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Habitat Use, Productivity, and Fruit Selection of Birds in Early-Successional Habitats in Western Massachusetts

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HABITAT USE, PRODUCTIVITY, AND FRUIT SELECTION OF BIRDS IN EARLY-
SUCCESSIONAL HABITATS IN WESTERN MASSACHUSETTS

A Thesis Presented

By

MICHELLE A. LABBE

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

MASTER OF SCIENCE

FEBRUARY 2011

Department of Environmental Conservation

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DEDICATION

Dedicated to my parents, and Memere

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ABSTRACT

HABITAT USE, PRODUCTIVITY, AND FRUIT SELECTION OF BIRDS IN EARLY-SUCCESSIONAL HABITATS IN WESTERN MASSACHUSETTS

FEBRUARY 2011

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Early-successional habitats have become rare in much of the eastern United States, largely due to landuse change, forest maturation and the disruption of natural disturbance regimes. As a result, populations of shrubland songbirds that depend on these habitats are also undergoing severe declines. To address these declines managers have initiated programs for the creation of and maintenance of shrubland habitats termed “wildlife openings.” In addition to providing nesting habitat for shrubland species of high conservation concern, wildlife openings may be important habitat for mature-forest birds during the postfledging period (after the young fledge and prior to migration). The postfledging period is a critical phase in the avian lifecycle with the potential for high mortality, yet the habitat requirements of birds during this time are poorly understood. In addition to habitat characteristics postfledging birds could also be affected by landscape factors, which are known to have strong effects on nesting birds. Finally, wildlife openings may be particularly vulnerable to invasions from exotic invasive plant species, due to the frequent disturbance regimes require to maintain them and thus, there is a concern among managers as to the effects of invasive species on native animal communities.

My study examined the relationships between characteristics of managed shrublands, and the birds that utilize them. In Chapter One, I examined how habitat and landscape affected the abundance of forest birds in wildlife openings during the postfledging period. In Chapter Two, I examined the relationship between these characteristics and the reproductive success of shrubland species that nest in wildlife openings. In Chapter Three, I examined the consequences of fruit choice and fruit abundance on avian body condition and seed dispersal. I also examine these relationships in the context of native vs. invasive plants.

In all chapters, mistnets were used to survey birds in wildlife openings during the postfledging season (July - August). I measured vegetation characteristics, fruit abundance and the prevalence of invasive plants for study site, and I calculated landuse composition within the surrounding landscape (1, 2km). In Chapter One, I used point count surveys to estimate breeding bird densities in the forests adjacent to wildlife openings. In Chapter Two, I examined the reproductive success of shrubland birds using age ratio indices, which incorporate nest success and juvenile survival. In Chapter Three, I recorded foraging observations for common frugivorous bird species.

My results from Chapter One indicated that landscape composition was an important predictor of forest bird abundance in wildlife openings. Captures of forest birds were positively related to residual trees, shrub cover, and fruit abundance, and negatively related to the graminoid cover and invasive plants. My findings support the suggestion made by previous studies, that structurally complex vegetation and abundant food resources are important components of habitat for postfledging forest birds. In Chapter Two I found that shrubland bird species varied in their responses to habitat, patch, and landscape characteristics. Overall, productivity was positively related to taller vegetation structure and

negatively related to the density of low vegetation. Some of my results were inconsistent with studies that have measured nest success. Because the index of productivity that I used integrated nest success and fledging survival, some of these inconsistencies may reflect differences in the habitat characteristics that contribute to nesting success versus those that affect fledgling survival. Patterns in fruit selection indicated that birds chose the fruit of native species over those of invasive species. Consequently, native plants received greater dispersal services from frugivores than invasive plants. Dispersal was not limited by fruit preference, however, and frugivores consumed the fruits of many species other than those they preferred, including those of invasive plants. While there are some purported benefits of invasive fruit as a component of wildlife habitats, my findings indicate the contrary. Not only did many of the most important dispersers prefer native fruits, but also the condition of these birds decreased in sites with a higher prevalence of invasive species.

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CHAPTER 1

THE EFFECT OF LOCAL AND LANDSCAPE-LEVEL CHARACTERISTICS ON THE ABUNDANCE OF FOREST BIRDS IN MANAGED SHRUBLAND HABITATS DURING THE POSTFLEDGING SEASON IN WESTERN MASSACHUSETTS

Introduction

Early-successional habitats have become critically uncommon in much of the eastern United States (Askins 2000, Thompson and DeGraaf 2001, Trani et al. 2001), particularly in the Northeast (Brooks 2003). This decline is attributed in part to forest maturation and the reduced occurrence of natural disturbance regimes (e.g. fire, wind, flooding, and beavers), which historically created openings throughout the predominantly forested landscape across a range of patch sizes (Litvaitis 2001, Lorimer 2001). The northeastern landscape is now dominated by human uses (e.g. agriculture and residential development), and the effect of these disturbance regimes on this altered landscape may no longer be sufficient in providing suitable early-successional habitat (Litvaitis 2001). In response, many agencies have initiated programs for the creation and maintenance of “wildlife openings” by reclaiming abandoned fields and agricultural lands and maintaining them in an early-successional state using periodic mowing.

In addition to providing nesting habitat for numerous shrubland species of high conservation concern (King et al. 2007, Chandler et al. 2009), wildlife openings may also provide important habitat for mature-forest birds during the postfledging period – the

time period after the young fledge from the nest and before initiation of migration (Vega Rivera et al. 1998b, Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Chandler 2007, Vitz and Rodewald 2007). The postfledging period is considered a critical phase of the avian lifecycle with the potential for high mortality (Anders et al. 1997, Kershner et al. 2004, King et al. 2006, Berkeley et al. 2007). Survival of juvenile birds can be particularly low during the postfledging period, which is generally attributed to their limited mobility and inexperience at foraging and evading predators (Sullivan 1989, Anders et al. 1997, Naef-Daenzer et al. 2001). The pronounced change in habitat use observed among forest-breeding birds following the breeding season is attributed to birds seeking out areas with increased understory vegetation and fruit abundance, resources presumed to enhance survival (Anders et al. 1998, Vega Rivera et al. 1998b, Pagen et al. 2000, King et al. 2006).

Despite the potential for high mortality during the postfledging period, it remains one of the least understood phases of the avian lifecycle. This is largely due to the difficulty in tracking birds during the postfledging season, which are no longer singing and become particularly furtive as they feed young and undergo molt (Vega Rivera et al. 1998, Faaborg et al. 1996). Although radio-telemetry studies have increased our understanding of postfledging ecology (e.g. Anders et al. 1998, Vega Rivera et al. 1998a, Kershner et al. 2004, White et al. 2005, King et al. 2006, Rush and Stutchbury 2008), these studies have each focused on only a single species and information remains lacking for the majority of forest birds. To date, there have been few community-level studies of forest birds during the postfledging period (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006, Chandler 2007, Vitz and Rodewald 2007). Furthermore, these

studies have been inconsistent in identifying the important factors explaining early-successional habitat use, suggesting that the habitat requirements of forest bird species during the postfledging season are more variable than is currently assumed. Thus, additional community-wide studies are essential in order to better understand the postfledging ecology of forest birds, and effectively manage for these imperiled populations.

The difficulty in identifying the factors involved in postfledging habitat selection by forest birds may partly be due to variation among studies in the landscape context. The composition of the surrounding landscape is known to have a strong influence on the nesting bird abundance and reproductive success of forest birds (Donovan et al. 1995, Freemark et al. 1995, Robinson and Robinson 1995, Rodewald and Yahner 2001b). The effect of landscape composition on postfledging ecology of birds is uncertain, however, and studies have reported both low (Rush and Stutchbury 2008) and high (Fink 2003) fledgling survival rates for birds occupying highly fragmented landscape. While the influence of landscape composition on forest birds during the postfledging period has been largely overlooked, it may be an important factor in explaining the selection and use of postfledging habitat.

The objective of my study was to determine the relative importance of habitat characteristics and landscape factors in predicting the abundance of mature-forest birds in early-successional habitat during the postfledging season. Specifically, I studied how captures of forest birds in managed shrubland habitats related to; (1) local habitat characteristics, including vegetation structure and composition, fruit abundance, and the prevalence of invasive plants, (2) the abundance of breeding birds in forests adjacent to

habitat patches, and (3) the composition and configuration of forest in the landscape surrounding habitat patches. Lastly, (4) I examined the effects of local and landscape characteristics on the body condition of postfledging birds.

Methods

Study area

This study was conducted in 10 wildlife openings managed either by the Massachusetts Division of Fish and Wildlife, or the Department of Conservation and Recreation (DCR) in Berkshire, Franklin, Hampden, Hampshire, and Worcester counties in western Massachusetts. Forests in the region were predominantly transitional and northern hardwoods dominated by maples (*Acer rubrum*, *Acer saccharum*), birches (*Betula lenta*, *Betula papyrifera*, *Betula alleghaniensis*), red oak (*Quercus rubra*), eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobes*), American beech (*Fagus grandifolia*), and white ash (*Fraxinus americana*), with spruce (*Picea* spp.) and fir (*Abies* spp.) at higher elevations. Wildlife openings ranged in size from 5 to 19 hectares, were a minimum distance of 4 km apart, and were characterized by shrubs, herbaceous plants and scattered trees. Common shrub species included native species of genera *Cornus*, *Rubus*, *Rhus*, *Vaccinium*, and *Spiraea*, as well as non-native species such as honeysuckle (*Lonicera* sp.), common buckthorn (*Rhamnus cathartica*), glossy buckthorn (*Frangula alnus*), autumn olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*). Residual trees were apple (*Malus* spp.), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). Common saplings were red maple (*Acer rubra*), birches (*Betula*

spp.), white ash (*Fraxinus americana*), pin cherry (*Prunus pensylvanica*), black cherry (*Prunus serotina*), white pine (*Pinus strobes*), and red oak (*Quercus rubra*).

Bird surveys

Bird abundance, species and age composition were surveyed using standardized mist netting at each site. Ten (12 m long, 3 m high, 32 mm denier) mist-nets were placed 50 m apart on a 200x150 m grid at each site between mid-July and mid-August, 2007. Survey sites were each sampled twice, with one sample day each at the beginning and end of the postfledging period. During the second cycle of sampling, sites were visited in the same order as during the original sampling. Nets were opened at sunrise and operated for 5 hours per visit (weather permitting). All birds captured (except Ruby-throated Hummingbirds) were banded with a USGS aluminum band, and information on age, sex, mass, tarsus length, and unflattened wing chord were collected. Age (juvenile or adult) was determined by degree of skull ossification, plumage, molt patterns, and evidence of cloacal protuberance or brood patch (Pyle 1997).

Forest point counts

Breeding bird surveys were conducted at five points in the forest adjacent to the site using 10-minute, 50 m radius point counts (Ralph et al. 1997). Points were located using a random starting point 150 m from the patch edge (defined as the center of the outermost canopy tree (Brothers and Spingarn 1992), and at that same distance from the edge 250 m apart thereafter. Each point was surveyed 3 times between 0500-1000 hours on calm days with no precipitation in June and early July 2007.

Data analysis

I used the 2005 MassGIS statewide land use layer in ArcGIS 9.2 (ESRI) to quantify the percent cover of forest, agriculture, development, and areas dominated by early-successional vegetation within 1, 2 and 5 km radii of the center of each study plot. I chose these distances because other studies have shown them to correspond to landscape-scale phenomena in passerines during the nesting season and migration (Hagan et al. 1997, Hartley and Hunter 1998, Driscoll and Donovan 2004, Buler et al. 2007). MassGIS categories representing developed or human-disturbed land use were grouped into the single category “developed,” and all agricultural categories were grouped as “agriculture.” The values for land use classes were highly correlated at the 1, 2, and 5 km radii; therefore I selected the 2 km buffer because it was the intermediate measure, and buffers were non-overlapping at this scale. I then calculated two forest composition metrics in ArcView 9.2 (ESRI); the total number of forest patches and mean patch size. A PCA performed on land use and configuration metrics resulted in one component (PC1) that accounted for 73.8 % of the variation among sites (eigenvalue 4.43). The first principal component, hereafter “fragmentation,” described a gradient with increasing percent cover of agricultural and developed land, and decreasing contiguous forest cover and mean forest patch size (Table 1.1).

Estimates of forest breeding bird abundance were calculated for species that occurred at >30% of sites as determined by both point count and mist net data. These estimates were corrected for heterogeneity of detection probabilities using N-mixture models (Royle 2004). N-mixture models estimate both the mean probability of detection

and an adjusted mean number of birds per plot. Detections by sight, song and call were all included in the analysis

The point-intercept method was used to measure vegetation characteristics at ten random points established from the center of each net. At each point, height and species was recorded for the dominant substrate. Fruit was counted within one meter diameter circles centered on each of the 10 random points and categorized as unripe, ripe, or desiccated. Although I counted fruits of native versus exotic invasive plants separately, for the analyses I combined them because they were correlated ($r = 0.66$, $P = 0.04$) and because invasive fruit was correlated with the cover of invasive plant ($r = 0.71$, $P = <0.01$). Vegetation data was combined into life form categories that reflected vegetation type and structure and included graminoids, ferns and forbs, low broadleaved shrubs (<2m), broadleaved shrubs (2-5m), and broadleaved trees (>5m). Non-native plants were primarily tree and shrub species; thus invasive cover was calculated as a percentage of total tree and shrub cover. A principal components analysis (PCA) was used to reduce the dimensionality of vegetation life form and density variables. The original variables proved more parsimonious (lower AIC_c), and therefore were retained for analysis.

