicksissel (*Spiza americana*) movements during the first 4 weeks post-fledging were not explained by morphometric characteristics or habitat features (Berkeley et al. 2007). We found no evidence that habitat features, risk of predation, or the number of nestlings at the time of fledging influenced fledgling movements.

Natal Home Range

Natal home range sized differed markedly between Ovenbirds and Worm-eating Warblers. For birds with similar diets, an allometric relationship has been found in respect to adult home range size (Ottaviani et al. 2006), and a similar pattern has been demonstrated for natal home range size of grassland songbirds (Wells et al. 2008). In contrast, we found the opposite pattern for two forest breeding species. Interestingly, Wood Thrush employ either a 'stationary' (mean home range = 4.46 ha) or 'drifting' (mean home range = 19.5 ha; Anders et al. 1998) pattern for their natal home range, and this same phenomenon was reported for Swainson's Thrush (*Catharus ustulatus*; White & Faaborg 2008). In the Wood Thrush study, natal home ranges were calculated using multiple radio-tagged fledglings from the same brood. A potential explanation for this bimodal pattern is that larger home ranges resulted from tracking fledglings in split broods, whereas the smaller home ranges represented unified broods or individuals fed by the same parent within split broods. Brood

division is a strategy to increase the chance that some fledglings will survive and appears to be common during the post-fledging stage (Yackell Adams et al. 2001). However, brood division or movement outside of the breeding territory may not be beneficial if another brood is attempted, and this may explain small natal home ranges for some Wood (Anders et al. 1998) and Swainson's Thrush (White & Faaborg 2008). In fact, double-brooding Wood Thrush have been documented remaining an average of 62 m (SE = 5 m) from the first nest, and 13 days following fledging females began incubating a second clutch while males continued to feed all of the fledglings from the initial brood (Vega Rivera et al. 2000). Other examples of small natal home ranges have been reported for the Gray Catbird (0.38 ha, *Dumetella carolinensis*) and Yellow-breasted Chat (0.89 ha, *Icteria virens*), two species also known to double brood (Maxted 2001).

Movements and Dispersal

As Ovenbird and Worm-eating Warbler fledglings aged, the distance between daily locations increased as did the distance to their nest location. This pattern is consistent with studies of Swainson's Thrush (White & Faaborg 2008), Dicksissels (Berkeley et al. 2007; Wells et al. 2008), Eastern Meadowlarks (*Sturnella magna*, (Guzy & Ribic 2007), Lark Buntings (*Calamospiza melanocorys*; Yackell Adams et al. 2001) and White-throated Robins (*Irania gutturalis*; Cohen & Lindell 2004). Similar to other ground nesting species (Yackell Adams et al. 2001), Ovenbird and Worm-eating Warbler fledglings initially were restricted in their movements because of their inability of sustained flight. Upon fledging, Ovenbirds are flightless and have limited hopping ability (Van Horn and Donovan 1994), and Worm-eating Warblers

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are only slightly more developed (Hanners and Patton 1998). This pattern is typical for nidicolous ground nesting species, which are thought to have adapted to high nest predation by reducing incubation and brooding periods and fledging young at a lower mass relative to adults (Remes & Martin 2002; Roff et al. 2005).

The mean dispersal distances of 1314 m for Ovenbirds and 1141 m for Worm-eating Warblers were in the middle of the range documented for other species. Mean dispersal distances away from the natal area have ranged from 292 m for White-throated Robin (Cohen & Lindell 2004), 242 m for Swainson's Thrush (White & Faaborg 2008), and between 825 m – 2189 m for Wood Thrush (Anders et al. 1998; Lang et al. 2002; Vega Rivera et al. 1998). In addition, dispersal movements of 12.8 km and 8.8 km have been reported for juvenile Eastern Meadowlarks in Illinois and Wisconsin, respectively (Guzy & Ribic 2007; Kershner et al. 2004). The maximum moved distance we recorded was 3,695 m for Ovenbirds and 1,799 m for Worm-eating Warblers. However, the possibility exists that longer movements occurred but went undetected because the final destinations were outside of the study area.

Ovenbirds and Worm-eating Warblers demonstrated dispersal movements an average of 29.2 and 21.8 days after fledging. Fledglings of a number of species have been found to gain independence between 2-4 weeks after leaving the nest (Vega Rivera et al. 2000; Wells et al. 2008), and dispersing away from the natal territory 3-5 weeks after fledging (Lang et al. 2002; Vega Rivera et al. 2000). However, it may take longer in some cases. Peak dispersal movements ranged between 33-45 days following fledging for juvenile Dicksissels and between 34-60 days for meadowlarks (Wells et al. 2008). The age at dispersal for fledgling songbirds may be influenced by

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sex, as females have been documented dispersing at a younger age (Green &

Cockburn 2001) and moving a farther distance, (Greenwood & Harvey 1982; Small

& Rusch 1989; Tyler et al. 1990) than males. Differential dispersal distances by sex

are largely thought to be a strategy to reduce inbreeding depression (Greenwood &

Harvey 1982; but see Moore & Ali 1984). Although we were unable to determine the

sex of fledgling Ovenbirds and Worm-eating Warblers, differences between the sexes

could explain some of the variation in our data.

CONSERVATION IMPLICATIONS

The objective of this study was to improve our understanding regarding the

movements undertaken by fledgling songbirds. Our study shows that natal home

ranges are generally much larger than breeding territories of the same species. In

addition, fledglings frequently move several kilometers once they leave their natal

area. Collectively, these behaviors may, at least partially, explain patterns of area-

sensitivity in some species. Conservation strategies should focused on preserving

forest patches greater than 10 ha in size in order to support natal home ranges.

Furthermore, habitat connectivity may be an important landscape attribute when

fledglings move away from their natal area. Despite having long flight capabilities

songbird movements may be constrained by fragmentation (Belisle et al. 2001), and

this may be especially relevant for birds during the post-fledging period (Desrochers

& Hannon 1997). However, additional studies are necessary to examine how

landscape features influence fledgling movements.

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A)

Model	K	AIC_c	ΔAIC_c	Akaike Weight	R^2
Condition	2	494.154	0	0.739	0.179
Null	1	497.993	3.839	0.108	.
Site DSR	2	498.540	4.386	0.082	0.056
# Nestlings	2	500.0733	5.919	0.038	0.013
Nest habitat	2	500.444	6.290	0.032	0.005

B)

Model	K	AIC_c	ΔAIC_c	Akaike Weight	R^2
Condition	2	494.4927	0	0.727152	0.109
Null	1	497.7782	3.28554	0.140663	.
Site DSR	2	499.9769	5.4842	0.046854	0.006
# Nestlings	2	500.1051	5.6124	0.043945	0.003
Nest habitat	2	500.2251	5.7324	0.041386	0.001

Table 4.1. Models examining the influence of biological variables on the distance

fledgling A) Ovenbirds (n = 51) and B) Worm-eating Warblers (n = 50) moved from

their nest 2 days following fledging in southeast Ohio between 2004-2006. In these

models condition represents energetic condition of the bird at the time of fledging,

site DSR represents the overall daily survival rate at each site (this variable was

treated as a categorical variable with low DSR < 0.960, and high DSR > 0.960), #

nestlings refers to the number of nestlings at the time of fledging for each brood, and

nest habitat represents low vegetation structure around the nest location.

A)

B)
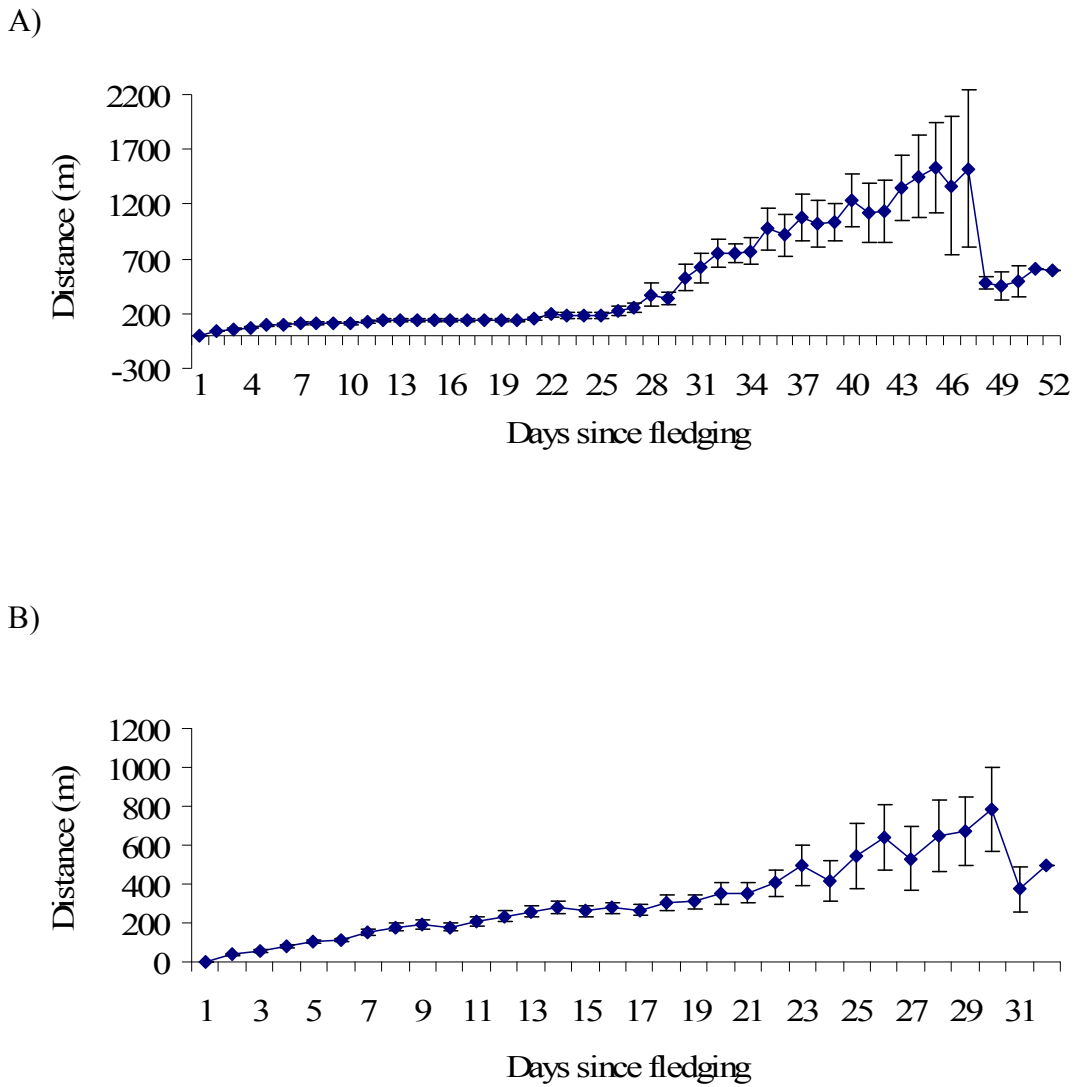
Figure 4.1. Cumulative distance moved from the nest by fledgling age for A)