Models were constructed separately for adult and juvenile birds, and separately for the 6 species that had at least 5 captures at 30% or more of sites. I analyzed juvenile and adult birds separately because they may experience different ecological pressures during the postfledging season and I expected them to respond differently to environmental variables. Sample sizes were too small to analyze individual species by age class. Only the captures of birds classified as mature-forest species according to Gough et al. (1998) and Schlossberg and King (2007) were included in the analysis. I

refined these classifications based on knowledge of the local breeding bird community. Paired t-tests were used to test whether capture rates differed between first and second survey dates for each site. Since there were no significant differences in captures between survey days, captures were summed over survey days for each study site.

The influence of local and landscape-level factors on the captures of postfledging forest birds was examined using generalized linear mixed models (GLMM) with site included as a random effect. Captures of adult birds were specified by negative binomial distribution, and captures of juvenile birds and focal species captures were specified with a Poisson distribution. Due to inclement weather conditions, survey effort was not consistent across all nets and sites. Therefore, to standardize bird captures for unequal survey effort (net hours), I included the total number of net hours per visit as an offset in models for juveniles and individual species, and as a covariate in the models for adults (offset was not available for the R function used to perform this analysis, `glmm.admb`). Explanatory variables that were measured at nets were nested within sites, and included vegetation life form classes, fruit abundance, and tree density. Redundancy of variables was evaluated using correlation matrices. There were no variables with a correlation greater than 0.5, therefore all were included in analyses. Prior to analysis, distributions for all variables were examined using histograms and scatter plots. Predictive variables were subsequently log-transformed, centered, and scaled to unit variance to improve normality and model interpretation (Gelman and Hill 2006). Analyses were performed in R version 2.9.1 with the functions `lmer` and `glmm.admb` (R Development Core Team. 2009).

I analyzed the relationship between mistnet captures and habitat characteristics using a manual stepwise selection process (Sokal and Rohlf 1995), and compared models based on Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson, 2002). The model with the smallest AIC_c was considered the best explanatory model; models with AIC_c values within two of the best model were considered to be supported and model with terms with 95% confidence intervals that did not include zero were considered to be strongly supported.

Body condition

To complement my analysis of forest bird abundance, I examined the body condition indices of forest bird species (Johnson 2007). Body condition indices were calculated for focal species with at least 10 captures in at least 50% of sites by first performing a PCA on morphometric variables (tarsus and wing length) to account for body size (Freeman and Jackson 1990). Mass was then regressed against the first component (body size metric), and the residuals were used as an index of body condition. Sample sizes were not sufficient for an analysis that would account for the correlation between individuals captured within the same site. Therefore, for each focal species, Pearson's correlation analysis was used to examine the relationship between site-averaged values of body condition and habitat and landscape variables.

Results

A total of 1,110 individuals of 52 species were caught during the study period

(Appendix 2). Of the total captures, 23% of the individuals (56% of the species) were birds that are considered to be mature-forest nesting species (Gough et al. 1998, Schlossberg and King 2007). The remainders of the captures were birds that nest in early-successional habitat. Many of the birds occupying these sites have been identified as having significant population declines by the Breeding Bird Survey (Sauer et al. 2005), have received high priority ratings from Partners in Flight (Dunn et al. 2005), or are species of special concern in the state of Massachusetts (Appendix 2). Mature-forest birds for which I had sufficient samples were; American Redstart, Black-capped Chickadee, Ovenbird, Rose-breasted Grosbeak, Red-eyed Vireo, and Veery (scientific names in Appendix 2). I encountered 832 individuals of 29 species of mature-forest birds in the forest adjacent to the wildlife openings during the breeding season point count surveys.

Landscape and habitat analysis

All four supported models for adults showed a positive relationship with tree density and fruit abundance, three showed a negative relationship with invasive plants and two models included a positive relationship with the nesting-season abundance of birds in the adjacent forests, and a negative relationship with the fragmentation index and graminoid cover (Table 1.2). Each of the three top models for juveniles indicated strong support for a positive relationship with the nesting-season abundance of birds in the adjacent forests and tree density, and a negative relationship with graminoid cover. One of the three supported models for captures of juveniles included low broadleaved shrub (<2 m) cover, and one included the fragmentation index.

All species were positively related to the density of broadleaved trees (Table 1.3), and four of six species were positively related to their estimates of nesting season abundance as measured by point count surveys (Tables 1.3 and 1.4). Three species were also related to the landscape composition (Table 1.3). All species, except American Redstart, were related to some measure of shrub cover. Black-capped Chickadees and Veeries were positively related to the cover of shrubs 2-5 m tall, and Ovenbirds, Rose-breasted Grosbeaks, and Red-eyed Vireos were positively related to the cover of low (<2 m) shrubs. American Redstarts, Rose-breasted Grosbeaks and Veeries were negatively related to cover of graminoids, and Black-capped Chickadees and Red-eyed Vireos were negatively related to the cover of invasives. Finally, Red-eyed Vireos and Veeries were positively related to fruit abundance, and Red-eyed Vireos were positively related to fern and forb cover. Of these, the relationship of American Redstarts with graminoids, Black-capped Chickadees with tree density, nesting season abundance, and invasive plants, Red-eyed Vireo with tree density and ferns and forbs, and Veery with tree density, graminoids and landscape composition received strong support (95% confidence intervals did not include zero).

Body condition

American Redstarts, Black-capped Chickadees, Red-eyed Vireos, and Veeries each had a sufficient number of observations for inclusion in the body condition analysis (Table 1.4). The body condition indices of American Redstarts were significantly and positively related to the site-level abundance of fruit. Body condition of Black-capped Chickadees was positively related to the site-level cover of low broadleaved shrubs and

Veery body condition was positively related to the site-level cover of ferns and forbs and negatively related to the cover of graminoids. There were no significant relationships between habitat or landscape variables and the body condition of Red-eyed Vireos.

Discussion

My findings are consistent with previous observations that forest-nesting birds shift their habitat use to early-successional areas during the postfledging period (Anders et al. 1998, Lang 1998, Vega Rivera et al. 1998b, Vega Rivera et al. 1999, Vitz and Rodewald 2006, Chandler 2007, Vitz and Rodewald 2007, Lehnen and Rodewald 2009). Moreover, the large number of species captured in wildlife openings during this study provides further evidence that this shift in habitat use is a widespread and general phenomenon among North American forest-nesting passerines.

The relationship I observed between captures of postfledging forest birds and vegetation characteristics are also consistent with previous studies that have found structurally complex low-strata vegetation to be an important component of postfledging habitat (Anders et al. 1998, Vega Rivera et al. 1998b, King et al. 2006, Rush and Stutchbury 2008). My finding that juvenile birds, but not adults, were positively associated with low broadleaved shrubs further supports the suggestion that dense understory vegetation may provide critical protective cover from predators for postfledging birds (King and DeGraaf 2006, Rush and Stutchbury 2008), particularly for young fledglings, which are highly vulnerable due to their poor flight capability and limited mobility (Sullivan 1989, Anders et al. 1997, Vega Rivera et al. 1998b).

The consistent support for models incorporating remnant trees in wildlife openings may reflect their value for providing perch sites and foraging substrates (Yahner 1986, 2003). The retention of residual trees in silvicultural openings has been found to attract forest birds during the nesting season (Rodewald and Yahner 2000). During the postfledging period, trees may be important for adults with dependant broods, by providing perches that allow them to be vigilant of predators while feeding young that may still be on the ground and unable to fly. Lastly, many of the trees within my study sites were species of *Prunus* that were fruiting during course of this study, and this concentrated food resource may have attracted birds.

The strong, negative relationship between captures and the cover of graminoids (grasses, sedges, and rushes), is similar to previous studies that have noted the avoidance of grassy areas by postfledging forest birds (Anders et al. 1998, White et al. 2005). While graminoids may create areas of low, dense vegetation, which are the characteristics generally associated with suitable postfledging habitat (King et al. 2006), extremely dense graminoids could inhibit foraging movement and even increase the risk of predation by concealing terrestrial predators such as snakes, which are often abundant in early-successional and grassland habitats (Thompson III and Burhans 2003, Berkeley et al. 2007). Similarly, Akresh et al. (2009) reported that postfledging birds in Michigan did not use areas of low dense vegetation that was composed of an understudy of bracken fern, possibly because it lacked adequate structure to provide protection from predators.

Fruit

Previous studies have suggested that dense cover and abundant fruit resources may best explain patterns in the habitat use of forest birds during the postfledging period (Anders et al. 1998, Vega Rivera et al. 1998b, Marshall et al. 2003). However, the relative importance of these resources to birds, and whether their importance differs between postfledging juveniles and adults, is unclear. Studies that have examined the habitat use of Wood Thrush (*Hylocichla mustelina*) and Swainson's Thrush (*Catharus ustulatus*) during the postfledging season have suggested that for juveniles, fruit is an important food resource (Anders et al 1997, Vega Rivera et al 2000, White et al. 2005) and a primary driver of habitat selection (Anders et al. 1998, Vega Rivera et al. 1998b, White and Faaborg 2008). While less attention has been focused on the habitat use of postfledging adults of these species, one study that examined molting adult Wood Thrush found no association between their habitat use and the presence of fruiting plants (Vega Rivera et al. 1998a). In one study that examined another thrush species, the Veery, McDermott and Wood (2010) found only weak evidence that captures of postfledging juveniles and adults were related to measurements of fruit abundance, and studies by Vitz and Rodewald (2006; 2007) found no evidence that captures of either juveniles or adults were related to fruit. Collectively, the high amount of variation in these findings suggests that age-specific differences may exist for some species, but any general patterns remain unclear.

One potential explanation for the variation in these results is that the importance of fruit for postfledging forest birds varies among species. While it appears that fruit is important for some species, it may not be for the majority of species. For example Vitz and Rodewald (2006; 2007) found that for forest species as a group, captures of juveniles

and adults were best explained by vegetation characteristics rather than fruit abundance, but when forest birds species were analyzed separately, they found that fruit was strongly related to captures of only one species, the Scarlet Tanager (Vitz and Rodewald 2007). Of the six species of forest birds that I examined individually, only captures of the Veery and Red-eyed Vireo were related to the abundance of fruit. Thus, while my findings may differ from those of earlier studies (Anders et al. 1998, Vega Rivera et al. 1998b, Marshall et al. 2003), they appear consistent with more recent studies (Vitz and Rodewald 2006; 2007), in that individual species differ in their use of fruit during the postfledging period.

Invasive species

The negative relationship between invasive plants and bird abundance is consistent with previous studies that have linked invasives to reduced abundance and diversity of native bird species (Mills et al. 1989, Germaine et al. 1998, Hunter et al. 1998, Benoit and Askins 1999, Rottenborn 1999), greater nest predation, and decreased breeding productivity (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). While many of these invasive shrubs (e.g., autumn olive, multiflora rose, and exotic honeysuckles) were intentionally planted to benefit wildlife by providing food and cover (Gill and Healy 1974), my findings indicate that an increased prevalence of these species may lead to reduced habitat quality for postfledging forest bird. Although the mechanism of this relationship is unclear, many invasive plant species have been linked to reduced invertebrate abundance (Tallamy 2004, Flanders et al. 2006, Ortega et al. 2006), which may be a more important food resource than fruit for many species during the

postfledging season (Vitz 2008). Thus, while it has been suggested that invasive shrubs may provide adequate vegetation structure and fruit resources to serve as functional replacement of native species (Walker 2008), this does not appear to be the case in terms of providing suitable postfledging habitat.

Landscape composition

The relationship I observed between captures of postfledging forest birds and the fragmentation index probably reflects greater abundance and productivity of forest birds, and subsequently, a greater source population in the landscape that may seek out early-successional habitats in the postfledging period. Abundance and reproductive success are known to be negatively related to increasing forest fragmentation (Donovan et al. 1995, Freemark et al. 1995, Robinson and Robinson 1995, Marzluff and Restani 1999, Howell et al. 2000, Rodewald and Yahner 2001a), and increasing with forest cover (e.g. Askins and Philbrick 1987). Lehen and Rodewald (2009) reported that in Ohio, captures of forest birds in clearcuts during the postfledging season was positively related to the cover of forest in the surrounding landscape. Lastly, the fact that the fragmentation index had a greater effect on the abundance of adults than juveniles, suggests that adult birds are moving to these openings from a greater distance than the periphery of the openings, where the point counts were located.

Alternatively, fragmentation could constrain (Lima and Dill 1990, Haas 1995), or channelize movements of birds within a landscape (Machtans et al. 1996, Desrochers and Hannon 1997, Belisle et al. 2001), either of which could affect a bird's ability to locate or encounter suitable postfledging habitat. The constraining effects of fragmentation on

movements may be caused by a bird's reluctance to venture into open areas, possibly because they perceive a greater predation risk in doing so (Lima and Dill 1990). Several studies have reported that fledglings and family groups remained within boundaries of their natal forest patch, apparently due to a reluctance to leave the forest fragment (Belisle et al. 2001, Norris and Stutchbury 2001). Bayne and Hobson (2001) and Rush and Stutchbury (2008) reported that Ovenbirds and Hooded Warblers, respectively, rarely took their dependant broods outside of the forest fragments where they nested. Similarly, Lens and Dhondt (1994) reported delayed dispersal of juvenile Crested Tits out of forest fragments due to their reluctance to cross gaps, and Berkeley et al. (2007) found that the dispersal movements of juvenile Dickcissel appeared to be a function of size and connectivity. The fact that adult birds, which are more mobile, were more affected than juveniles by fragmentation argues against this explanation.

Breeding bird abundance

The most obvious explanation for the positive association between the abundance of forest birds in the openings and their abundance in the adjacent forest during the nesting season is that the point counts reflected the size of the source populations producing juveniles to colonize openings. Juvenile captures were less strongly related to landcover, possibly because their movements occur at a much smaller scale (100s of meters; Kershner 2001, Kershner et al. 2004, Chandler 2007, Rush and Stutchbury 2008 than the landscape scale at which I detected effects of fragmentation on adults (1000s of meters). During the first week after leaving the nest juveniles are particularly limited in their mobility (Kershner et al. 2004) and consequently, the movements of family groups

are constrained by the limited flight capacity of recently fledged young (Sullivan 1989, Anders et al. 1997). Marshall et al. (2003) found that family groups of forest birds that were banded during the breeding season moved short distances into clearcuts adjacent to the forests where they nested. Due to the limited mobility of juveniles (and thus family groups), the accessibility of habitat that will provide protective cover for fledglings may be critical during the early part of the postfledging period, when juvenile mortality is highest (Anders et al. 1997, King and DeGraaf 2006, Yackel Adams et al. 2006, Berkeley et al. 2007, Rush and Stutchbury 2008).

I also found a consistent relationship between captures of focal forest bird species, and estimates of their breeding abundance in the surrounding forests, which indicates that the community of forest birds using early-successional habitats during the postfledging season reflect the local breeding bird community of forest species. However, several forest species were detected during the breeding season point counts that I did not capture in mistnets during the postfledging season. Two of these species were detected infrequently, Blue-headed Vireo (*Vireo solitarius*) and Myrtle Warbler (*Dendroica coronata*), while the rest belonged to a group of habitat specialists that included Hairy Woodpecker, Brown Creeper, Pileated Woodpecker, and Yellow-bellied Sapsucker. Although research devoted to postfledging ecology of these habitat specialists is limited, a study conducted in Spain found that Middle-spotted Woodpeckers (*Dendrocopos medius*) use similar habitats during the nesting and postfledging periods (characterized by high densities of large trees), and that postfledging woodpeckers avoided early-successional forest (Ciudad et al. 2009). Thus, while this group of habitat specialist may be the exception, my results provide additional evidence that the use of early-

successional habitat by forest-nesting passerines during the postfledging season is a generalized phenomenon that occurs across a wide range of species (Vitz and Rodewald 2007).

Body condition

There were no strong patterns among the relationship between habitat or landscape variables and the body condition indices of forest bird species, nor did the results of condition analysis reflect the patterns evident in the analysis of forest bird abundance. Similarly, Vitz (2008) did not find evidence that diet influenced energetic condition for several species of forest birds during the postfledging season. These results, combined with those of the abundance analysis, suggest that fruit resources are not a key factor influencing habitat selection by forest bird during the postfledging period.

Alternatively, food may not have been limited in these habitats to the extent that it would have an effect on the body condition of forest birds. However, because small sample sizes required pooling age and sex classes and using site-averaged values of condition indices and habitat variables, it is possible that the analysis was too coarse to detect the presence of subtle relationships. In any case, further research with larger sample sizes will be required to understand the relationships between habitat use and the condition of forest birds during the postfledging season.

While I have attempted to account for as many variables as possible in the design and implementation of my study, an important caveat is that I cannot account for the possibility that postfledging forest birds selected early-successional habitats other than my study site. The probability of this is most likely related to the proportion of suitable,

early-successional habitat in the landscape. Unfortunately, I did not specifically measure this and thus cannot account for how it may have affected my captures.

Conclusions

My findings support previous recommendations made for postfledging habitat use and further highlight the importance of structurally complex vegetation in providing suitable postfledging habitat (Anders et al. 1998, Vega Rivera et al. 1998b, King and DeGraaf 2006, Chandler 2007, Vitz and Rodewald 2007). In addition, my results indicate that grassland habitats, or habitats with excessively dense vegetation cover, may not have suitable structure to provide quality postfledging habitat for forest birds. Therefore, maintaining low densities of residual trees in early-successional habitat may be beneficial for postfledging forest birds; as well early-successional species that breed in these habitats (Rodewald and Yahner 2001a, Chandler 2006).

Mature-forest birds will likely benefit from management focused on providing habitat for shrubland birds, and conservation strategies may be greatly improved by accounting for habitat requirements during the postfledging period. Some level of interspersed of various stages of successional habitat types will help provide accessible habitat for postfledging birds (Anders et al. 1998, Pagen et al. 2000). Maintaining continuity and movement corridors may also be important for ensuring that habitat patches are accessible to postfledging forest birds. Finally, accounting for landscape contexts can help target management efforts, such as in the acquisition, creation, and maintenance of openings (Saab 1999), by identifying areas prone to edge and area effects, and colonization by invasive species (Borgmann and Rodewald 2005, Johnson et

al. 2006). These results will hopefully help encourage other studies of this important, but poorly understood stage of the avian lifecycle.

Table 1.1. Results from a principle component analysis (PCA) performed on land use classes and forest configuration metrics. Variables were measured within a 2km radius of each study site and included the percent cover of; forest (% Forest), agriculture (% Agriculture), human-disturbed and/or developed land (% Developed), and areas dominated by early-successional vegetation (% Early-successional); and the forest configuration metrics, total patches (# Forest patches) and mean patch size (Mean patch).

PC1 (Fragmentation)	
<hr/>	
Variance eigenvalue)	4.425
Proportion of variance explained	0.738
<i>Structure Correlations (component loadings)</i>	
% Forest	-0.977
% Agriculture	0.732
% Early-successional	0.602
% Developed	0.851
# Forest patches	0.956
Mean patch (ha.)	-0.967

Table 1.2. Model selection results and parameter estimates for negative binomial (adults) and Poisson (juvenile) regression analysis of adult and juvenile mature-forest bird captures in early-successional habitats during the postfledging season. Data were collected for 9 wildlife openings during June-Aug., 2007 in Berkshire, Franklin, Hamden, Hampshire, and Worcester counties, MA. Only models within 2 ΔAIC_c units of top model are shown. Bold text indicates coefficients with 95% confidence intervals that do not include zero. BLSH, FRNFRB, GRAM, LBLSH = % cover vegetation classes, FRT = fruit abundance, INV = non-native trees and shrubs, TREE = tree density, BRDCNT = N-mixture estimates of breeding bird abundance in forest adjacent to study sites, LNDCVR = Principal component for forest fragmentation.

Model	AIC _c	ΔAIC_c	ω	Intercept	BLSH	FRNFRB	GRAM	LBLSH
Juvenile mature-forest birds								
BRDCNT + TREE + GRAM	89.41	0	0.40	-3.05 (0.19)			-0.85 (0.19)	
BRDCNT + TREE + GRAM + LBLSH	90.37	0.10	0.25	-3.07 (0.19)			-0.87 (0.19)	0.14 (0.13)
BRDCNT + LNDCVR + TREE + GRAM	90.88	1.50	0.19	-3.05 (0.19)			-0.88 (0.20)	
Adult mature-forest birds								
LNDCVR + TREE + FRT + GRAM + INV	232.16	0	0.31	3.64 (4.66)			-0.34 (0.16)	
BRDCNT + TREE + FRT	233.71	1.55	0.14	3.03 (4.75)				
BRDCNT + TREE + FRT + INV	234.12	1.96	0.10	3.61 (4.70)				
BRDCNT + LNDCVR + TREE + FRT + GRAM + INV	234.12	1.97	0.12	2.06 (4.98)			-0.31 (0.17)	

Table 1.2 Continued

FRT	INV	TREE	BRDCNT	LNDCVR
		0.56 (0.15)	0.53 (0.14)	
		0.55 (0.14)	0.52 (0.13)	
		0.51 (0.15)	0.48 (0.16)	-0.05(0.05)
0.48 (0.27)	-0.38 (0.19)	0.53 (0.15)		-0.16 (0.07)
0.55 (0.27)		0.72 (0.16)	0.49 (0.20)	
0.72 (0.31)	-0.28 (0.19)	0.77 (0.17)	0.43 (0.02)	
0.52 (0.28)	-0.35 (0.20)	0.60 (0.18)	0.17 (0.23)	-0.13 (0.08)

Table 1.3 Model selection results and parameter estimates for candidate Poisson regression analysis for captures of mature-forest bird species in early-successional habitats during the postfledging season. Data were collected for 9 wildlife openings during June-Aug., 2007 in Berkshire, Franklin, Hamden, Hampshire, and Worcester counties, MA. Only models within 2 ΔAIC_c units of top model are shown. Bold text indicates coefficients with 95% confidence intervals that do not include zero. BLSH, FRNFRB, GRAM, LBLSH = % cover vegetation classes, FRT = fruit abundance, INV = non-native trees and shrubs, TREE = tree density, BRDCNT = N-mixture estimates of breeding bird abundance in forest adjacent to study sites, LNDCVR = Principal component for forest fragmentation.

Model	AIC _c	ΔAIC_c	ω	Intercept	BLSH	FRNFRB	GRAM
Rose-breasted Grosbeak							
null	40.41	0	0.21	-5.35 (0.57)			
GRAM	40.57	0.16	0.20	-5.42 (0.60)			-0.65 (0.54)
TREE	41.50	1.09	0.12	-5.26 (0.55)			
LBLSH + GRAM	42.20	1.79	0.09	-5.53 (0.64)			-0.67 (0.54)
GRAM + TREE	42.26	1.85	0.08	-5.38 (0.59)			-0.56 (0.54)
Black-capped Chickadee							
BRDCNT + INV + LNDCVR + TREE	93.22	0	0.41	-4.02 (0.30)			
BRDCNT + INV + TREE	93.89	0.67	0.29	-3.98 (0.30)			
BRDCNT + INV + LNDCVR + BLSH + TREE	94.75	1.53	0.19	-4.01 (0.30)	0.21 (0.25)		
American Redstart							
BRDCNT + GRAM	52.27	0	0.31	-5.00 (0.65)			-1.68 (0.65)
GRAM	53.28	1.01	0.19	-4.91 (0.64)			-1.73 (0.65)
BRDCNT + TREE + GRAM	53.92	1.65	0.14	-4.99 (0.64)			-1.61 (0.66)

Table 1.3 Continued

LBLSH	FRT	INV	TREE	BRDCNT	LNDCVR
			0.53 (0.5)		
0.32 (0.47)			0.36 (0.51)		
		-0.84 (0.20)	0.83 (0.25)	0.91 (0.28)	-0.20 (0.12)
		-0.81 (0.21)	0.96 (0.26)	0.58 (0.17)	
		-0.84 (0.20)	0.78 (0.26)	0.82 (0.30)	-0.20 (0.12)
				0.41 (0.24)	
			0.18 (0.24)	0.39 (0.23)	

Table 1.3 Continued

Model	AIC _c	ΔAIC _c	ω	Intercept	BLSH	FRNFRB	GRAM
Ovenbird							
BRDCNT + TREE	50.86	0	0.26	-5.41 (0.70)			
BRDCNT + LBLSH + TREE	51.40	0.54	0.20	-5.49 (0.72)			
null	51.72	0.86	0.17	-6.27 (1.14)			
Veery							
LNDCVR + TREE + GRAM	83.47	0	0.27	-3.59 (0.23)			-0.55 (0.22)
LNDCVR + BLSH + GRAM + TREE	83.94	0.47	0.21	-3.62 (0.24)	0.36 (0.28)		-0.40 (0.25)
LNDCVR + BLSH + LBLSH + GRAM + TREE	84.13	0.67	0.19	-3.68 (0.25)	0.46 (0.29)		-0.37 (0.25)
LNDCVR + FRT + GRAM + TREE	84.68	1.22	0.15	-3.64 (0.24)			-0.52 (0.23)
Red-eyed Vireo							
BRDCNT + TREE + FRNFRB + INV + LBLSH	73.99	0	0.26	-4.50 (0.46)		0.83 (0.40)	
BRDCNT + FRNFRB + TREE + LBLSH	74.48	0.49	0.20	-4.44 (0.45)		0.72 (0.40)	
TREE + FRNFRB + INV + LBLSH	74.77	0.78	0.18	-4.54 (0.52)		0.81 (0.39)	
BRDCNT + TREE + FRNFRB + LNDCVR + INV + LBLSH	74.90	0.90	0.16	-4.43 (0.43)		0.82 (0.41)	
BRDCNT + LNDCVR + TREE + FRNFRB + FRT + INV + LBLSH	75.89	1.90	0.10	-4.47 (0.43)		0.87 (0.44)	

Table 1.3 Continued

LBLSH	FRT	INV	TREE	BRDCNT	LNDCVR
0.60 (0.55)			1.04 (0.69) 1.07 (0.69)	0.80 (0.79) 0.67 (0.75)	
0.35 (0.25)	0.31 (0.35)		0.58 (0.19) 0.49 (0.20) 0.49 (0.20) 0.53 (0.19)		-0.26 (0.07) -0.27 (0.07) -0.23 (0.07) -0.25 (0.07)
0.84 (0.43)		-0.47 (0.28)	1.06 (0.38)	0.82 (0.48)	
0.80 (0.43)			0.86 (0.35)	0.87 (0.47)	
0.79 (0.44)		-0.53 (0.29)	0.89 (0.46)		
0.75 (0.43)		-0.45 (0.28)	0.96 (0.31)	0.80 (0.51)	-0.19 (0.14)
0.66 (0.42)	0.59 (0.52)	-0.58 (0.30)	0.92 (0.24)	1.01 (0.56)	-0.18 (0.10)

Table 1.4 Pearson's correlation coefficients (and p-values) between habitat and landscape variables and the body condition of forest bird species captured in wildlife opening during the postfledging season in western Massachusetts, 2007. Significant correlations ($P < 0.05$) are in bold print. Number of sites with observations, and total observations (N) were: Black-capped Chickadee (Sites = 8, N = 35), American Redstart (Sites = 8, N = 22), Veery (Sites = 8, N = 38), and Red-eyed Vireo (Sites = 6, N = 39).