Ovenbirds (n = 51) and B) Worm-eating Warblers (n = 60) in southeast Ohio between

2004-2007. The bars represent standard errors.

A)
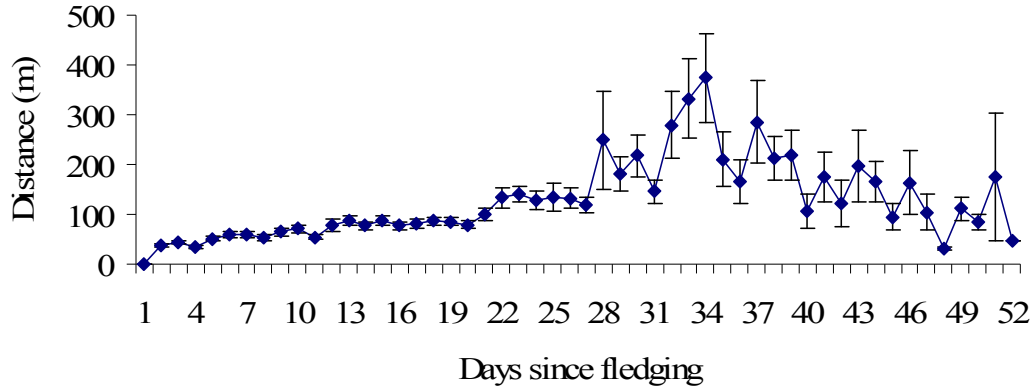
B)
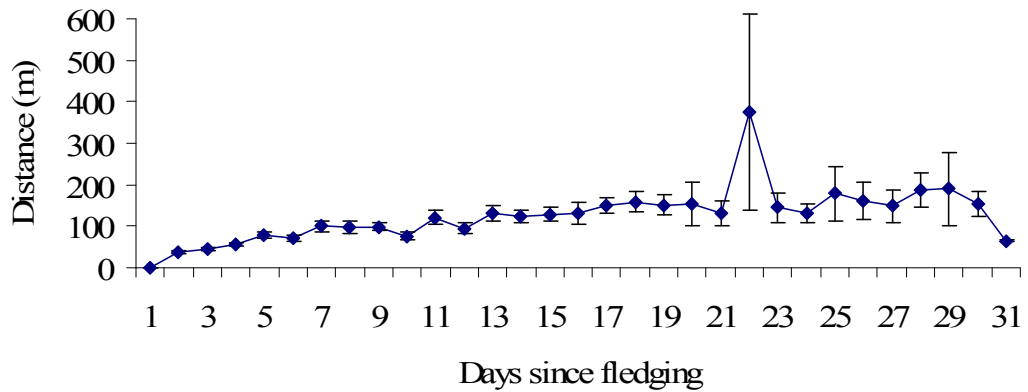
Figure 4.2. Successive distance moved between daily locations for fledgling A)

Ovenbirds (n = 51) and B) Worm-eating Warblers (n = 60) in southeast Ohio between

2004-2007. The bars represent standard errors.
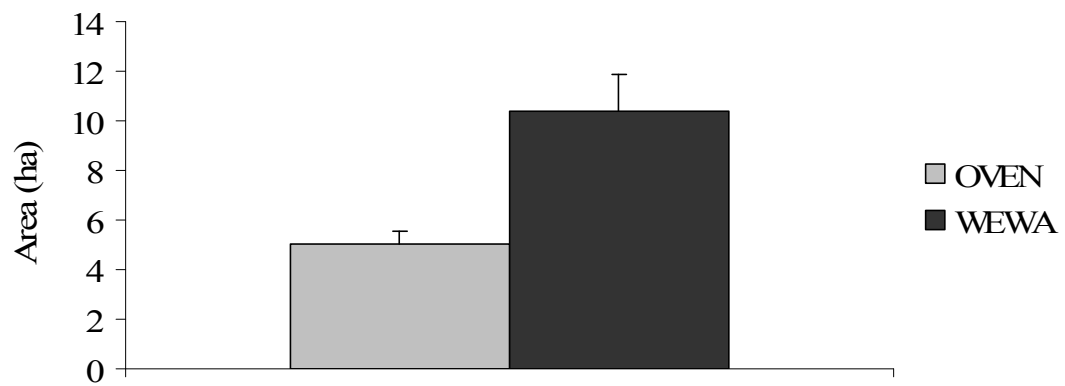
Figure 4.3. Comparison of mean Minimum Convex Polygon natal home range size (+ SE bars) for Ovenbirds (n = 37) and Worm-eating Warblers (n = 36) in southeast Ohio between 2004-2007.

A)

B)
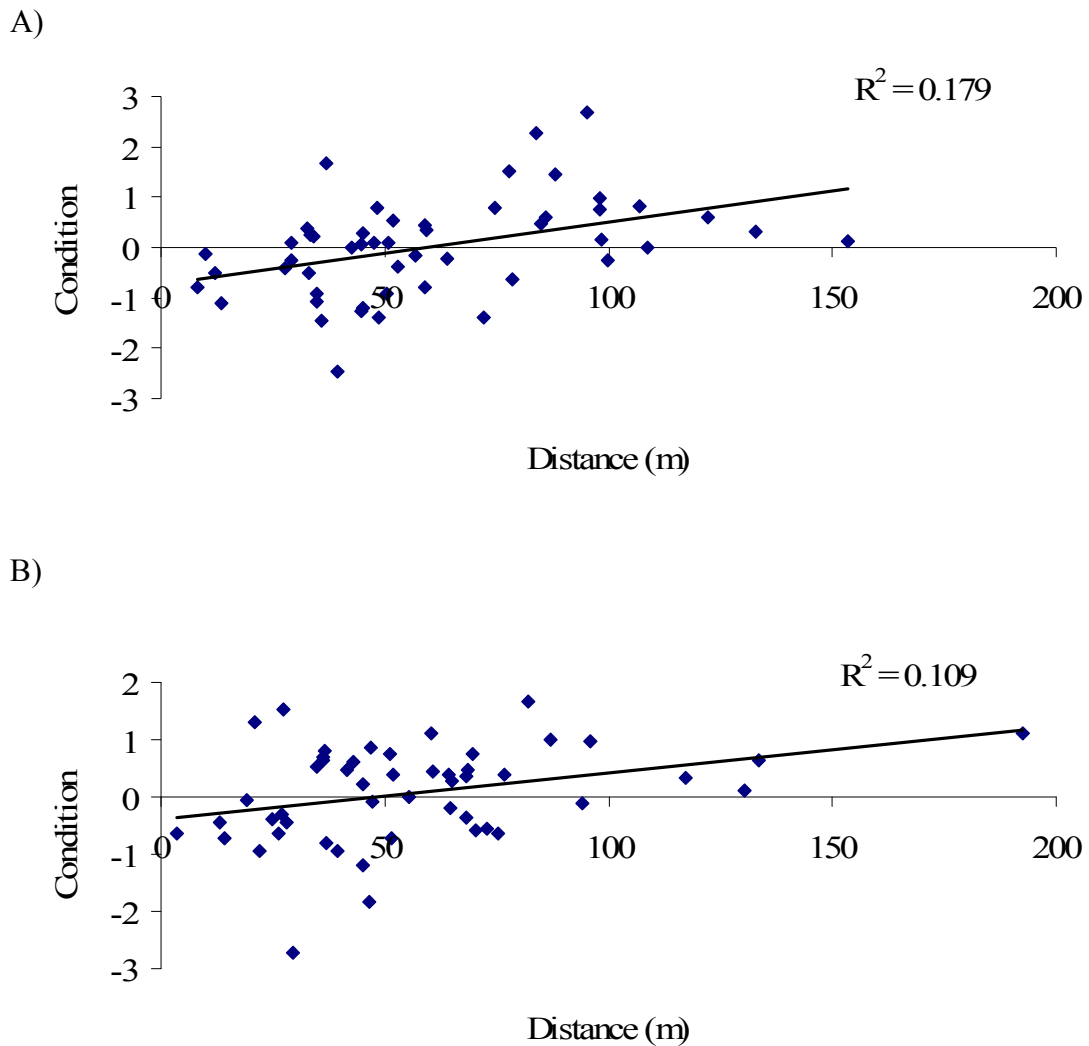
Figure 4.4. The relationship between energetic condition (residual from a regression of tarsus on mass) and the distance between daily fledgling locations on the second day after leaving the nest. This is displayed for A) Ovenbirds (n = 51) and B) Worm-eating Warblers (n = 60) in southeast Ohio between 2004-2007.