	Black-capped Chickadee	American Redstart	Veery	Red-eyed Vireo
BLSH	-0.53 0.18	0.15 0.73	0.30 0.47	0.44 0.39
FRNFRB	-0.35 0.40	0.34 0.41	0.82 0.01	-0.09 0.87
GRAM	0.54 0.17	-0.22 0.60	-0.77 0.03	-0.17 0.75
LBSH	0.71 0.05	-0.27 0.53	0.15 0.73	-0.34 0.51
FRT	-0.26 0.54	0.80 0.02	-0.21 0.61	-0.68 0.13
INV	-0.50 0.20	0.56 0.15	-0.22 0.61	-0.28 0.60
TREE	-0.52 0.19	0.26 0.53	-0.17 0.69	-0.18 0.73
LNDCVR	-0.33 0.42	0.41 0.31	-0.10 0.81	0.38 0.46

CHAPTER 2
HABITAT CHARACTERISTICS ASSOCIATED WITH PRODUCTIVITY OF
SHRUBLAND BIRDS IN MANAGED SHRUBLANDS IN WESTERN
MASSACHUSETTS

Introduction

Shrubland songbirds are undergoing severe population declines in the northeastern United States, and in New England these declines are strongly associated with declines in habitat availability (Litvatis 1993, Hunter et al. 2001, Thompson and Degraaf 2001). Many of these species are habitat specialists and are restricted to specific habitat characteristics present only 10-15 years post-disturbance (Schlossberg and King 2007). Such early-successional habitat types have now become critically uncommon in much of the Northeast (Brooks 2003), and in Massachusetts suitable habitat for shrubland birds has declined >90% since 1950 (Trani et al. 2001). Historically, natural disturbance agents such as fire, wind, flooding, and beavers created shrubland habitat in New England (Lorimer 2001, Litvatis 2001). Much of this landscape, however, is now dominated by human land uses. As a result, there is less available open land that is subject to natural disturbance regimes, and the small remnant patches of disturbed areas that are embedded in this landscape may not provide suitable habitat for many of these imperiled bird species (Litvatis 2001).

In response to the regional declines in shrubland bird populations, many state and federal land management agencies have initiated activities to create and maintain early-successional habitat. This is often accomplished through the creation or modification of existing early-successional habitat (including old fields, clearcuts, and orchards), which are maintained in an early-seral state through mowing or burning (DeGraaf and Yamasaki 2003, Oehler 2003). The restoration, creation, and maintenance of early-successional habitats is expensive however (Askins 1994), and given the critical state of these bird populations, an understanding of what factors are limiting shrubland bird populations is required to efficiently and successfully manage these declining populations under the constraints of limited resources.

Reproductive success, which is a critical component of annual fecundity, is central to population viability and can be affected by habitat characteristics at multiple spatial scales. Predation is considered the greatest cause of nest failure for passerines (Ricklefs 1969, Martin 1992) and the probability of nest predation is influenced by vegetation characteristics of the nest site and the area immediately surrounding the nest site. Microhabitat characteristics such as nest height, and attributes of the nesting substrate, including height, the presence/absence of thorns, branching structure, and stem density may affect how accessible a nest is to predators (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Schmidt et al. 2005). Vegetation structure in the area immediately surrounding the nest site may influence the concealment and accessibility of nests to predators (Martin and Roper 1988, Yahner and Scott

1988, Kelley 1993, Martin 1993). Previous studies have found that the importance of these habitat characteristics for the nest success of shrubland birds can vary by both species and geographic location (reviewed in Schlossberg and King 2007).

Patch-level factors, including patch area, edge, and shape may also affect the reproductive success of birds (e.g., Robbins et al. 1989, Brodhead et al. 2007). Patch area is positively related to the reproductive success of forest birds (Hoover et al. 1995) and grassland birds (Winter and Faaborg 1999, Johnson and Igl 2001, Davis 2004), although, studies of shrubland birds have found inconsistent results regarding the effects of patch size on abundance and reproductive success (Krementz and Christie 2000, King & DeGraaf 2004, Rodewald and Vitz 2005, Chandler 2006, Lehnen and Rodewald 2009). Reduced reproductive success in small patches may be attributable to edge effects, which refer to the general phenomena of higher rates of nest predation (reviewed in Paton 1994) and parasitism (Faaborg et al. 1995, Hoover et al. 2006, Brodhead et al. 2007) that are associated with the edges of a habitat patch. Among the few studies that have examined the influence of edge effects on shrubland birds, results suggest that edge effects at the scale of the entire patch may be more relevant than measurements of distance-to-edge for an individual nest (Donovan et al. 1997). For example, smaller patches, and those with more complex shapes have proportionally more edge and less core habitat (Temple 1986), which presumably may lead to increased edge-effects. Previous studies (Weldon and Haddad 2005, Chandler 2006) have found evidence that birds nesting in more complex patches had lower nest success than those nesting in patches with simpler shapes, and that

patches with high interior core-to-edge ratio were positively related to productivity (Perkins et al. 2003).

Landscape-scale factors can also have a profound influence on avian reproductive success. Among forest birds, many studies have documented lower rates of nest success in landscapes fragmented by human land uses (i.e. agriculture, residential development) than those with contiguous tracts of forest. These observations of reduced productivity are frequently attributed to elevated rates of nest predation and parasitism that occur in fragmented and human-dominated landscapes (Donovan et al. 1995b, Robinson et al. 1995, Bayne and Hobson 1997b, Rodewald and Yahner 2001, Batary and Baldi 2004). Indeed, the abundance of nest predators may be higher along edges in fragmented landscapes (Chalfoun et al. 2002) and numerous studies have found positive relationships between fragmentation, edge, urbanization, and the abundance of Brown-headed Cowbirds (*Molothrus ater*) (Gates and Geysel 1978, Robinson 1997, Thompson et al. 2000, Burhans and Thompson 2006). While the effects of landscape fragmentation on forest birds are well documented, few studies have examined how shrubland birds respond to factors at the landscape-scale and consequently, the effects of landscape composition on the reproductive success of shrubland birds are less clear. Similar to forest species, there is evidence that the nest success of shrubland birds may be lower in landscapes fragmented by permanent disturbances such as human-development (Lloyd et al. 2005). In heavily forested regions, however, where landscape disturbance is due to ephemeral processes like silviculture, studies have found that fragmentation has either little effect, or a

positive effect on the reproductive success of shrubland birds (Chandler 2006, Morgan et al. 2007).

An additional concern regarding the management of habitat for shrubland bird species is the presence of invasive plant species. Invasive plants can be particularly problematic in managed shrublands due to the frequent disturbance applications required to maintain habitats in an early successional state, which increase the vulnerability of these habitats to exotic plant invasions (Hobbs and Huenneke 1992, Mack et al. 2000). Invasive plants have been found to negatively affect nesting success by altering habitat structure, which in turn has been linked to increased rates of nest predation and brood parasitism (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Rodewald 2009) Yet many studies have also reported that there was no difference in the rates of nest predation between invasive and native plant substrates (Maddox and Wiedenmann 2005, Schmidt et al. 2005, Schlossberg and King 2009) or that some species even had greater nest success when nesting in invasive plants (Schmidt et al. 2005, Schlossberg and King 2009). In fact, many invasive shrubs were planted by managers during the early and mid 1900's in an effort to enhance habitat quality for wildlife by providing additional resources of food and cover (Gill and Healy 1974, Mehrhoff et al. 2003).

In order to evaluate the effectiveness of management practices in providing quality habitat for birds, estimates of productivity are required (Thompson et al. 2001). Most researchers have used the metric of nest success (the proportion of nests that fledge young) or nest survival (the probability of a

nest surviving a specified time interval) as a measure of avian reproductive success. However, because nest success does not account for the fate of nestlings after they leave the nest, it may be a poor predictor of productivity (Underwood and Roth 2002, Anders and Marshall 2005). Upon leaving the nest, fledgling birds receive care from their parents for several weeks, and during this time period, referred to as the “postfledging period,” they are extremely vulnerable to mortality from predation (Anders et al. 1997, King et al. 2006, Yackel Adams et al. 2006, Rush and Stutchbury 2008). Recent studies using radio-tracking, have revealed that survival rates during the postfledging period are lower than previously believed, and that the juvenile survival rates that are currently used in demographic models have been overestimated for many species (Norris and Stutchbury 2001, Yackel Adams et al. 2006, Whittaker and Marzluff 2009). Despite the critical importance of juvenile survival for population recruitment, the postfledging period is poorly understood. To date, studies have found that the predation risks (Schmidt et al. 2008) and habitat requirements of birds during the postfledging season can be significantly different from the requirements of the nesting season (King et al. 2006). Thus, the habitat characteristics that contribute to nesting success may not be the same as those that enhance the survival of fledgling birds. Research has primarily focused on species of forest birds (e.g., Anders et al. 1998, Vega Rivera et al. 1998) and grassland birds (e.g., Yackel Adams et al. 2006, Berkeley et al. 2007, Kershner et al. 2004, Suedakamp Wells et al. 2007), and few have examined the habitat characteristics that affect the survival of fledgling shrubland birds (but see Maxted 2001, Vitz and Rodewald

2010). Consequently, our knowledge of the habitat characteristics that affect the productivity of shrubland birds is currently defined by measures of abundance and nest success, neither of which account for the survival of fledgling birds.

Early-successional species are the focus of considerable conservation concern, yet as is evident from the foregoing, there are significant gaps in our understanding of the effects of microhabitat, patch and landscape influences on reproductive success, and how these interact with invasions by exotic plants. Due to the limited availability of early-successional habitat in the Northeast, understanding how habitat characteristics affect shrubland birds is important for the effective management of remaining habitat (Askins 1994). Many early-successional bird species may benefit from some types of silviculture techniques (reviewed in Schlossberg and King 2007) and given the potential for forestry practices to be used as an economically viable tool in conservation management, understanding how patch area and edge affect habitat suitability may have implications for the design of conservation practices. Finally, given the known effects of landscape factors for forest birds, and the expense of habitat restoration, understanding the potential consequences of land use change and the effects of invasive plants on the habitat quality and productivity of shrubland birds can aid in prioritizing management efforts for the conservation of shrubland bird populations.

This study examined the reproductive success of shrubland birds using indices of productivity based on the age ratio of juvenile to adult birds, which incorporates survival during both the nesting and the postfledging period. When

measured at the end of the breeding season, this index of productivity may better reflect recruitment rates than metrics of nest success by accounting for high postfledging mortality. In addition, this index incorporates multiple components of productivity including the proportion of the population that breeds, the number of breeding attempts, clutch size, hatching success, and fledging success (Ricklefs 1973, Newton 1999, Beissinger and Peery 2007). The aim of this study is to augment previous research on shrubland bird habitat quality and nesting success, and potentially elucidate additional factors that may be important for birds during the postfledging period. Specifically, I examined these productivity indices in relation to vegetation structure and composition, patch and landscape characteristics and the prevalence of invasive plants, in order to understand the factors critical for effective management of these declining populations.

Methods

Study area

This study was conducted in 10 wildlife openings that are managed by either the Massachusetts Division of Fish and Wildlife or the Department of Conservation and Recreation (DCR) located in Berkshire, Hamden, Hampshire, Franklin, and Worcester counties of western Massachusetts. Wildlife openings ranged in size from 5 to 19 hectares, and were characterized by shrubs, herbaceous plants and scattered trees. Common shrub species included native species of *Cornus*, *Rubus*, *Rhus*, *Vaccinium*, and *Spirea*, as well as non-native

species such as honeysuckle (*Lonicera* spp.), common buckthorn (*Rhamnus cathartica*), glossy buckthorn (*Frangula alnus*), autumn olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*). Trees were naturalized species of apple (*Malus* spp.), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). Common saplings were red maple (*Acer rubra*), birches (*Betula* spp.), white ash (*Fraxinus americana*), pin cherry (*Prunus pensylvanica*), black cherry (*Prunus serotina*), white pine (*Pinus strobes*), and red oak (*Quercus rubra*).

Bird surveys

Bird abundance, species, and age composition were surveyed using standardized mist netting at each site. Ten (12m long, 3m high, 32mm denier) mist-nets were placed 50 meters apart on a 200x150m grid at each site between mid-July and mid-August 2007. Each survey site was sampled once during the early postfledging season (July 17th – 31st) and once during the later part of the postfledging season (Aug 1st – 20th) and site was visited in the same order for each of the two cycles. Nets were opened at sunrise and operated for 5 hrs per visit (weather permitting). All birds captured (except Ruby-throated Hummingbirds) were banded with a USGS aluminum band, and information on age, sex, mass, tarsus length, and unflattened wing chord were collected. Birds were classified either as juvenile (0-1 years old) or adult (≥ 1 years old) based on characteristics of plumage, molt pattern, skull ossification, cloacal protuberance, brood patch, and feather wear. Only initial captures of individuals were included in the analysis

(recaptures were excluded). In addition, I excluded individuals from analysis that exhibited any indication of breeding characteristics (e.g. fluid-filled brood patch).

Vegetation composition and structure

The point-intercept method was used to measure vegetation characteristics at ten random points that were established from the center of each net. At each point, height and species were recorded for the dominant substrate and vegetation density was measured by counting the total number of stem and leaf hits within six height class intervals marked on a 3m transect pole. Vegetation data was combined into lifeform categories that reflected vegetation type and structure and included; graminoids, ferns and forbs, low broadleaved shrubs (<2m), broadleaved shrubs (2-5m), and broadleaved trees (>5m). The height interval classes used for vegetation density measurements were highly correlated, therefore I combined them into one of two classes, 'high' (>2m) or 'low' (<2m). The majority of invasive plants at the study sites were trees and shrubs species, therefore invasive cover was calculated as a proportion of total tree and shrub cover. Fruit may be an important food resource for postfledging birds and the availability of food resources can have implications for survival (Anders et al. 1997, Parrish 1997, Vega Rivera et al. 1998, Studds and Marra 2004). Therefore, I measured fruit abundance at each study site by counting all fruits within one meter diameter circles centered on each of the 10 random points.

Patch and landcover metrics

I used the 1999 MassGIS statewide land use layer in ArcGIS 9.2 (ESRI) to calculate patch area and patch-perimeter of each study site, and to quantify the landscape composition within a 1 km radius centered on the mistnet grid at each site. The buffering distance of 1 km was chosen because previous studies of shrubland birds in the Northeast have found that birds respond to landscape characteristics at this scale (Hagan and Meehan 2002, Chandler et al. 2009). The patch-level variable, the ratio of patch area-to-edge, represents the relative proportion of core and edge habitat of a given study site and was calculated as: $\text{patch area} / \text{patch perimeter}$.

Landscape composition can exert a strong influence on avian reproductive success, and landscapes with less forest cover and higher proportions of human-caused disturbance are associated with elevated nest predation and parasitism (Robinson et al., 1995a; Rodewald and Yahner, 2001). Some shrubland generalists, however, which utilize a wide range of habitat types for nesting, have greater nest success in landscapes with human-caused disturbances (Lloyd et al. 2005, Askins et al. 2007). Therefore, given this uncertainty about the effect of disturbance in this system, and to examine the effects of landscape across multiple species of shrubland birds – which may vary in their response to landscape composition and configuration (Hagan et al. 1997, Chandler 2006) – I examined all the landscape variables that have been shown by previous studies to affect avian reproductive success. However, because these variables were highly

correlated, I chose to use a metric that would characterize the landscapes context of this study.

The landscape-level metric was obtained by performing a principle component analysis (PCA) on percent cover of the landuse classes: forest, agriculture, residential development and open land, and the total number of distinct landuse patches within the 1 km buffer of each study site. This resulted in one component (PC1) that explained 79.6 % of the total variation in landscape composition (eigenvalue 3.98). This first component (hereafter, ‘disturbance’ metric) loaded positively for total patches (0.96), percent cover of agriculture (0.81), residential development (0.93), and open land (0.84), and negatively for forest cover (-0.90). The disturbance metric was significant based on Monte-Carlo randomization test, and the broken stick and latent root criteria. Prior to the PCA, assumptions of normality and linearity were evaluated using scatter plots and Q-Q plots; variables that failed to meet assumptions were log-transformed. All analyses were performed in the statistical package R v. 2.9.1 (R Development Core Team 2009).

A principal components analysis (PCA) was used to reduce the dimensionality of vegetation life form and density variables. The original variables proved more parsimonious (lower AIC_c), and therefore were retained for analysis. Explanatory microhabitat variables were log-transformed, centered, and scaled to unit variance to improve equality of variances and model interpretation (Gelman and Hill 2006).

Productivity analysis

I examined the influence of habitat, patch and landscape variables on shrubland bird productivity, measured as the index of juvenile to adult birds, using generalized linear mixed models (GLMM) with a binomial error distribution and a logistic link function. The binomial dependent variable was age ratio, juvenile to adults. Mistnets, which were the unit of measurement for bird captures and microhabitat variables, were nested within each site; therefore, site was included as the random effect in each of the models to account for the non-independence of these observations. Due to inclement weather conditions, survey effort was not consistent across all nets and sites. Therefore, I included the total number of net hours per visit as an offset in all models in order to standardize bird captures for unequal survey effort (net hours).

Model selection

To keep the number of candidate models low, I started with a global model that included additive combinations of habitat variables only, and to evaluate the effect of landscape and patch characteristics on productivity, I included patch and landscape metrics as additive terms in the top-ranked habitat models. I analyzed the relationship between productivity and habitat characteristics using a manual stepwise selection process (Sokal and Rohlf 1995). Candidate models were evaluated using Akaike's Information Criteria adjusted for small sample size (AIC_c ; Akaike 1973). The model with the smallest AIC_c was considered the best explanatory model; models with $\Delta AIC_c \leq 2$ of the best model

were considered to be supported, and model with terms with 95% confidence intervals that did not include zero were considered to be strongly supported (Burnham and Anderson 2002). Analyses were performed using the lmer function in R v. 2.9.1 (R Development Core Team. 2009).

Body condition

Body condition indices have been used to assess non-breeding season habitat quality (Strong and Sherry 2000, Marra and Holmes 2001, Johnson et al. 2006, Johnson 2007). Therefore, to complement my analysis of productivity, I also used indices of body condition to assess habitat quality. In order to standardize body mass for body size, I first performed a PCA on two morphometric variables, tarsus and wing length (Freeman and Jackson 1990). Mass (g) was then regressed against the first component (PC1) and the residuals, which represent the deviation from expected weight given a particular body size, were used as an index of body condition (hereafter, 'body condition'). Male and female birds were analyzed separately for species that had sufficient sample sizes (Green 2001). Because juvenile birds face different ecological constraints than adults during the postfledging period, and thus may respond differently to habitat resources, I examined the condition of juvenile and adult birds separately for each species (sexes were pooled for this analysis). Analyses were restricted to species with >20 captures at >30% of sites and with sufficient records of morphometric measurements (complete data for tarsus, wing, mass). Species with sufficient data to be included in the condition analysis were Cedar Waxwing, Song Sparrow,

Gray Catbird and Common Yellowthroat. Sample sizes were not sufficient for an analysis that would account for the correlation between individuals captured within the same site. Therefore, I used Pearson's product moment correlations to examine the relationships between body condition and habitat and landscape variables. All variables were averaged by site and vegetation variables and were arcsine-transformed. An alpha level of 0.05 was considered statistically significant.

Results

I captured a total of 1,110 individuals of 52 species during the study period (Appendix 2). Of these, 853 of the individuals and 23 of the species were birds that are considered to be early-successional species (Schlossberg and King 2008). Nine of these species are listed as having significant population declines over the past five decades by the Breeding Bird Survey (BBS) (Sauer et al. 2005) (Appendix 2), and one, the Mourning Warbler (*Oporonis philadelphia*), is listed as a species of special concern in the state of Massachusetts. Shrubland species with >20 captures, and for which juvenile and adults each had a minimum frequency of occurrence of >10% of observation were included in the analysis of productivity. Eight species met these criteria; Cedar Waxwing, Field Sparrow, Song Sparrow, Gray Catbird, Chestnut-sided Warbler, Common Yellowthroat, Yellow Warbler and Alder Flycatcher (scientific names in Appendix 2).

Productivity

Productivity as indicated by age ratios was affected by microhabitat, patch and landscape variables (Table 2.1). For all species combined, productivity was positively related to the cover of tall shrubs and tree density and negatively related to vegetation density <2m and invasives. Of these, the relationship of productivity with tree density and with the density of low vegetation (<2m) received strong support (95% confidence intervals did not include zero).

The cover of tall shrubs (>2m) was positively related to the productivity of Yellow Warblers while the cover of low shrubs (<2m) was negatively associated with the productivity of Cedar Waxwings, Field Sparrows (strongly supported) and Yellow Warblers, and positively related to the productivity of Alder Flycatchers (strongly supported) and Chestnut-sided Warblers. The density of low vegetation (<2m) was negatively associated with the productivity of Common Yellowthroats, and the density of tall shrubs (>2m) was positively related to the productivity of Common Yellowthroats and Field Sparrows (both strongly supported). Tree density was positively related to the productivity of Song Sparrows and Cedar Waxwings. The cover of ferns and forbs was positively related to the productivity of Cedar Waxwings (strongly supported) and Chestnut-sided Warblers, and negatively related to the productivity of Common Yellowthroats. Fruit abundance was positively associated with the productivity of Field Sparrows and Gray Catbirds (both strongly supported), while the prevalence of exotic, invasive shrubs was negatively related to the productivity of Song

Sparrows, Field Sparrows (strongly supported), and Common Yellowthroats. The patch-level metric, the ratio of patch area-to- edge, was positively related to the productivity of Song Sparrows and negatively related to the productivity of Cedar Waxwings and Alder Flycatchers (strongly supported). Lastly, the landscape disturbance metric was negative associated with the productivity of Common Yellowthroats, Chestnut-sided Warblers, and Field Sparrows and positively associated with the productivity of Cedar Waxwings and Gray Catbirds (strongly supported).

Body condition

The condition of juvenile Cedar Waxwings was positively related to the cover of ferns and forbs and vegetation density $>2m$ (Table 2.2). The condition of juvenile catbirds was positively related to the cover of invasive trees and shrubs. The condition of juvenile Song Sparrows was negatively related to the cover of invasive plants and landscape disturbance. Finally, the condition of juvenile Common Yellowthroats was negatively related to vegetation density $<2m$. Lastly, the condition of adult female Gray Catbirds was positively related to fruit abundance and the condition of adult female Song Sparrows was marginally related to the cover of low shrubs ($<2m$); both of these relationships were marginally significant.

Discussion

Using age ratios of shrubland birds as an index of reproductive success, which integrates both nesting success and fledging survival, I have shown that shrubland birds were affected by variables at multiple environmental scales, information that managers can use to increase the value of habitat for shrubland birds in managed wildlife openings. Shrubs are widely believed to be in jeopardy, leading managers and conservationists to create and maintain shrubland habitat in managed “wildlife openings.” Despite the fact that most state and federal management entities have active wildlife openings, there is only a single study other than mine that quantitatively relates habitat characteristics in wildlife openings to the productivity of shrubland birds (Chandler et al. 2009).

The age ratios I applied as an index of reproductive success integrated nest success and fledging survival, and thus, some of the patterns between this index and habitat characteristics could reflect the associations between these habitat variables and nesting success. Insofar as habitat structure influences nest-site selection and the placement of nests in nesting substrate (Bowman and Harris 1980, Martin 1985, Knopf and Sedgwick 1992), my finding that productivity indices were positively related to taller vegetation is consistent with previous studies that found a positive effect of height on nest success, perhaps because higher nests are less accessible to some terrestrial predators (Best and Stauffer 1980, Schmidt and Whelan 1999, Budnik et al. 2002, Burhans et al. 2002, Borgman and Rodewald 2004, Schmidt et al. 2005).

If the age ratios do indicate nest success, than my observation that productivity of shrubland birds was negatively related to vegetation density <2m in height is not consistent with studies that report that increased structure and density of woody vegetation decreases nest predation by interfering with nest predators' ability to detect and access nests (Martin 1993, Holway 1991, Murphy et al. 1997). However, the effect of habitat structure on nest success is also reported to increase nest predation, possibly by facilitating the movements of predators (Schmidt and Whelan 1999, Borgmann and Rodewald 2004).

Alternatively, because the index of reproductive success I used incorporates survival during the postfledging period, the relationships with habitat conditions I found could reflect the effects of habitat on fledgling survival rather than nesting success. Juveniles are poor flyers relative to adults and are highly vulnerable to predation (Anders et al. 1997, Sullivan 1989, Yackel-Adams et al. 2001) and dense understory vegetation has been suggested to be critical to juvenile survival by providing protective cover from predators (King et al. 2006). The associations between productivity and tall vegetation could also be a reflection of the effect of habitat on fledgling survival. Fledglings have been observed to move into elevated vegetation layers as they gain greater flight capabilities, presumably in search of greater protection from predators (Moore et al. 2010). Terrestrial small mammals are thought to be important predators of fledging birds in the northeast (King et al. 2006), and seeking elevated perches could help fledglings evade these species. Consistent with this result, Vitz and

Rodewald (2007) found that captures of postfledging forest birds were positively related to sapling canopy height. .

Finally, my finding that residual trees had a positive effect on the productivity of shrubland birds indicates that shrubland species are able to tolerate low densities of large trees. Residual trees and snags, which are often left standing in wildlife management areas, may be beneficial to shrubland birds by providing song posts, perches, and foraging substrates (Yahner 2003, Chandler 2006). In addition, during the postfledging period, trees may benefit adults with dependant young by providing perches from which they can assess predation risks prior to delivering food to concealed fledglings (Pers. Obsv). Despite the positive relationships with trees that I observed in this study, several studies have reported a positive correlation between snags and standing trees and snags and the abundance of Brown-headed Cowbirds (Askins et al. 1997). In areas in the Midwest where cowbirds are a problem it is thought that standing trees and snags could lead to increased rates of nest parasitism by providing observation perches for cowbirds (Johnson and Temple 1990, Freeman et al. 1990), however I caught only two cowbirds during this study and productivity was positively related to tree density, indicating that trees do not contribute to cowbird parasitism in this region.