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CHAPTER 5

THE EXTENT OF FRUGIVOROUS BEHAVIOR IN FLEDGLING SONGBIRDS:

AN INVESTIGATION USING STABLE ISOSTOPES

ABSTRACT

Use of early successional habitat by mature forest birds during the post-fledging period is well documented, but reasons for this habitat shift remain elusive. The objectives of this study were to evaluate whether use of fruit resources may be the mechanism attracting fledglings of three species of forest breeders to regenerating clearcuts and to link diet to energetic condition. We accomplished this by using stable isotopes to identify the trophic level of fledgling diet using stable isotopes. For both nitrogen and carbon the heavier isotope is preferentially incorporated into the consumer tissue resulting in a systematic enrichment with increasing trophic level. We collected outer right retrix and several basic plumage body feathers from juvenile Scarlet Tanagers (*Piranga olivacea*), Wood Thrush (*Hylocichla mustelina*), and Ovenbirds (*Seiurus aurocapilla*) captured in regenerating clearcuts in southeastern Ohio, 2005-2006. We also collected fruit and arthropod samples from each clearcut. Stable isotope values for $\delta^{15}N$ and $\delta^{13}C$ of both feather types revealed that arthropods were the primary source of protein during the period of growth for retrix and body feathers. Compared to the retrices, basic plumage body feathers were more enriched

in $\delta^{15}N$ and $\delta^{13}C$ values, suggesting that independent juveniles primarily consumed both lepidopteran and predatory arthropods rather than primarily lepidopteran larvae. Because stable isotope signature was unrelated to size-adjusted mass of the birds, we have no evidence to suggest that dietary trophic level strongly affected energetic condition. Our results suggest that mature forest birds during the post-fledging period are not specifically using regenerating clearcuts for fruit resources.

INTRODUCTION

There is increasing evidence that many mature-forest birds move into early successional habitats during the post-fledging period. Although this habitat shift is thought to be at least partly the consequence of seeking protective cover to avoid predators (Anders et al. 1997; Vitz & Rodewald 2007), the role of food resources in determining habitat use remains unclear (Vega Rivera et al. 1998; Vitz & Rodewald 2006). Availability of and access to food resources should be especially important for juvenile passerines that must quickly learn to exploit their surroundings while meeting the dietary and metabolic requirements for molting and fat deposition to fuel migration. As such, fledglings of mature-forest species are thought to be somewhat opportunistic foragers, consuming a combination of fruits and arthropods (Martin 1951; Parrish 1997). This tendency to consume fruit during the post-fledging period (Stiles 1980) may explain the use of early successional forests given that they produce fruit long before they are widely available in mature forests (Willson 1986). However, empirical data describing the relative amounts of fruit and arthropod matter in diets of juvenile birds are lacking.

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Although strictly frugivorous birds are largely absent in eastern North America, many species that are primarily insectivorous while breeding show dietary plasticity outside of the breeding season, when they consume both fruit and arthropods (Martin 1951; McCarty et al. 2002; Parrish 2000). Once juveniles are fully-grown, their protein requirements are greatly reduced while their lipid and carbohydrate requirements increase (Stiles 1980). Therefore, frugivory during the post-fledging period may be an important strategy for many North American passerines. Frugivory offers several advantages as a foraging strategy, including ease with which birds can find and obtain fruits, reduced search movements compared to insect foraging, and high-energy content (McCarty et al. 2002; Parrish 2000). These advantages may especially benefit hatch-year birds that lack foraging proficiency (Desrochers 1992; Vanderwerf 1994; Wunderle 1991) and are vulnerable to starvation (Husby & Slagsvold 1992; Sullivan 1988). Conversely, birds may select habitat and be drawn to regenerating clearcuts during the post-fledging period based on arthropod resources. Arthropods have been found to be positively correlated with selection of breeding territories (Burke & Nol 1998), reproductive success (Zanette et al. 2000), and abundance on the breeding (Forsman et al. 1998) and wintering grounds (Johnson & Sherry 2001).

Stable isotope analysis can be used to evaluate dietary trophic level because the heavy isotope of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are preferentially incorporated into the consumer's tissue. As a result, with each increase in trophic level there exists an average of 3-4‰ (parts per thousand) enrichment for $\delta^{15}N$ and 1-2‰ enrichment for $\delta^{13}C$ relative to the diet (Kelly 2000). Compared to traditional dietary analysis

(i.e, content analysis of stomach, esophagus, feces) isotope analysis has the advantage of evaluating assimilated material (rather than ingested), and enables the evaluation of the importance of plant and animal sources of protein in the diet (Herrera et al. 2003). Another advantage is the ability to examine isotope values from different timescales depending on the tissue collected (Podlesak et al. 2005). For example, feathers become inert once grown, and their isotope signatures reflect diet during the period of feather growth. The primary disadvantage is the inability to examine diet at a fine scale, with the limitation of discriminating between trophic level food resources.

Objectives

We evaluated fledgling diet of three species of forest birds that heavily use regenerating clearcuts during the post-fledging period. Specifically, we examined the extent to which (1) post-fledging birds concentrated on arthropod or fruit resources and (2) N and C isotopic signatures were associated with energetic condition of birds.

METHODS

Study Area

This study was conducted in southeast Ohio within Athens and Vinton counties located in the Ohio Hills physiographic region. The region is approximately 70% forest covered, and the Zaleski State Forest (10,857 ha), where the study sites were located, was nearly completely composed of forest habitat.

Birds were captured between 3 July – 1 August 2005 and 2006 using passively managed mist-nets (12 m long, 2.6 m high, 30 mm mesh) in 3 regenerating clearcuts. Clearcuts were 6-10 years post-harvest and were separated by a minimum

of 5 km. Mist-netting occurred each day for 4.5 hours beginning 0.5 hour before

sunrise, and nets were checked for birds every 30 minutes. Upon capture, birds were

identified to species, age, and sex (if possible) and banded with a USGS aluminum

band, and morphological measurements (i.e., mass, wing length) were recorded. A

bird's energetic condition was evaluated using the residual from a regression of wing

cord by body mass to standardize mass for the structural body size (Green 2001). A

residual value for each point was calculated where a positive number indicated a

greater mass than expected given a particular body frame (i.e., good condition), and a

negative value indicated a lower mass than expected given its size (i.e., poor

condition).

Feather Samples

We collected the outer right retrix and several body feathers from the first

basic plumage from juvenile Scarlet Tanagers, Wood Thrushes, and Ovenbirds.

Retrices begin growing during the nestling phase and finish soon after fledging.

However, to ensure retrices reflected the diet of nestlings or very young fledglings we

only analyzed the tips of the feathers, which are the first portion of the feather to be

grown. Body feathers from the first basic plumage replace the juvenile plumage and

begin growing around the time juveniles reach adult size and continue through much

of the post-fledging period. Many individuals were molting at the time of capture and

feathers in the process of growing were collected whenever possible. Fruit and

invertebrate samples from the same sites were collected in 2007. Arthropod samples

were collected throughout the site by using a branch clipping method (Johnson 2000).

Ripe fruit also were gathered throughout each site and included several species of

Rubus, which represented the only abundant, fleshy fruit available in the sites during the period (Vitz pers. obs.). Only a single arthropod or fruit sample was collected from a particular plant because items from the same plant may not be independent. All samples were stored in a freezer for several weeks before being prepared for analysis.

To remove oils and foreign particles, feathers were rinsed with distilled water, submerged for 48 hours in a 3:1 chloroform:methanol solution, and air dried for at least 24 hours. Feathers were cut into small pieces using scissors and forceps and were weighed to the nearest $\pm$ 1 µg. Invertebrate and fruit samples were washed in distilled water, dried in a drying oven at 60˚C for 48 hours, and ground with a mortar and pestle to acquire representative samples from bulk material. Feather and arthropod samples weighing between 0.80 – 1.20 mg and fruit samples weighing 4.00 – 6.00 mg were packaged into 5x9 mm tin capsules, stored in a well plate, and shipped to the University of California Stable Isotope Facility where they were combusted (1020˚C) and analyzed using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Final $\delta^{15}N$ and $\delta^{13}C$ values were determined by adjusting provisional results such that correct values for laboratory standards were obtained (2 laboratory standards were analyzed after every 12 samples). Stable isotope ratios were expressed in δ notation $[(R_{sample}/R_{standard})-1]*1000$, as deviations from atmospheric Nitrogen (international standard for N) and Peedee Belemnite (PDM) limestone formation (standard for C) in parts per thousand (‰). R_{sample} and $R_{standard}$ represent the proportion of heavy to light isotopes in the sample and standard, respectively.

Statistical Analyses

We tested for yearly differences in stable isotope values for N and C in both body and retrix feathers for all species combined using a chi square analysis (proc npar1way, SAS Institute). Annual differences in $\delta^{13}C$ values were not detected in body [$\chi^2(1, N = 103) = 2.15, p = .142$], but differences were revealed for $\delta^{13}C$ in retrix feathers [$\chi^2(1, N = 103) = 7.13, p = 0.008$] and for $\delta^{15}N$ values in body [$\chi^2(1, N = 103) = 15.55, p < 0.001$] and retrix feathers [$\chi^2(1, N = 103) = 10.67, p = 0.001$]. Values for $\delta^{13}C$ and $\delta^{15}N$ were consistently more enriched in feathers grown in 2005 compared to 2006 (Fig. 5.1) so separate analyses were performed by year unless stated otherwise. We tested for differences in stable isotope values among sites separately for arthropods, fruit, and body and retrix feathers for each species using general linear models (Proc Glm). To compare dietary trophic level of nestlings/young fledglings to that of older/independent fledglings we examined differences between stable isotope values of $\delta^{15}N$ and $\delta^{13}C$ between body and retrix feathers (Proc Glm). For this analysis, we combined data from the two years because the trend for more enriched body feathers was similar in both years. In order to examine all species in a single analysis we used a multivariate analysis of variance (MANOVA). If a significant value was found in this overall test species were examined separately (Proc Glm). Finally, to evaluate whether diet influenced condition we examined whether there was a significant relationship between $\delta^{15}N$ or $\delta^{13}C$ isotope values of body or retrix feathers and energetic condition (Proc Glm). All data met the assumption of normality.