Patch characteristics

While most species exhibited no relationship with the ratio of area-to-edge, my finding that the productivity of Song Sparrows was positively related to

higher proportions of core area-to-edge habitat is consistent with others who found that shrubland birds nest success was lower in patches with more complex shapes (lower proportions of core area and more edge) (Weldon and Haddad 2005, Chandler 2006).

The negative relationships of Cedar Waxwings and Alder Flycatchers with the area-to-edge ratio may reflect the association of these species with taller shrubs and saplings, which are abundant on the edges of wildlife openings. Cedar Waxwings and Alder Flycatchers nest in tall vegetation (shrubs and saplings), and are thus probably less susceptible to edge-related nest predation than ground nesters (i.e. Song Sparrows) (Chalfoun et al. 2002, Lloyd et al. 2005, Flaspohler et al. 2001).

Landscape

Similar to previous studies of shrubland birds, I found that the effect of landscape composition on the productivity indices of shrubland birds was variable (MacFaden and Capen 2002, Hagan and Meehan 2002, Chandler 2006, Lehnen 2009). For Cedar Waxwings and Gray Catbirds, the amount of disturbance in the landscape surrounding habitat patches had a positive influence on productivity. Both of these species are known to utilize resources associated with human development, such as food provided by fruiting ornamental plants that are commonly used in residential landscaping (Putnam 1949). In particular, the Gray Catbird appears to be one of the few species to benefit, or at least be resilient to anthropogenic disturbance (Lloyd et al. 2005, Askins et al. 2007, Morgan et al.

2007). Species such as Chestnut-sided Warblers and Common Yellowthroats, which unlike catbirds and waxwings are not frugivorous, may receive little benefit from the potential resources provided by human-landuse (e.g. fruit), and development in the landscape may present only negative consequences from increases in the abundance of predators and nest parasites (Burhans and Thompson 2006). Field Sparrows and Common Yellowthroats are also ground nesters and thus may be more sensitive to increased edge-effects (Chalfoun et al. 2002, Lloyd et al. 2005).

Variation among species in the relationship between productivity and landscape composition may also explain why I detected no significant effect of landscape composition on the productivity of shrubland birds combined. Results reported by the few studies that have analyzed productivity of shrubland birds relative to landscape-scale habitat features, have also found these relationships vary among shrubland species (Chandler 2006, Lloyd et al. 2005), and no association between landscape characteristics and nest survival for shrubland birds as a group (Chandler 2006). The weak response of shrubland birds to landscape composition is in contrast with the strong, negative effects of landscape disturbance on nesting success of forest birds in the eastern United States (Robinson et al. 1995). The different responses of shrubland birds likely reflect their adaptation to successfully colonize small, ephemeral patches of early-successional habitat (Askins 2000, Askins 2001).

Invasive plants

The negative effect of invasive trees and shrubs on the productivity indices of shrublands species and on all shrubland birds combined is consistent with previous studies that documented the negative effects of invasives on avian abundance (Mills et al. 1989, Germaine et al. 1998) and reproductive success (Schmidt and Whelan 1999, Borgmann and Rodewald 2004). Invasive plants have been found to affect the productivity of birds directly and indirectly, often through altering vegetation structure and food availability. For example, two invasive species that were common in my study sites, *Rosa multiflora* and *Lonicera* spp., have been found to lead to an overall increase in foliage density in the habitats they invade (Hecksher 2004). In Ohio, nests in invasive shrubs were found to be twice as likely to be depredated as those in native shrubs, and this was partially attributed to greater vegetation volume surrounding nests in invasive plants (Borgman and Rodewald 2004). Schmidt and Whelan (1999) also observed higher rates of nest predation in invasive shrubs (species of *Rhamnus* and *Lonicera*) and suggested this was related to the architecture and greater structure of the branches of these invasives, which may have enabled greater access for terrestrial predators to nests. In addition, both Borgman and Rodewald (2004) and Schmidt and Whelan (1999) reported that the heights of nests built in invasive shrubs were generally lower than nests built in native species, and both studies suggested that this factor may also have contributed to increased predation of nests in invasive substrates, possibly because lower nests were more accessible to terrestrial predators. Lastly, invasive plants could also negatively affect reproductive

success by reducing the availability of insect food (Tallamy 2004, Jones and Bock 2005), because native insects may not be adapted to overcome the chemical defenses of exotic plant species (Orians 1986).

Body condition

There were multiple instances in which associations between habitat variables and condition reflected relationships between productivity and habitat variables, particularly for juveniles, suggesting that in some cases body condition can provide a useful indicator of non-breeding habitat quality (Marra and Holberton 1998, Strong and Sherry 2000, Marra and Holmes 2001, Latta and Faaborg 2002, Johnson et al. 2006, Johnson 2007). Indices of condition have been linked to the probability of fledgling survival in some passerine species (Sullivan 1989, Naef-Daenzer et al. 2001, Berkeley 2004, Yackel Adams et al. 2006, Suedekamp Wells et al. 2007, Vitz 2008). The fact that the consistent relationships I observed between relationships of habitat variables and condition and those with productivity existed primarily among the juveniles of the species I examined, suggests that the factors involved in these relationships may be of particular importance for juvenile survival.

The positive effect of invasives on the condition of juvenile Gray Catbirds further supports the observation of Schlossberg and King (2009) that catbirds experience greater reproductive success when they nest in invasive plants versus when they nest in native plants. However, by examining these factors separately for each juveniles and adult females, my findings may offer further insight to this

relationship. In particular, that adult female catbirds may incur other benefits from invasive plants, as suggested by the positive relationship between adult condition and fruit abundance – a variable correlated with the prevalence of invasive plants ($r_{(8)} = 0.63$, $P = 0.05$). Furthermore, the correlation between landscape disturbance and invasive plants prevalence (With 2004, Johnson et al. 2006), which was evident in my study system ($r_{(8)} = 0.63$, $P = 0.04$), is reflected by the positive relationship between catbird productivity indices and landscape disturbance. These relationships are similar to Morris (2005), who found that female Indigo Buntings nesting in fragmented landscape were able to regain mass more quickly than birds nesting in more forested landscapes, possibly because there were more foraging opportunities in disturbed landscapes, such as the abundant fruit crops of invasive plants. In contrast to catbirds, the negative correlation between Song Sparrows and invasives and landscape disturbance suggest that Song Sparrows may be particularly sensitive to the effects of development.

Conclusions

In this study, I examined the reproductive success of shrubland birds using indices of productivity (ratio of juveniles to adults), which incorporate survival during the nesting season and the postfledging season, when mortality of juvenile is high (Anders et al. 1997, King et al. 2006). While age ratio indices have the advantage of providing a measure of productivity that incorporates survival during both the nesting and postfledging season, this also precludes me from

determining whether microhabitat, patch and landscape factors had different implications for these two lifecycle periods. Nonetheless, my findings are consistent with the current literature on shrubland birds, in that birds responded to characteristics at the microhabitat, patch, and landscape levels, and that the relative importance of these scales varied among species. However, inconsistencies between the relationships I observed using productivity indices and those based on measurements of abundance or nest success, draws attention to our lack of understanding about how landscape patterns and disturbance-related factors affect the reproductive success and postfledging survival of shrubland birds. This discrepancy emphasizes to the need for accurate estimates of season-long productivity and adult and juvenile survival rates, which are critical for the effective conservation management of these declining populations. Future studies should address the need for this information and for basic demographic data, which is currently lacking for many species of shrubland birds in the Northeast. In addition, collecting this data across a range of habitats and landscape conditions will enable a better understanding how changes in landuse patterns may affect the populations of shrubland birds.

Table 2.1 Model selection results and parameter estimates for logistic mixed-model regression analysis of the productivity indices (juvenile: adult) of shrubland birds captured during the postfledging season. Data were collected for 10 wildlife openings during July-Aug., 2007 in Berkshire, Franklin, Hamden, Hampshire, and Worcester counties, MA. Only models within 2 ΔAIC_c units of top model are shown. Bold text indicates coefficients with 95% confidence intervals that do not include zero. BLSH, FRNFRB, GRAM, LBLSH = % cover vegetation classes, FRT = fruit abundance, INV = non-native trees and shrubs, TREE = tree density, HDEN = vegetation density >2m, LDEN = vegetation density <2m, AREA:EDGE = ratio of patch area(ha) to edge(m), LNDCVR = Principal component for landscape disturbance.

Species	Formula	K	AICc	ω	$\Delta AICc$	Intercept	BLSH	FRNFRB	FRT
Cedar Waxwing									
(N = 59)	FRNFRB + TREE + LNDCVR	5	19.99	0.19	0	-6.69 (1.59)		1.86 (1.15)	
	FRNFRB + LBLSH + TREE	5	20.67	0.13	0.68	-5.74 (0.97)		1.45 (0.72)	
	FRNFRB + TREE	4	21.47	0.09	1.48	-5.13 (0.66)		0.77 (0.54)	
	FRNFRB + LBLSH + TREE + AREA:EDGE	6	21.98	0.07	1.99	-6.99 (2.02)		2.63 (1.51)	
Field Sparrow									
(N = 49)	FRT + INV + LBLSH	5	33.71	0.24	0	-2.81 (0.36)			1.25 (0.61)
	FRT + INV + HDEN	5	34.01	0.20	0.30	-2.79 (0.36)			1.56 (0.66)
	FRT + INV + HDEN + LNDCVR	6	34.56	0.16	0.85	-3.31 (0.55)			1.74 (0.67)
Song Sparrow									
(N = 150)	TREE	3	96.69	0.26	0	-1.85 (0.18)			
	NULL	2	97.38	0.18	0.70	-1.95 (0.17)			
	TREE + AREA:EDGE	4	98.28	0.12	1.59	-1.89 (0.19)			
	INV + TREE	4	98.57	0.10	1.88	-1.85 (0.18)			
Gray Catbird									
(N = 148)	FRT + LNDCVR	4	76.90	0.54	0	-2.29 (0.21)			0.56 (0.25)

Table 2.1 Continued

GRAM	INV	LBLSH	TREE	HDEN	LDEN	AREA:EDGE	LNDCVR
			1.68 (0.80)				0.78 (0.48)
		-1.05 (0.56)	1.29 (0.58)				
			1.06 (0.45)				
		-1.95 (1.22)	1.84 (0.98)			-1.79 (1.67)	
	-0.70 (0.41)	-0.78 (0.33)					
	-1.19 (0.56)			0.99 (0.46)			
	-0.50 (0.69)			0.87 (0.47)			-0.59 (0.39)
			0.43 (0.26)				
			0.45 (0.26)			0.15 (0.17)	
	-0.11 (0.17)		0.41 (0.26)				
							0.37 (0.12)

Table 2.1 Continued

Species	Formula	K	AICc	ω	Δ AICc	Intercept	BLSH	FRNFRB	FRT
Chestnut-sided Warbler									
(N = 59)	NULL	2	45.26	0.27	0	-2.18 (0.38)			
	FRNFRB	3	46.23	0.17	0.97	-2.16 (0.37)		0.35 (0.29)	
	LNDCVR	3	47.08	0.11	1.83	-2.14 (0.36)			
	LBSH	3	47.22	0.10	1.97	-2.13 (0.38)			
Yellow Warbler									
(N = 27)	BLSH	3	22.81	0.41	0	-3.06 (0.86)	2.48 (1.12)		
	BLSH + LBSH	4	24.66	0.16	1.85	-2.17 (1.01)	1.86 (1.00)		
Common Yellowthroat									
(N = 174)	FRNFRB + LDEN	4	103.19	0.20	0	-2.53 (0.24)		-0.38 (0.18)	
	FRNFRB + HDEN + LDEN	5	104.12	0.12	0.93	-2.54 (0.23)		-0.31 (0.18)	
	FRNFRB + INV + LDEN	5	104.24	0.12	1.04	-2.53 (0.22)			
	FRNFRB + LDEN + LNDCVR	5	105.03	0.08	1.84	-2.51 (0.23)		-0.39 (0.18)	
Alder Flycatcher									
(N = 27)	LBSH + AREA:EDGE	4	30.64	0.46	0	-2.05 (0.48)			
Shrubland birds									
(N = 746)	BLSH + TREE + LDEN	5	142.93	0.37	0	-2.41 (0.08)	0.25 (0.09)		
	BLSH + INV + TREE + LDEN	6	144.36	0.18	1.43	-2.42 (0.08)	0.25 (0.09)		

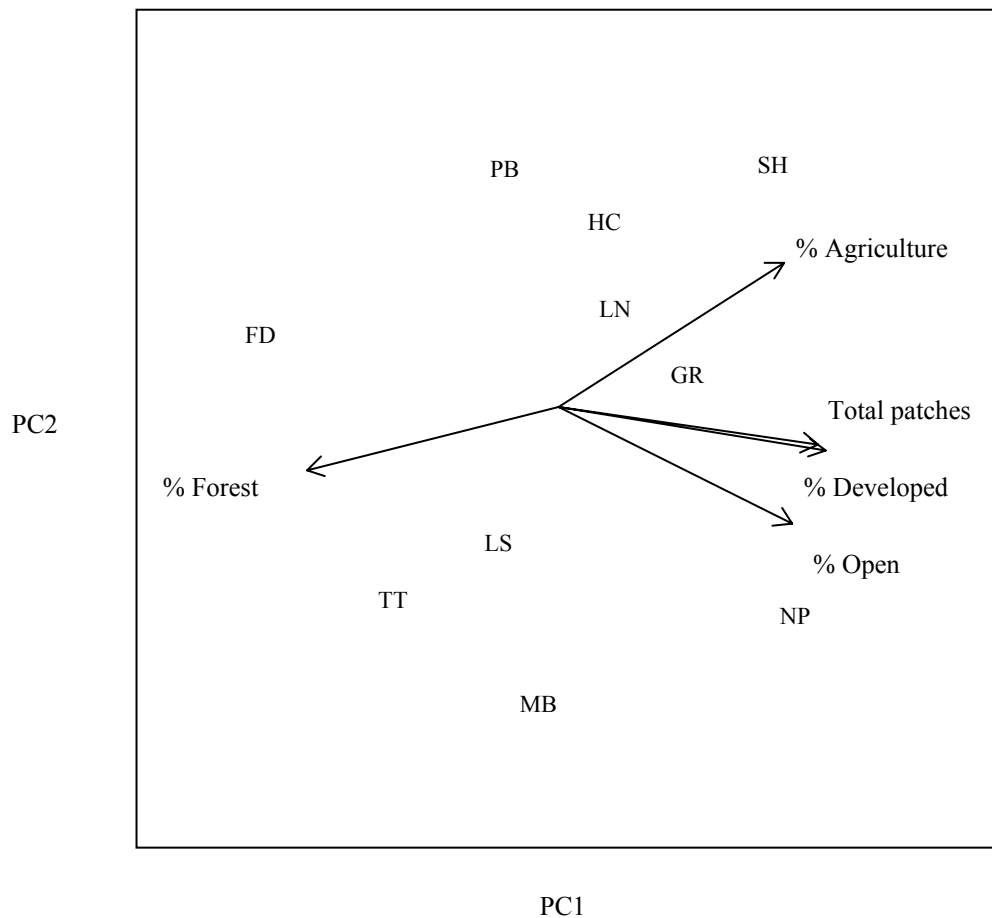
Table 2.1 Continued

GRAM	INV	LBLSH	TREE	HDEN	LDEN	AREA:EDGE	LNDCVR
		0.19 (0.25)					-0.14 (0.16)
		-1.25 (1.31)					
					-0.42 (0.19)		
				0.24 (0.20)	-0.47 (0.20)		
	-0.32 (0.19)			0.39 (0.19)	-0.39 (0.20)		
					-0.39 (0.19)		-0.09 (0.12)
		1.73 (0.76)				-2.78 (1.25)	
	-0.07 (0.08)		0.12 (0.08)	-0.22 (0.09)			
			0.11 (0.08)	-0.24 (0.09)			

Table 2.2 Pearson's correlation coefficients between habitat, patch, and landscape variables and body condition indices of juvenile (juv) and adult shrubland birds captured in wildlife openings in western MA during July-Aug., 2007. CEDW is Cedar Waxwing, SOSP is Song Sparrow, GRCA is Gray Catbird, and COYE is Common Yellowthroat. BLSH, FRNFRB, GRAM, LBSH = % cover vegetation classes, FRT = fruit abundance, INV = non-native trees and shrubs, TREE = tree density, HDEN = vegetation density >2m, LDEN = vegetation density <2m, AREA:EDGE = ratio of patch area(ha) to edge(m), LNDCVR = Principal component for landscape disturbance.

	adultCEDW	juvCEDW	adultSOSP	juvSOSP	adultGRCA	juvGRCA	adultCOYE	juvCOYE
BLSH	-0.05 0.91	0.95 0.21	0.33 0.39	-0.32 0.38	0.58 0.10	-0.09 0.82	0.15 0.67	0.01 0.99
FRNFRB	-0.01 0.98	0.96 0.03	0.36 0.35	0.15 0.68	-0.10 0.81	0.16 0.69	-0.24 0.51	-0.24 0.50
FRT	0.23 0.62	-0.31 0.80	-0.54 0.14	-0.45 0.20	0.65 0.06	-0.02 0.96	0.21 0.56	0.04 0.91
GRAM	0.19 0.69	-0.66 0.54	0.06 0.89	0.11 0.77	-0.56 0.11	0.39 0.30	-0.09 0.81	0.17 0.64
INV	-0.57 0.19	-0.61 0.58	0.22 0.57	-0.68 0.03	-0.25 0.51	0.66 0.05	-0.02 0.96	0.17 0.64
LBSH	-0.09 0.85	-0.86 0.34	-0.61 0.08	0.29 0.42	-0.15 0.71	-0.36 0.34	-0.07 0.85	-0.06 0.86
TREE	-0.24 0.61	-0.82 0.39	-0.20 0.61	-0.30 0.40	0.50 0.17	-0.33 0.39	0.36 0.31	0.03 0.94
HDEN	0.24 0.60	0.96 0.03	0.36 0.34	-0.22 0.53	0.43 0.24	0.06 0.89	0.17 0.64	-0.12 0.74
LDEN	0.09 0.85	-0.31 0.80	-0.47 0.20	-0.05 0.89	-0.02 0.96	0.11 0.77	-0.29 0.42	-0.65 0.04
AREA:EDGE	-0.40 0.37	0.07 0.96	-0.07 0.86	0.30 0.40	-0.32 0.40	-0.15 0.69	-0.44 0.21	-0.32 0.37
LNDCVR	-0.06 0.90	0.81 0.40	-0.16 0.68	-0.64 0.05	0.53 0.14	0.38 0.31	0.12 0.74	0.24 0.51

Figure 2.1 Biplot of PC1 and PC2 showing component scores from principal components analysis (PCA) of landscape “patchiness” and percent cover of landuse classes calculated within a 1km radius for 9 wildlife openings located in Berkshire, Franklin, Hamden, Hampshire, and Worcester counties in Massachusetts. The first component (PC1), or the “disturbance” metric, described 76.6% of the variation and represents a gradient of less disturbed to more disturbed and fragmented (“patchy”) landscapes. %Forest = forest cover, %Open = open land, %Developed = residential development, %Agriculture = agriculture, Total patches = total number of patches. Site codes are: FD=Fox Den, HC=Herman Covey, GR=Green River, LN=Leyden North, LS=Leyden South, MB=Muddy Brook, NP=Natty Pond, PB=Poland Brook, SH=Stafford Hill, TT=Taconic Trail.



CHAPTER 3

AVIAN FRUIT SELECTION BY SHRUBLAND BIRDS AND CONSEQUENCES FOR SEED DISPERSAL AND BODY CONDITION

Introduction

Fruit is consumed by a large number of North American bird species and may provide an important food resource during seasons or lifecycle periods when energy demands are high (Baird 1980, Parrish 1997, Vega Rivera et al. 1998, Suthers et al. 2000, McCarty et al. 2002, Drummond 2005). Access to food resources outside of the breeding season can have implications for survival (Strong and Sherry 2000) and food availability is considered to be a key factor limiting avian populations (Wiens 1989). Likewise, birds' use of fruit and their choices in fruit selection has implications for the reproductive success of their food plants. This has led plants that rely on frugivore dispersers to produce nutritious fleshy fruits in return for the dispersal of their seeds, and competition among plants for the services of the same dispersers has led to plant fruit traits that influence frugivore choice (morphology, display, phenology) (Snow 1971).

The success of many invasive species can be partly attributed to exaggerated life-history traits, such as fruit traits, that make them particularly effective competitors for avian dispersal services. Birds are the major dispersal agents of many invasive plant species (Glyphis et al. 1981, Buchanan 1989, Renne et al. 2002, White and Stiles 1992, McCay et al. 2009), and in the northeastern United States nearly all fruit-bearing invasives rely on birds for seed dispersal (Silander and Klepeis 1999). Birds are highly

mobile, and move between similar habitats (Moody and Mack 1988) and thus have the potential to facilitate the rapid spread of invasive species. This potential depends, in part, on the extent to which they select the fruits of invasive plants. If birds select invasive fruit over the fruits of native plants, natives may be out-competed for dispersal services, which could have serious consequences for native plant communities (Bass 1990, Sallabanks 1992).

Exotic plant invasions can have substantial impacts on native ecosystems, native biodiversity (Daehler and Strong 1994, Wilcove et al. 1998) and ecosystem functions (Vitousek 1990, D'Antonio and Vitousek 1992). By altering the vegetation characteristics and food availability in native habitats, invasive plants can be detrimental to populations of native vertebrates (Tallamy 2004, Ortega et al. 2006). For avian communities, the direct and indirect effects of plant invasions on habitat quality have been linked to reduced species abundance and diversity (Mills et al. 1989, Germaine et al. 1998, Hunter et al. 1998), and lower reproductive success (Schmidt and Whelan 1999, Borgmann and Rodewald 2004, Jones and Bock 2005).

While there are many examples by which invasive plants can be detrimental to native biota, it is suggested that invasives can also have positive impacts, by providing habitat or food resources for native animals (Sax et al. 2005, Gosper and Vivian-Smith 2006). In fact, many of the more problematic invasive plant species in North America today were intentionally planted during the early and mid 1900's to provide food and cover for wildlife (Gill and Healy 1974), and the abundant fruit produced by these invasive plants is readily consumed by birds (Baird 1980, Stiles 1992, White and Stiles 1992, Suthers et al. 2000, Renne et al. 2002, Drummond 2005, Munoz et al. 2007).

Currently, our understanding of the value of invasive fruit as a food resource for birds is largely inferential, and based on observations that birds forage on invasive fruits (Williams 1997). While birds may use invasive fruit, the observation of use alone is not a sufficient indication of its importance as a food resource, and its abundance does not necessarily indicate its nutritional quality. In order to determine whether the use of invasive fruits by birds actually reflects its value as a food resource, rather than a response to its high abundance (Loiselle and Blake 1990), additional information about the relative availability of other food resources and effects on fitness is required. In addition, there is a concern among wildlife managers as to whether invasive fruits constitute “junk food,” (i.e. nutritionally inferior to native fruits; Oehler 2006).

Lastly, while understanding the factors that influence avian fruit choice is key to the effective management of invasives, not all bird species that consume fruit are necessarily seed dispersers. Bird species can vary in their effectiveness as dispersers, due to differences in their foraging behaviors, and relative abundance (Courtney and Sallabanks 1992, Ramirez and Slack 1994). Species-specific data on the foraging behaviors of frugivores that affect dispersal is currently lacking for bird-dispersed plants in the Northeast, which limits our ability understanding of the dispersal ecology of invasives.

Despite increased awareness of the impacts of invasives, there has been no empirical evidence that the use of invasive fruits by birds has a positive or negative effect on survival during the postfledging or pre-migratory period. And, despite the important role that avian frugivores play in the dispersal of fruit bearing plant, there have been few studies that have examined how the fruit preferences of birds may contribute to the

spread of invasives (Gosper 2005, Buckley et al. 2006). In order to understand the dispersal ecology of bird-dispersed invasive plants in the Northeast, and to effectively manage for their control, knowledge is needed about the suite of potential disperser species that exist, the relative importance of these species, and what plant species they are dispersing.

To address these issues, I undertook a study of avian frugivory in managed shrubland habitats in the northeastern United States with the following objectives: (1) evaluate invasive plant food resources as a component of habitat quality and (2) identify important avian seed dispersers of fruit-bearing native and invasive plants. In order to address my first objective, I (a) determined whether frugivores preferentially selected fruits of either native or invasive species, and (b) examined the effect of native and invasive fruit abundance on avian body condition. To address my second objective I (c) examined foraging behavior considered to be important determiners of species disperser efficiency and (d) evaluated the relationships between avian dispersers and fruit bearing plants in terms of patterns of fruit selection and foraging behaviors.

Methods

Study Area

This study was conducted during mid-July through August, 2006 through 2008 at 15 sites in Berkshire, Hamden, Hampshire, Franklin, and Worcester Counties in Western Massachusetts. Eleven of these sites were wildlife openings managed by the Massachusetts Division of Fish and Wildlife, and four were silviculture openings owned

either by the state of Massachusetts, or private landowners. Wildlife openings ranged in size from 5 to 19 hectares, were a minimum distance of 4km apart, and were characterized by shrubs, herbaceous plants and few trees. All surveys were conducted after the nesting season during a peak in the abundance of fruit. This time period also corresponds to a peak in the abundance and species diversity of birds in wildlife openings, when they are utilized by both shrubland and forest bird species (Chapter 1 and 2).

Residual large trees in the study sites were typically apple (*Malus* spp.), black cherry (*Prunus serotina*), and white ash (*Fraxinus americana*). In this study, I focused on the eight most common genera of bird-dispersed, native and invasive woody plants that co-occur in shrubland habitats in the northeastern United States and have overlapping fruiting schedules. Focal native genera included *Cornus*, *Prunus*, *Rubus*, and *Vaccinium*, and focal invasive genera were *Lonicera*, *Elaeagnus*, *Rhamnus*, and *Rosa*. Focal frugivore species were: American Robin (*Turdus migratorius*), Baltimore Oriole (*Icterus galbula*), Cedar Waxwing (*Bombycilla cedrorum*), Gray Catbird (*Dumetella carolinensis*), and Scarlet Tanager (*Piranga olivacea*). These species are not territorial during the postfledging/pre-migratory period and often forage together in flocks.