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RESULTS

Nitrogen and Carbon isotopic values were identified for body and retrix feathers collected and analyzed from 34 Wood Thrush and Ovenbirds and 35 Scarlet Tanagers. Of these, feathers from 14 Wood Thrush, 17 Ovenbirds, and 17 Scarlet Tanagers were collected in 2005, and 20, 17, and 18 were collected in 2006, respectively (Table 5.1). In 2007, arthropod and fruit samples were collected from each site, and their $\delta^{15}N$ and $\delta^{13}C$ stable isotope values were identified (Table 5.2).

We found little evidence of among-site differences in body or retrix feathers for Scarlet Tanager, Wood Thrush or Ovenbirds after applying a Bonferroni correction for multiple comparisons (adjusted alpha = 0.002; Table 5.3). In 2007, isotope values for arthropods did not vary by site for either carbon ($F_{2,44} = 2.46$, P = 0.097) or nitrogen ($F_{2,44} = 1.78$, P = 0.181). However, isotope values for non-lepidopteran larvae (n = 33) were more enriched than lepidopteran larvae (n = 14) by 2.1‰ for $\delta^{13}C$ ($F_{1,45} = 14.07$, P < 0.001) and 2.5‰ for $\delta^{15}N$ ($F_{1,45} = 14.97$, P < 0.001, Fig. 5.2; Appendix G). In contrast to the arthropod results, isotope values of fruit differed by site for $\delta^{13}C$ ($F_{2,44} = 5.15$, P = 0.010) and $\delta^{15}N$ ($F_{2,44} = 4.64$, P = 0.015; Table 5.2).

Enrichment

When examining all species together, mean isotopic values differed between feather type, and body feathers were 0.11 – 0.84 ‰ and 0.47 – 0.68 ‰ more enriched than retrix feathers in $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Wilks' Lambda $F_{6,55} = 7.75$, P < 0.001). Individually, isotopic differences between feather type in $\delta^{15}N$ values were revealed for Scarlet Tanager ($F_{1,60} = 16.26$, P < 0.001), Wood Thrush

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($F_{1,60} = 6.61$, $P = 0.013$), and Ovenbird ($F_{1,60} = 22.82$, $P < 0.001$), and in $\delta^{13}C$ values for Scarlet Tanager ($F_{1,60} = 15.66$, $P < 0.001$) and Wood Thrush ($F_{1,60} = 4.70$, $P = 0.034$). No difference was detected for $\delta^{13}C$ values between feather types for Ovenbird ($F_{1,60} = 1.01$, $P = 0.318$). In all cases, the isotope values of body feathers (grown on older juveniles) reflected a diet from a higher trophic level compared to retrix feather (grown on young fledglings; Table 5.4). We found no evidence that energetic condition was related to N or C isotope signatures of either feather type (Table 5.5).

DISCUSSION

Despite using fruit-rich habitats during the post-fledging period, isotope values for retrix and body feathers from Ovenbird, Wood Thrush, and Scarlet Tanager reflected a primarily arthropod-based diet. In addition, all three species consistently showed a pattern where body feathers grown during the first pre-basic molt contained more enriched values of $\delta^{15}N$ and $\delta^{13}C$ relative to the retrix grown as nestlings or young fledglings. Thus, our results do not support the idea that post-fledging birds heavily consumed fruit during the period when juveniles were molting into their juvenile and first pre-basic plumages.

Our findings contrast with anecdotal reports that juveniles of several species include substantial amounts of fruit in their diet during the post-fledging period. In a related study involving radio-telemetry we documented fledgling Ovenbirds and Worm-eating Warblers (*Helmitheros vermivorum*) occasionally foraging on *Rubus* fruit (Vitz pers. obs.). In addition, we documented a positive relationship between

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captures of Scarlet Tanagers and the number of ripe fruit associated with mist-nets, adult tanagers feeding fruit (*Rubus* spp) to fully grown fledglings, independent juvenile tanagers frequently foraging on fruit in clearcuts, and fruit stains on the bills of nearly all tanagers captured in clearcuts (Vitz & Rodewald 2007). Moreover, in the same study area, captures of tanagers during the post-fledging period were positively related to the abundance of ripe fruit (Vitz & Rodewald 2007). These results are similar to those found for both fledgling Wood Thrush (Vega Rivera et al. 1998) and Swainson's Thrush (White et al. 2005), which are thought to select post-fledging habitat based on fruit abundance. Juveniles may include fruit and other easily captured food items in their diet to compensate for their lack of foraging proficiency (Breitwisch et al. 1987). Indeed, juvenile European Starlings (*Sturnus vulgaris*) have been documented foraging on fruit while adults continued to prey on insects (Stevens 1985). Although a number of species may consume some fruit during the post-fledging period, the extent of frugivory does not appear to rival that demonstrated by songbirds during fall migration (Parrish 1997).

The isotopic signatures coupled with patterns of habitat use suggest that post-fledging birds may use early-successional habitats, such as regenerating clearcuts, at least partially due to the high number of arthropods they support. Arthropods may be attracted to regenerating clearcuts because compared to mature trees, saplings are more palatable (Farji-Brener 2001) and produce fewer secondary compounds in their leaves (Coley 1983). Furthermore, abundant summer flowers and fruits found in clearcuts may attract arthropods. There is not only evidence that arthropods have a strong positive correlation with numbers of saplings and shrubs (Jokimäki et al.

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1998), but that abundances are higher in regenerating clearcuts compared to adjacent mature forest (Keller et al. 2003). One possible explanation for the more enriched isotope values of body feathers is that older juveniles may have consumed more predatory arthropods and fewer lepidopteran larvae than nestlings. For many species the nesting phase coincides with the time of peak lepidopteran larvae biomass (Naef-Daenzer & Keller 1999), which composes the majority of the diet for nestlings (Rodenhouse & Holmes 1992) and young fledglings (Vitz pers. obs.). However, later in the season as juveniles gain independence, caterpillars become increasingly scarce as many have pupated (Naef-Daenzer & Keller 1999), and birds may be forced to concentrate on alternate prey.

An important caveat of our results is they do not necessarily indicate that forest songbirds fail to consume fruit during the post-fledging period given that evidence of fruit consumption may not be found in feathers if they are primarily being used for their lipid and carbohydrate content and not for their proteins. Furthermore, the δ^{15}N value of feather tissue is influenced by both the N concentration and signature of prey items (Pearson et al. 2003). Compared to arthropods most fruits have both lower N concentration and δ^{15}N value, and as a result, a shift to incorporating fruit in the diet may not substantially change the δ^{15}N value of the consumer's tissue unless it is dramatic, making partial frugivory difficult to detect (Pearson et al. 2003). Furthermore, 90-95% of feather material is composed of proteins (Murphy 1996), and the protein signatures of the diet largely dictate the isotopic value of feathers (Bearhop et al. 2002). Because fruit contains substantially less protein than arthropods, fruit consumed as part of an omnivorous diet should be

less involved in protein synthesis and the isotopic signatures composed of proteinaceous tissue (Herrera et al. 2003). Nonetheless, using a N stable isotopic analysis of feathers, numerous species were classified as employing a frugivorous, insectivorous, or an intermediate strategy (Herrera et al. 2003).

One interesting pattern that we documented in this study was that isotopic values of feathers differed by year. Such annual variation in the isotopic value may result from weather patterns, with bird tissue having more enriched isotopic values during times of drought (Kelly 2000). This relationship is thought to result from birds having to resort to protein catabolism (resulting in enriched isotope values) in order to produce new feathers during periods of nutritional stress (Graves et al. 2002). However, we did not measure precipitation or soil moisture as part of this study and are unable to address this possibility. Although annual differences in stable isotope signatures were detected, within a year, we found only limited evidence of differences in isotope values among sites. Plants from the same area are known to vary substantially in their $\delta^{15}N$ value, which may result from the $\delta^{15}N$ value of the soil and root depth (Kelly 2000).

Differences in dietary protein reflected in $\delta^{13}C$ and $\delta^{15}N$ isotope values of either body or retrix feathers were not related to energetic condition of birds at the time of capture. This is not surprising as our results suggest that all fledglings primarily consumed an arthropod diet through their first pre-basic molt. Fruit intake may become more important as the initiation of migration approaches because it may facilitate the accumulation of fat reserves (Parrish 1997; but see Long & Stouffer

2003). However, none of the birds sampled in our study showed evidence of being in a pre-migratory state (i.e., storing fat reserves) when fruit intake may become crucial.

CONCLUSIONS

The objectives of this study were to evaluate whether use of fruit resources may be the mechanism attracting fledglings of three species of forest breeders to regenerating clearcuts and to link diet to energetic condition. Use of stable isotopes from two generations of feathers from juvenile birds allowed us to evaluate fledgling diet and, in this way, provide insight into the mechanisms responsible for mature forest bird use of regenerating clearcuts during the post-fledging period. Because juvenile birds appear to focus heavily on arthropod resources through the first pre-basic molt, their shift from late- to early-successional forest may not reflect selection of fruit-rich habitats. Instead, regenerating clearcuts may be especially suited for juvenile birds because they provide abundant arthropods for foraging and dense cover providing cover from predators (Keller et al. 2003). Still, we can not rule out that juveniles are consuming fruit resources for non-protein based requirements such as lipids and carbohydrates or heavily forage on fruit once their molt is complete and protein requirements reduced.

Site	Scarlet Tanager *Piranga olivacea*		Wood Thrush *Hylocichla mustelina*		Ovenbird *Seiurus aurocapilla*	
	2005	2006	2005	2006	2005	2006
WT	6	4	4	6	6	7
WH	6	6	9	7	6	2
CC	5	8	1	7	5	8
Total	17	18	14	20	17	17

Table 5.1. Number of individuals from which feather samples were collected from each site and year for Scarlet Tanager, Wood Thrush, and Ovenbird in southeast Ohio.

		Arthropods			Fruit	
	n	δ^{13}C ratio	δ^{15}N ratio	n	δ^{13}C ratio	δ^{15}N ratio
WT	18	-25.976 (0.392)	-0.342 (0.576)	16	-26.039 (0.395)	-2.048 (0.463)
WH	17	-26.146 (0.514)	0.792 (0.483)	20	-27.300 (0.193)	-3.068 (0.143)
CC	12	-24.692 (0.494)	1.059 (0.641)	11	-26.069 (0.431)	-3.161 (0.241)

Table 5.2. Arthropod and fruit sample sizes and mean (SE) values for δ^{13}C and δ^{15}N isotope ratios from each site in southeast Ohio during early July, 2007.

A)

	CC	WH	WT	Test Results
2005				
SCTA$_{body}$	5.88 (0.28)	5.36 (0.36)	5.47 (0.15)	$F_{2,14} = 0.93$, $P = 0.418$
SCTA$_{retrix}$	5.01 (0.16)	4.97 (0.19)	4.92 (0.30)	$F_{2,14} = 0.04$, $P = 0.959$
WOTH$_{body}$	4.84 (.)	5.70 (0.14)	5.94 (0.06)	$F_{2,11} = 3.57$, $P = 0.064$
WOTH$_{retrix}$	4.77 (.)	5.20 (0.15)	4.97 (0.03)	$F_{2,11} = 0.91$, $P = 0.430$
OVEN$_{body}$	5.50 (0.26)	5.56 (0.20)	5.35 (0.11)	$F_{2,14} = 0.33$, $P = 0.724$
OVEN$_{retrix}$	4.30 (0.28)	4.93 (0.24)	4.79 (0.23)	$F_{2,14} = 1.73$, $P = 0.213$
2006				
SCTA$_{body}$	5.31 (0.17)	5.66 (0.18)	4.74 (0.17)	$F_{2,15} = 5.00$, $P = 0.022$
SCTA$_{retrix}$	4.11 (0.21)	5.06 (0.18)	4.57 (0.11)	$F_{2,15} = 6.26$, $P = 0.011$
WOTH$_{body}$	4.91 (0.30)	5.20 (0.24)	4.93 (0.29)	$F_{2,17} = 0.34$, $P = 0.718$
WOTH$_{retrix}$	4.46 (0.28)	5.19 (0.37)	4.20 (0.20)	$F_{2,17} = 2.92$, $P = 0.081$
OVEN$_{body}$	5.07 (0.21)	5.12 (0.27)	4.93 (0.15)	$F_{2,14} = 0.19$, $P = 0.827$
OVEN$_{retrix}$	4.42 (0.19)	4.64 (0.17)	4.54 (0.13)	$F_{2,14} = 0.24$, $P = 0.787$

B)

	CC	WH	WT	P-value
2005				
SCTA$_{body}$	-22.59 (0.46)	-22.89 (0.33)	-22.34 (0.10)	$F_{2,14} = 0.85$, $P = 0.448$
SCTA$_{retrix}$	-23.61 (0.58)	-23.68 (0.45)	-23.65 (0.31)	$F_{2,14} = 0.01$, $P = 0.995$
WOTH$_{body}$	-23.20 (.)	-22.33 (0.10)	-22.40 (0.30)	$F_{2,11} = 2.09$, $P = 0.171$
WOTH$_{retrix}$	-23.55 (.)	-22.59 (0.13)	-22.87 (0.37)	$F_{2,11} = 1.75$, $P = 0.219$
OVEN$_{body}$	-22.82 (0.15)	-23.09 (0.21)	-23.07 (0.22)	$F_{2,14} = 0.53$, $P = 0.601$
OVEN$_{retrix}$	-23.28 (0.16)	-23.08 (0.16)	-23.18 (0.23)	$F_{2,14} = 0.26$, $P = 0.774$
2006				
SCTA$_{body}$	-22.48 (0.20)	-22.44 (0.09)	-22.75 (0.30)	$F_{2,15} = 0.60$, $P = 0.563$
SCTA$_{retrix}$	-23.24 (0.32)	-23.13 (0.14)	-23.10 (0.11)	$F_{2,15} = 0.07$, $P = 0.929$
WOTH$_{body}$	-22.30 (0.13)	-22.35 (0.08)	-22.04 (0.08)	$F_{2,17} = 2.64$, $P = 0.100$
WOTH$_{retrix}$	-22.50 (0.26)	-22.57 (0.24)	-22.12 (0.13)	$F_{2,17} = 1.13$, $P = 0.347$
OVEN$_{body}$	-22.64 (0.19)	-22.75 (0.07)	-22.86 (0.15)	$F_{2,14} = 0.40$, $P = 0.676$
OVEN$_{retrix}$	-22.82 (0.19)	-22.28 (0.08)	-22.89 (0.13)	$F_{2,14} = 1.50$, $P = 0.256$

Table 5.3. Mean (SE) stable isotope values for body and retrix feathers by site for Scarlet Tanager (SCTA), Wood Thrush (WOTH), and Ovenbird (OVEN) in 2005 and 2006. Test results are given from general linear models examining differences among sites. A Bonferroni correction was used to control for the family-wise type 1 error rate for 24 multiple comparisons and provided an adjusted alpha of 0.002, resulting in little evidence for differences in stable isotope values among sites in either year. Results are shown for A) $\delta^{15}N$ values and B) $\delta^{13}C$ values.

	SCTA$_R$	SCTA$_B$	WOTH$_R$	WOTH$_B$	OVEN$_R$	OVEN$_B$	Fruit	Arthro
$\delta^{15}N$	4.74	5.42	4.83	5.30	4.60	5.24	-2.86	0.43
	(0.10)	(0.10)	(0.12)	(0.12)	(0.09)	(0.087)	(0.16)	(0.33)
$\delta^{13}C$	-23.41	-22.57	-22.55	-22.31	-22.98	-22.87	-26.59	-25.71
	(0.14)	(0.10)	(0.10)	(0.06)	(0.08)	(0.08)	(0.21)	(0.28)

Table 5.4. Mean (SE) values of $\delta^{15}N$ and $\delta^{13}C$ for retrix ($_R$) and body ($_B$) feathers of each species and fruit and arthropod (Arthro) samples.

	Body feather		Retrix feather	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
SCTA				
2005	$F_{1,15}=1.55$, P=0.23	$F_{1,15}=1.23$, P=0.29	$F_{1,15}=0.04$, P=0.85	$F_{1,15}=1.14$, P=0.30
2006	$F_{1,16}=0.65$, P=0.43	$F_{1,16}=0.02$, P=0.88	$F_{1,16}=0.12$, P=0.74	$F_{1,16}=2.51$, P=0.13
WOTH				
2005	$F_{1,12}=5.00$, P=0.05	$F_{1,12}=1.68$, P=0.22	$F_{1,12}=4.90$, P=0.05	$F_{1,12}=1.92$, P=0.19
2006	$F_{1,18}=1.08$, P=0.31	$F_{1,18}=0.04$, P=0.85	$F_{1,18}=0.00$, P=0.97	$F_{1,18}=0.05$, P=0.83
OVEN				
2005	$F_{1,15}=0.78$, P=0.39	$F_{1,15}=0.43$, P=0.52	$F_{1,15}=0.23$, P=0.64	$F_{1,15}=0.01$, P=0.93
2006	$F_{1,15}=0.10$, P=0.75	$F_{1,15}=1.03$, P=0.33	$F_{1,15}=0.52$, P=0.48	$F_{1,15}=0.08$, P=0.78

Table 5.5. Test statistics for the relationship between $\delta^{15}N$ and $\delta^{13}C$ values of body and retrix feathers and the energetic condition of independent juvenile Ovenbirds. After adjusting for multiple comparisons to control for the family-wise type 1 error rate (Bonferroni adjusted alpha = 0.002), we did not find any significant relationships between the isotopic signatures of the feathers and energetic condition for Scarlet Tanager (SCTA), Wood Thrush (WOTH), or Ovenbird (OVEN) in either 2005 or 2006 in southern Ohio.

A)

B)
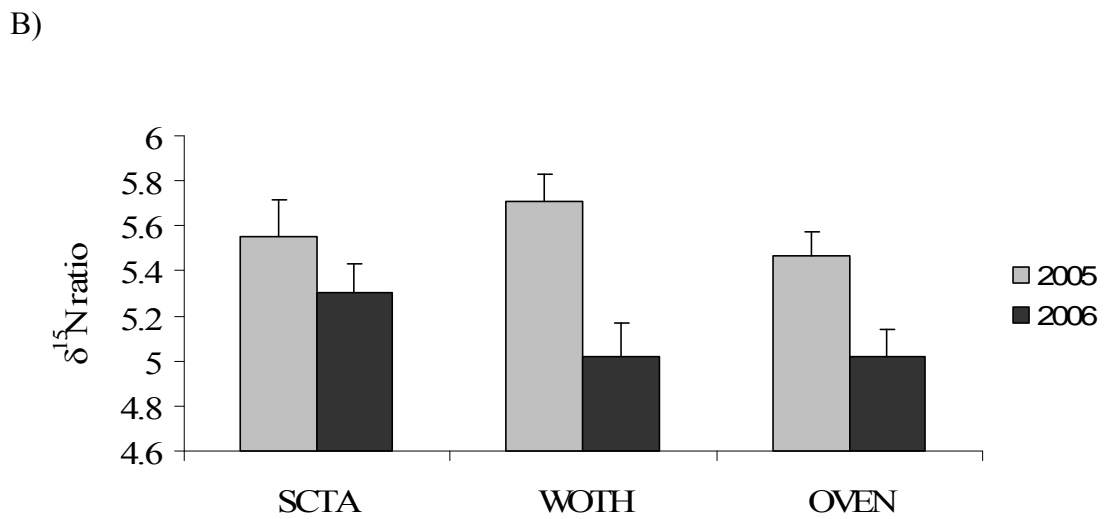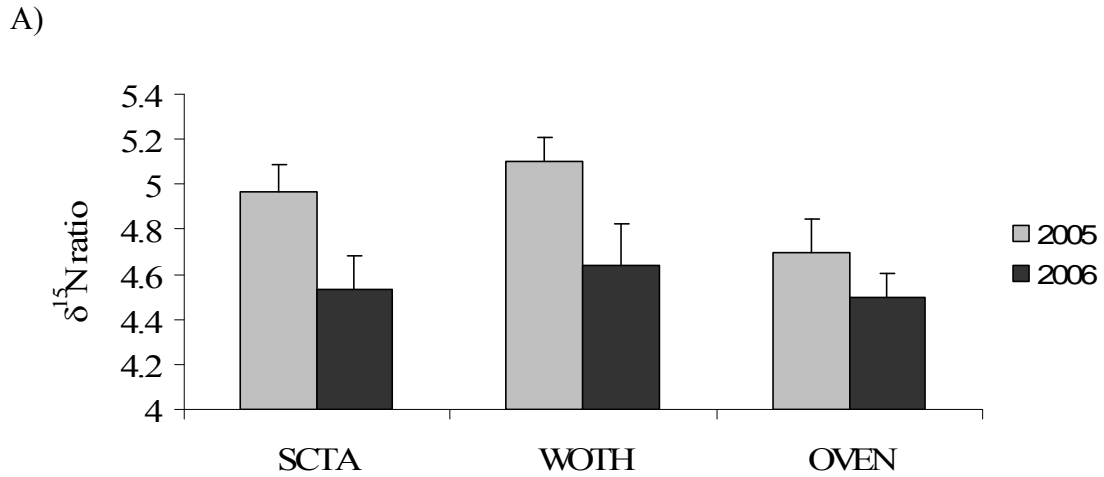
Figure 5.1. Annual values for Scarlet Tanager (SCTA), Wood Thrush (WOTH), and Ovenbird (OVEN) for A) δ^{15}N values in retrix feathers, B) δ^{15}N values in body feathers, C) δ^{13}C values in retrix feathers, and D) δ^{13}C values in body feathers between 2005 and 2006.

Figure 5.1 (continued).

C)
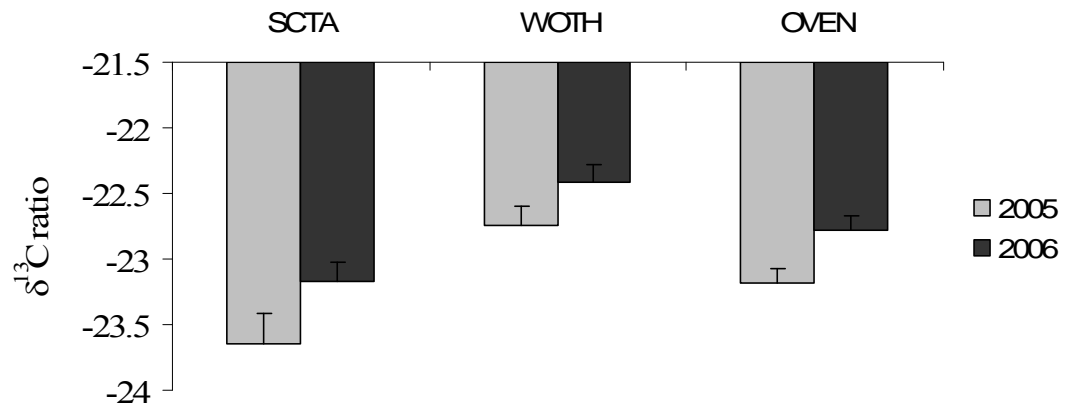
D)
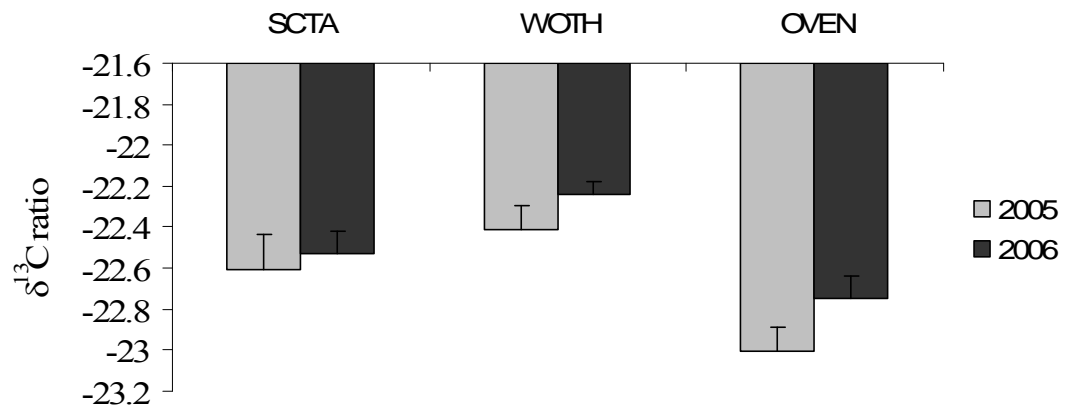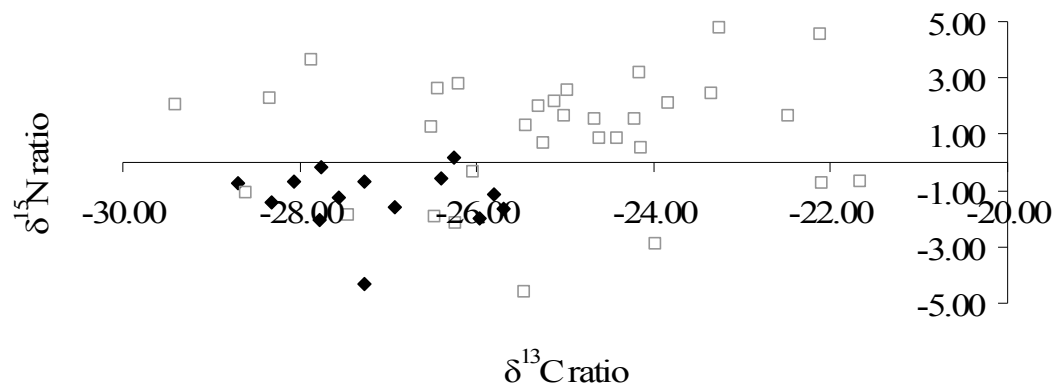
Figure 5.2. $\delta^{15}N$ and $\delta^{13}C$ isotope values for lepidopteran larvae (♦) and non-lepidopteran (□) arthropods in regenerating clearcuts in southeast Ohio in July, 2007.

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APPENDIX A. A list of all of the estimates for fledgling survival of passerines that we were able to find in the literature. All study regions represent U.S. state abbreviations except SW (Sweeden), SZ (Switzerland), ON (Ontario), SP (Spain), NO (Norway), and CR (Costa Rica). The methods used for data collection included capture/recapture (CR), radio-tracking (RT), and color-marking (CM).

Species	Survival	Days	Region	Method	Citation
Great-spotted Cuckoo (*Clamator glandarius*)	63%	59	SP	RT	Soler et al. 1994
Great and Coal Tit *Periparus ater*	47%	20	SZ	RT, CM	Naef-Daenzer et al. 2001
European magpie (*Pica pica*)	50%	47	NO	CM	Husby and Slagsvold 1992
Great Tit *Parus major*	22%	77	SW	CM	Dhondt 1979
Marsh Tit (*Parus palustris*)	4-19%	11	SW	CM	Nilsson and Smith 1985
White-throated Robin *Turdus assimilis*	67%	21	CR	RT	Cohen and Lindell 2004
Wood Thrush *Hylocichla mustelina*	42%	56	MO	RT	Anders et al. 1997
Wood Thrush	75%	100	GA	RT	Powell et al. 2000
Wood Thrush	68%	90	MO	RT	Fink 2003
Gray Catbird *Dumetella carolinensis*	60%	84	IN	RT	Maxted 2001
Brown Thornbill (*Acanthiza pusilla*)	64%	42	AU	CM	Green and Cockburn 2001
Ovenbird *Seiurus aurocapillus*	57%	40	NH	RT	King et al. 2006
Hooded Warbler *Wilsonia citrina*	19%	28	PA	RT, CM	Rush and Stutchbury 2008
Yellow-breasted Chat *Icteria virens*	39%	56	IN	RT	Maxted 2001

APPENDIX A (continued).

Rose-breasted Grosbeak					Stutchbury
Pheucticus ludovicianus	62%	.	ON	RT	(pers. comm.)
Dicksissel					
Spiza americana	56%	58	MO	RT	Wells et al. 2007
Dicksissel					Berkeley
Spiza Americana	33%	28	NE/IA	RT	et al. 2007
Eastern Meadowlark					
Sturnella magna	63%	72	MO	RT	Wells et al. 2007
					Kershner
Eastern Meadowlark	56-69%	90	IL	RT	et al. 2004
Lark Bunting					
Calamospiza melanocorys	37%	20	CO	RT	Adams et al. 2001
Yellow-eyed Junco					
Junco phaeonotus	27%	64	AZ	CR	Sullivan 1989

APPENDIX B. Location coordinates of mature forest study sites in the Ohio Hills Physiographic Province in southeast Ohio.

Site	Latitude	Longitude	Ownership	Adjacent Clearcut
Waterloo	39º20'N	82º16'W	Ohio Division of Wildlife	N
King Hollow	39º20'N	82º19'W	Ohio Division of Forestry	N
Lake Hope	39º20'N	82º21'W	Lake Hope State Park	N
Webb Hollow	39º18'N	82º24'W	Ohio Division of Forestry	Y
CCC	39º17'N	82º20'W	Ohio Division of Forestry	Y
Will Tract	39º15'N	82º24'W	Ohio Division of Forestry	Y
REMA 1	39º09'N	82º23'W	MeadWestvaco	Y

APPENDIX C. Map displaying the location of each study site on an aerial photo showing the greater landscape for these sites.

					Kilometers
0	4	8	12	16	20
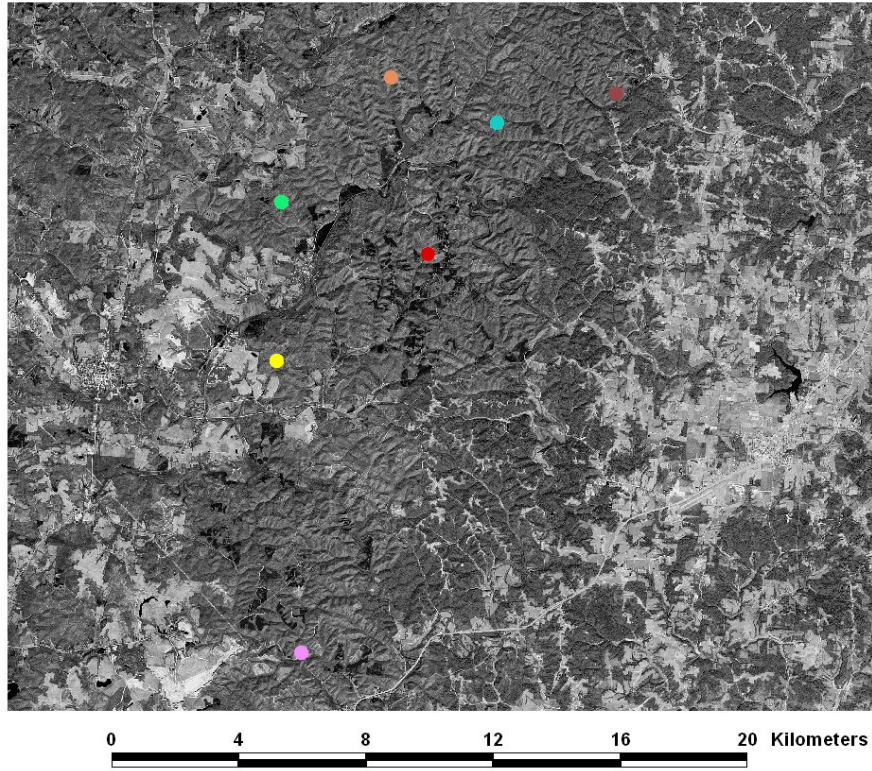
● Will Tract
● Webb Hollow
● Waterloo
● Rema
● Lake Hope
● King Hollow
● CCC

N

APPENDIX D. Information on each radio-tagged fledgling Ovenbird including the year, nesting site, number of days known to survive, the mean distance (m) between successive locations, the distance (m) between the nest location and the final documented location (final distance), and whether the fledgling survived (mortality).

Frequency	Year	Site	Days	Successive distance (SE)	Final distance	Mortality
150.840	2004	WT	34	134 (28)	808	y^s
150.860	2004	RE	40	155 (28)	380	n
150.870a	2004	WT	1	15	15	y^u
150.870b	2004	RE	36	174 (41)	1710	n
150.890	2004	CC	36	110 (11)	268	n
150.940	2004	WT	35	114 (17)	381	n
150.959	2004	RE	3	45 (5)	82	y^u
151.980	2004	CC	40	139 (22)	386	n
151.008	2004	RE	33	91 (36)	894	n
151.030	2004	KH	41	155 (30)	529	n
151.050	2004	KH	29	120 (16)	269	n
151.269	2004	CC	42	88 (7)	437	n
150.571	2005	KH	29	67 (9)	88	n
150.590	2005	CC	43	134 (26)	854	n
150.629	2005	RE	43	111 (29)	1264	n
150.650	2005	WT	41	167 (46)	1191	n
150.672	2005	WL	3	24 (1)	12	y^s
150.689	2005	RE	39	123 (24)	483	n
150.709	2005	WH	7	20 (3)	33	y^m
150.730	2005	WT	11	28 (4)	140	y^r
150.750	2005	WL	39	165 (37)	1700	y^m
150.768	2005	RE	32	91 (16)	686	n
150.790	2005	CC	7	35 (5)	25	y^m
150.810	2005	LH	45	149 (25)	701	n
150.829	2005	WL	46	123 (17)	809	n
150.851	2005	LH	38	95 (18)	506	n
150.870	2005	WL	1	23	23	y^u
150.891	2005	RE	34	74 (8)	279	n
150.910	2005	RE	4	14 (8)	22	y^m
150.931	2005	RE	3	44 (16)	62	y^m

APPENDIX D (continued)

150.970	2005	KH	45	169 (44)	2821	n
150.990	2005	WL	12	53 (13)	76	y^m
150.511	2006	WL	32	111 (22)	1003	n
150.709	2006	CC	30	90 (11)	3	n
150.730	2006	WL	40	167 (39)	1783	n
150.750	2006	KH	5	23 (3)	32	y^m
150.790	2006	WH	46	88 (11)	205	n
150.870	2006	KH	51	90 (12)	601	n
150.910	2006	CC	26	62 (7)	34	n
150.990	2006	KH	27	34 (5)	121	n
151.740	2006	WL	28	100 (15)	52	n
151.762	2006	CC	5	36 (5)	142	y^u
151.800	2006	WL	9	55 (12)	123	y^r
151.841	2006	WT	33	157 (71)	1743	n
151.861	2006	LH	40	180 (27)	1011	n
151.880	2006	KH	50	77 (9)	355	n
151.900	2006	CC	10	80 (21)	161	y^u
151.921	2006	CC	47	152 (49)	2764	n
151.941	2006	LH	45	144 (21)	1572	n
151.951	2006	KH	30	64 (6)	144	n
151.961	2006	WL	2	26 (13)	29	y^u
151.980	2006	LH	47	189 (80)	3708	n

y^s snake predation
y^u unknown mortality
y^m mammal predation
y^r raptor predation

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APPENDIX E. Information on each radio-tagged fledgling Worm-eating Warbler including the year, nesting site, number of days known to survive, the mean distance (m) between successive locations (Successive dist.), the distance (m) between the nest location and the final documented location (Final distance), and whether the fledgling survived (Mortality).

Frequency	Year	Site	Days	Successive dist. (SE)	Final distance	Mortality
150.870	2004	CC	22	76 (12)	375	n
150.138	2004	WL	8	181 (68)	770	y^u
150.159	2004	WL	23	120 (16)	435	n
150.500	2004	KH	27	94 (12)	327	n
150.137a	2005	CC	22	40 (6)	74	n
150.189	2005	WH	21	73 (13)	221	n
150.207	2005	RE	3	23 (7)	4	y^u
150.278	2005	CC	21	117 (22)	105	n
150.300	2005	RE	22	82 (12)	811	n
150.329	2005	WL	21	67 (11)	77	n
150.420	2005	WT	13	125 (23)	799	y^u
150.438a	2005	LH	2	16 (1)	30	y^u
150.438b	2005	CC	17	119 (21)	570	n
150.462	2005	WH	20	114 (23)	106	n
150.540	2005	LH	22	95 (19)	122	n
150.580	2005	WH	17	73 (15)	105	n
150.600	2005	CC	24	59 (12)	91	n
150.038	2005	RE	17	111 (22)	437	n
150.058a	2005	KH	23	120 (30)	357	y^u
150.098	2005	WL	22	109 (21)	258	n
150.158	2005	KH	21	458 (272)	642	n
150.228	2005	WL	4	52 (11)	192	y^u
150.359	2005	WH	23	245 (80)	1999	n
150.399a	2005	LH	16	69 (10)	77	y^r
150.479	2005	KH	20	137 (25)	358	n
150.519	2005	WH	22	95 (16)	448	n
150.558	2005	KH	26	82 (14)	88	n
150.058b	2006	KH	6	41 (9)	228	n
150.137b	2006	KH	10	29 (4)	58	n

APPENDIX E (continued)

150.207b	2006	WH	5	20 (1)	49	n
150.399b	2006	KH	5	66 (16)	17	n
151.017	2006	KH	9	51 (8)	57	n
151.039	2006	WH	31	98 (12)	492	n
151.060a	2006	LH	2	14 (2)	26	y[m]
151.060b	2006	WL	30	158 (35)	498	n
151.081	2006	LH	10	73 (13)	268	n
151.080	2006	WL	29	125 (26)	861	n
151.098	2006	CC	7	42 (9)	76	n
151.120	2006	LH	9	85 (16)	424	n
151.140	2006	CC	18	84 (19)	94	y[u]
151.159	2006	WT	6	94 (32)	190	n
151.179	2006	CC	27	174 (29)	874	n
151.198	2006	WT	11	190 (33)	368	n
151.219	2006	WL	5	48 (8)	65	y[m]
151.238	2006	CC	30	117 (10)	424	n
151.258	2006	WL	7	93 (18)	175	n
151.278	2006	CC	26	168 (39)	1712	n
151.296	2006	WT	5	89 (18)	96	n
151.320	2006	LH	7	86 (25)	159	n
151.338	2006	WL	6	54 (15)	20	n
150.057	2007	CC	20	92 (18)	469	n
150.138	2007	CC	3	23 (2)	63	y[u]
150.199	2007	LH	22	80 (12)	379	n
150.397	2007	CC	9	47 (7)	29	y[u]
150.420	2007	CC	21	146 (35)	516	n
151.020	2007	LH	16	75 (14)	331	n
151.160	2007	CC	29	88 (12)	609	n
151.259	2007	LH	5	67 (18)	71	y[u]
151.296	2007	CC	29	178 (33)	1591	n
151.319	2007	CC	24	60 (8)	18	y[u]

y[u] unknown mortality
y[r] raptor predation
y[m] mammal predation

APPENDIX F. Information on each radio-tagged independent juvenile Ovenbirds including the year, site of capture and release (Site), the treatment (Trt, 1 indicates the release in the original clearcut of capture, 2 the release into a different regenerating clearcut, and 3 the release into mature forest habitat), number of days known to survive, the distance (m) between the nest location and the final documented location (Final distance), and whether the fledgling survived (Mortality).

Frequency	Year	Site	Trt	Days	Final distance	Mortality
151.069	2004	WT→KH	3	25	695	n
151.080	2004	CC→CC	1	6	234	y[r]
151.117	2004	CN→WT	2	24	17855	n
151.140	2004	CN→KH	3	3	929	n
151.160	2004	CC→CC	1	20	4281	n
151.180	2004	KG→WH	2	20	7081	n
151.200	2004	KG→CC	2	36	5089	n
151.220	2004	WT→KH	3	43	9836	n
151.229	2004	GG→LH	3	25	1963	n
151.260	2004	CC→CC	1	5	878	n
151.288	2004	CN→CC	2	3	1787	n
151.300	2004	CC→LH	3	33	8077	n
151.309	2004	CC→WH	2	22	5983	n
151.319	2004	CC→WL	3	34	891	n
151.329	2004	KG→WT	2	38	1232	n
151.340	2004	CC→WH	2	2	105	n
151.380	2004	CN→WT	2	4	1427	n
151.388	2004	CN→WH	2	22	5914	n
151.400	2004	CC→CC	1	28	1174	n
151.428	2004	R1→CC	2	37	5332	n
151.518	2004	CC→CC	1	37	1266	n
151.538	2004	CC→LH	3	8	1585	n
151.720	2004	CC→CC	1	33	6469	n
151.760	2004	CC→WT	2	41	5505	n
151.767	2004	CC→WL	3	15	4262	n
151.798	2004	CN→KH	3	22	5811	n
151.806	2004	WT→WT	1	42	77	n
151.818	2004	CC→WL	3	11	4357	n
150.959	2005	CC→LH	3	26	2164	n

APPENDIX F (continued)

151.081	2005	WT→WT	1	17	627	n
151.101	2005	WH→WH	1	21	106	n
151.269	2005	WH→WH	1	34	418	n
151.478	2005	KG→WH	2	7	4305	n
151.558	2005	WH→KH	3	37	1495	n
151.571	2005	WT→WT	1	6	1069	n
151.621	2005	KG→CC	2	13	4969	n
151.961	2005	WH→WH	1	16	120	n
150.011	2005	CC→LH	3	28	10352	n
150.028	2005	CC→WH	2	29	3140	n
150.048	2005	CC→WL	3	23	2111	n
150.071	2005	WT→WT	1	28	203	n
150.090	2005	CC→CC	1	25	4766	n
150.110	2005	CC→LH	3	17	2798	n
150.170	2005	CC→WT	2	26	878	n
150.220	2005	CC→WT	2	24	2582	n
150.238	2005	CC→WL	3	18	716	n
150.261	2005	WH→WH	1	18	1885	n
150.292	2005	WH→CC	2	18	5497	n
150.311	2005	WH→WH	1	17	979	n
150.342	2005	WT→CC	2	28	4379	n
150.373	2005	WT→WT	1	25	716	n
150.390	2005	WT→WT	1	10	614	n
150.410	2005	CC→CC	1	17	846	n
150.468	2005	CC→WH	2	24	1408	n
150.491	2005	WH→WH	1	22	7146	n
150.511a	2005	CC→WL	3	2	998	y^v
150.511b	2005	WH→KH	3	11	8320	y^r
150.528	2005	KG→KH	3	1	.	n
150.548	2005	KG→WT	2	32	583	n
150.672	2005	WH→CC	2	13	4192	n
150.931	2005	WH→LH	3	11	5739	n
151.360	2006	WT→LH	3	23	5553	n
151.380	2006	CC→CC	1	30	861	n
151.419	2006	CC→WH	2	30	3211	n
151.439	2006	WT→WT	1	29	568	n
151.459	2006	CC→WT	2	31	813	n
151.478	2006	CC→WT	2	32	1087	n
151.489	2006	WT→KH	3	27	2533	n
151.499	2006	WH→WH	1	30	5875	n

APPENDIX F (continued)

151.519	2006	WT→WT	1	15	76	N
151.540	2006	WH→KH	3	30	7515	N
151.571	2006	CC→WH	2	35	377	N
151.582	2006	CC→LH	3	30	5333	N
151.600	2006	CC→WL	3	26	9631	N
151.681	2006	CC→WH	2	26	1103	N
151.700a	2006	CC→CC	1	4	1419	y^r
151.717	2006	CC→WL	3	24	2859	N
150.750	2006	CC→CC	1	29	1613	N
150.709	2006	WT→KH	3	11	4447	N
151.800	2006	WT→CC	2	33	1555	N
151.762	2006	WT→WT	1	14	4797	N
151.961	2006	WH→WH	1	20	5534	N
151.990	2006	CC→LH	3	33	5575	N
151.560	2006	CC→CC	1	9	865	y^r
151.700b	2006	WT→WH	2	25	1182	N

y^r Raptor predation
y^v Vehicle collision

APPENDIX G. A list of the invertebrates sampled with identification to their taxonomic family or order (Group), whether their diet was herbaceous (herb), predatory (pred), or unknown (ukn), isotopic values of δ^{15}N and δ^{13}C, and the site of collection (Site).

Type	Group	Diet	δ^{15}N Delta Air	δ^{13}C Delta PDB	Site
aphid spp	Aleyrodidae	herb	-0.32	-26.04	wh
beetle spp	Coleoptera (order)	ukn	1.55	-24.66	wh
firefly spp	Lampyridae	pred	-0.69	-21.67	cc
firefly spp	Lampyridae	pred	5.58	-23.49	cc
firefly spp	Lampyridae	pred	-0.73	-22.09	cc
firefly spp	Lampyridae	pred	1.65	-22.49	wt
firefly spp	Lampyridae	pred	4.78	-23.26	wt
firefly spp	Lampyridae	pred	4.55	-22.11	wh
firefly spp	Lampyridae	pred	1.53	-24.21	wh
firefly spp	Lampyridae	pred	-1.07	-28.61	wh
green lacewing spp	Chrysopidae	pred	2.79	-26.20	wh
green lacewing spp	Chrysopidae	pred	2.43	-23.35	wt
green lacewing spp	Chrysopidae	pred	1.99	-25.30	wh
ladybug spp	Coccinellidae	pred	0.69	-25.25	wt
ladybug spp	Coccinellidae	pred	2.59	-26.43	wh
leafhopper spp	Cicadellidae	herb	-1.95	-26.48	wt
leafhopper spp	Cicadellidae	herb	-4.59	-25.45	wt
leafhopper spp	Cicadellidae	herb	-2.92	-23.99	wh
leatherwing spp	Cantharidae	pred	3.63	-27.87	wt
leatherwing spp	Cantharidae	pred	2.04	-29.40	wh
lepidopteran spp	Lepidoptera (order)	herb	-1.16	-25.80	wt
lepidopteran spp	Lepidoptera (order)	herb	-0.57	-26.41	wt
lepidopteran spp	Lepidoptera (order)	herb	-0.67	-27.27	wt
lepidopteran spp	Lepidoptera (order)	herb	-4.31	-27.27	wt
lepidopteran spp	Lepidoptera (order)	herb	-1.59	-26.93	wt
lepidopteran spp	Lepidoptera (order)	herb	-2.07	-27.78	wt
lepidopteran spp	Lepidoptera (order)	herb	-1.97	-25.97	wt
lepidopteran spp	Lepidoptera (order)	herb	0.15	-26.26	wt
lepidopteran spp	Lepidoptera (order)	herb	-0.18	-27.75	wt
lepidopteran spp	Lepidoptera (order)	herb	-1.25	-27.57	wt

APPENDIX G (continued)

lepidopteran spp	Lepidoptera (order)	herb	-1.44	-28.31	wh
lepidopteran spp	Lepidoptera (order)	herb	-0.70	-28.07	wh
lepidopteran spp	Lepidoptera (order)	herb	-1.64	-25.69	wh
lepidopteran spp	Lepidoptera (order)	herb	-0.75	-28.70	wh
mosquito	Culicidae	pred	3.17	-24.15	cc
mosquito spp	Culicidae	pred	2.29	-28.33	wh
rose chafer	Scarabaeidae	herb	2.55	-24.98	cc
tussock moth	Lepidoptera (order)	herb	-1.89	-27.45	cc
weevil spp	Curculionidae	herb	2.14	-25.12	cc
weevil spp	Curculionidae	herb	1.25	-26.51	cc
weevil spp	curculionidae	herb	1.65	-25.00	cc
weevil spp	curculionidae	herb	1.31	-25.45	cc
weevil spp	curculionidae	herb	-2.15	-26.25	cc
wheelbug	Reduviidae	pred	0.52	-24.15	cc
wheelbug	Reduviidae	pred	0.83	-24.40	wt
wheelbug	Reduviidae	pred	0.85	-24.61	wh
wheelbug	Reduviidae	pred	2.13	-23.83	wh

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