Field methods

To determine whether frugivores preferentially selected fruits of either native or invasive species and to assess their importance as seed dispersers, I conducted foraging observations at 10 sites during 2007 and 5 sites during 2008. All observations were collected along a grid of transect lines (spaced by 25m) established within each study

plot. To record foraging events, observers walked slowly along transects while looking and listening for target species. Foraging observations were focused on the first foraging attempt after a bird was initially encountered (Hejl et al. 1990). To minimize dependence between foraging events, after each foraging observation, I proceeded along the transect line for a minimum distance of 25m until another individual of a focal species was located. The following data was recorded for each of the foraging observations; food type (insect/fruit) and species (only for fruit), substrate from which food was obtained (plant species and height), the foraging maneuver used to obtain and consume the food, and the number and species of other birds present in the foraging flock. Classifications of foraging observations for fruit were adapted from Remsen and Robinson (1990) and were recorded as either: bite, drop, swallow whole, or taken in flight. Insect prey was noted but not identified to further taxonomic level. Foraging observations were focused on focal species but were collected for other species opportunistically in accordance with the methods described above. All foraging observations were collected during the first 5 hours after sunrise. Foraging observations were not conducted during periods of high winds or in the rain.

To examine the effect of fruit abundance on avian body condition, I captured birds using standardized mist netting with ten (12m long, 3m high, 32mm denier) mist-nets placed 50 meters apart on a 200x150m grid at each site. Each site was sampled on two occasions, once during the early postfledging season (July 17th – 31st) and once during the later part of the postfledging season (Aug 1st – 20th) and visits occurred in the same order for each of the two cycles. Measurements of body size were taken for birds captured in mistnets and included: measured mass (to the nearest 0.1 g using an

electronic scale), tarsus length (to the nearest 0.01 mm), and unflattened wing chord (to the nearest 0.1 mm). Age was classified as hatch-year (HY) or after hatch-year (AHY) based on degree of skull ossification, plumage, molt patterns, and evidence of cloacal protuberance or brood patch (Pyle 1997). Only initial captures of individuals were included in the analyses (recaptures were excluded). Individuals that exhibited any indication of breeding characteristics (e.g. fluid-filled brood patch), which may have influenced body mass, were excluded from analyses. All birds captured (except Ruby-throated Hummingbirds) were banded with a USGS aluminum band.

Fruit abundance was measured at each site using the point intercept method. From the center-point of each mist net, a transect line was determined by a random compass bearing and random distance between 1 and 50m. A sample point was established at the end of each transect and fruit abundance was measured by counting all fruits within a one meter diameter circle centered on the sample point. Fruits were tallied by species and categorized as unripe, ripe, or desiccated. Ten points were sampled per net, for a total of 100 samples per study site.

Data analysis

To examine fruit selection, I identified focal frugivores that had ≥ 10 foraging observations and that were also observed foraging in ≥ 8 sites. For each focal frugivore species, I calculated the proportions of used fruit as the number of foraging events for each genus of plant divided by the total number of foraging events for that bird species. I calculated the proportion of available fruit as the total number of berries counted for a given fruit genus relative to the total berries counted for all focal fruit genera combined.

Compositional analysis was used to examine whether fruit was used disproportionate to its availability (Aebischer et al. 1993). This method of analysis is appropriate for datasets consisting of proportions. Deviations from random use of fruit were evaluated using Wilk's lambda multivariate analysis of variance (MANOVA). If use was found to be significantly different than random, then significant differences among fruit genera were determined using randomization tests (50,000 iterations) to compare the log-odds ratios of ranked "used" and "available" fruit (Aebischer et al. 1993). Foraging observations were combined within each study site for each frugivore species, so that a study site was an independent unit of measurement. Tests were two-tailed and used a significance level of $P = 0.05$. Analysis was performed in R v. 2.10.1 (R core Development Team 2009) with the function `compAna` in the library `adehabitat` (Calenge 2006). Significance was determined using an alpha value of 0.05 and results are reported as means \pm 1 SE.

Bird captures and habitat data from 2006 and 2007 were used to examine the relationship between fruit abundance and the body condition of common frugivores. Only focal frugivores with sufficient captures (>10) and a complete record of measurements (mass, tarsus and wing lengths) were included in the condition analyses. Prior to all analyses, a simple index of condition (mass/wing length) was used to test for a year effect by examining the difference in deviance between the null model, and a model including a term for year. No significant effects of year were found for any species or sex category; therefore data were pooled across years within each of the study sites for all subsequent analyses.

Indices of nutritional condition were calculated by first performing a principal component analysis (PCA) on two morphometric measurements, tarsus and wing length,

in order to derive a single measurement for body structure. The resulting body structure variable (PC1) was then regressed on body mass (“mass”) using linear regression and the residuals from the regression were used as an index of nutritional condition (hereafter “condition”) (Green 2001). The magnitude of the residuals is the deviation in the observed mass of an individual from the expected mass given structural size and the sign of the residual (+/-) indicates better or poorer condition. Data were tested for normality and log transformed as needed (mass of Cedar Waxwings combined and male Gray Catbirds) in order to meet assumptions of the regression analysis. Condition indices were calculated separately for each species and for sexes if sample sizes were sufficiently large.

The relationships between condition and fruit variables were analyzed using restricted maximum likelihood (REML) linear mixed models, which were fitted using the lmer function in R v. 2.10.1 .1 (R Development Core Team 2009). Predictor variables included in the analysis were net-level measurements of abundance of the focal fruit genera, the proportion of all fruit species that was invasive (“prpInv”), and a site-level measurement of total fruit abundance (“totalFruit”). Factors other than food resources can affect condition including, but not limited to, the age and sex of the bird, as well as environmental fluctuations. Therefore, to examine the effects of fruit variables relative to those factors, I included variables for sex, age and year in the analysis. Model fit was assessed by graphical inspection of residual plots, and Shapiro-Wilks normality tests were performed on residuals. Fruit abundance variables were log-transformed prior to analysis (untransformed counts varied from 0 - 70,000) and only fruits that occurred in >5% of observations were included in the condition analysis.

For each species and sex class, I constructed univariate models comprised of a fruit variable and site as a random effect term. Models were ranked in relation to each other based on their AICc scores and evaluated based on AICc weights (Akaike 1973). Models with AICc scores ≤ 2 AICc units of the top model were considered supported (Burnham and Anderson 2002). To determine the precision of parameter estimates, 95% Highest Posterior Density (HPD) confidence intervals were constructed from a Markov Chain Monte-Carlo sample (MCMC) generated from 50,000 iterations of fitted models. HPD intervals return the shortest interval with a 95% probability content in the empirical distribution. Model terms with 95% confidence intervals that did not include zero were considered to be strongly supported. Significance of fixed effects was determined from P-values calculated for each of HPD intervals; alpha = 0.05 was considered statically significant. For each of the focal frugivore species, a separate analysis was conducted for males and females and for all birds combined ('all birds' included male, female, and birds of 'unknown' sex).

Analyses of disperser importance focused on the most common frugivore species American Robin, Baltimore Oriole, Cedar Waxwing, Gray Catbird, Northern Cardinal and Scarlet Tanager. Frugivore species with >10 observation and that were observed foraging on ≥ 2 fruit species in ≥ 2 sites were analyzed separately, while the remaining species were pooled into the category "other." To examine how the frugivore community as a whole contributed to the seed dispersal of native and invasive plants, I pooled observations of all focal frugivores into a single additional category, "frugivores combined." To evaluate the dispersal importance of focal frugivore species and frugivores combined, I developed two indices based on Renne et al. (2000), which

incorporated behavioral traits that determine the quantity of seed dispersal services provided to a plant species and are necessary conditions for a species to be an effective seed disperser (e.g., fruit preference, foraging behavior, and overall abundance) (Schupp 1993, Ramirez and Slack 1994, Renne et al 2000; 2002). The first of these two parameters was the number of seed-swallowing events per a given species of bird within a site, and the second parameter was mean flock size (hereafter “AvgFlock”), which was the average number of individuals of a given species within in a foraging group. The index of flock disperser importance (FDI) was calculated as the product of these two parameters ($FDI = \sum OBS_{site} * AvgFlock$). In addition, an index for the overall dispersal importance of a species (ODI) was calculated to incorporate the species-specific frequency of occurrence by multiplying FDI times the total number of observations across all sites ($ODI = FDI * N_{obsv}$). Indices were calculated within each site for each frugivore and plant species that had sufficient data, and assume that all birds in the flock were foraging.

Dispersal indices (AvgFlock, FDI, ODI) were compared among focal frugivores, focal fruit-bearing plant genera, and plant genera grouped by their native or invasive statuses. Comparisons were made using t-tests or using Analysis of Variance (ANOVA) in R. Homogeneity of variances was examined using Fligner-Killeen tests and log-transformation were used as needed. Normality was examined using Shapiro-Wilk’s tests and variables that did not meet assumptions of normality were square-root transformed. Tukey's ‘Honest Significant Difference’ method was used when multiple comparisons were made.

Results

A total of 255 foraging events were recorded for individuals representing 31 bird species (Table 3.1). Thirty percent (76 obsv.) of these events were directed at fruit and the remaining 70% (179 obsv.) were for insects. In total I observed 12 species of birds forage on the fruits of seven different species of plants (Appendix 3). The focal frugivore species comprised 71% of all fruit foraging observations. American Robins and Scarlet Tanagers were the most frugivorous of the focal bird species, with fruit comprising 77% of recorded observation for American Robins and 67% of observations for Scarlet Tanagers. Cedar Waxwings and Gray Catbirds foraged on insects and fruit equally (47% fruit, 53% insects), Gray Catbirds (50% fruit, 50% insects), and to a lesser extent, so did Baltimore Orioles (42% fruit, 64% insects). Focal fruit species comprised 62%-100% of total available fruit among study sites, and 90% of available fruit overall. The percent of native fruit at sites ranged from 0.2% - 100%. *Lonicera* was found to be the most abundant fruit overall, followed by *Rosa* and *Rubus* (Appendix 4).

Fruit selection

Focal frugivores with a sufficient number of foraging observations for individual analysis of fruit selection were Cedar Waxwing and Gray Catbird. Fruit selection of Cedar Waxwings was found to be significantly different from random (Wilk's $\Lambda = 0.001$, $P = 0.016$), but there was no evidence of differential fruit selection for either Gray Catbirds ($\Lambda = 0.016$, $P = 0.166$) or frugivore species combined (Wilk's $\Lambda = 0.02$, $P = 0.23$) (Fig. 3.1a-c). Nonetheless, a general pattern in all analysis was similar to that

observed in Cedar Waxwings - that *Prunus* generally ranked highest in selection order, while *Rosa* was among the lowest ranked (Fig 3.2). Other patterns of selection, while not all significant, indicated frugivore-specific differences in selection rank among fruits. For example, while *Rubus* ranked high in preference for Gray Catbirds, it was generally avoided by Cedar Waxwings (Fig.3.1a and 3.1b).

Body condition

Four of the focal frugivore species had a sufficient number of captures (>10) and morphometric records (mass, tarsus, wing) for separate analysis of body condition: Baltimore Oriole, Cedar Waxwing, Gray Catbird, and Scarlet Tanager. Of these, male and female Baltimore Orioles, male and female Gray Catbirds, and female Cedar Waxwings had sufficient observations to be individually examined. Age class was omitted from the analysis of female Cedar Waxwing, female Gray Catbird and male Gray Catbirds because in each of these cases, all individuals were adults. Results are reported as Estimate \pm 1 SE and are presented in Table 3.2a-d and Table 3.3a-d.

Supported models for Baltimore Orioles combined were age and sex and indicated that adult condition was greater than juvenile condition, and that male condition was greater than female condition. However, only the model containing age received strong supported (95% confidence interval did not include zero). Supported models for female Baltimore Orioles were the null model and the proportion of invasive fruit. The latter of these indicated a negative relationship between invasive fruit and the condition of female orioles but this relationship was not strongly supported. The single supported model for the condition of male Baltimore Orioles was age class (strongly supported),

which indicated that the condition of adult males was greater than the condition of juvenile males

The one supported model for the condition of Cedar Waxwings combined was the proportion of invasive fruit (strongly supported), which indicated that invasive fruit had a negative effect on Cedar Waxwing condition. Confidence intervals also indicated negative relationships with the abundance of *Rosa* and *Rhamnus* (marginal), and positive relationships with the abundance of *Prunus* and *Rubus*. The top models for female Cedar Waxwing condition included the proportion of invasive fruit and *Rosa* (both strongly supported) and indicated that female waxwings condition was negatively related to invasive fruit and *Rosa*. Confidence intervals also indicated a positive (marginal) relationship with *Prunus*.

The top models for the condition of Gray Catbirds combined included sex (strongly supported) and *Rhamnus* (both strongly supported) and indicated that the condition of female catbirds was greater than that of males and that the condition of Gray Catbirds combined was negatively related to the abundance of *Rhamnus*. Confidence intervals also indicated a (marginal) negative relationship between the condition of catbirds combined and *Elaeagnus*. The only supported model for the condition of female Gray Catbirds was the null model. The single supported model for male Grey Catbird condition was the proportion of invasive fruit (strongly supported), which indicated a positive relationship between male catbird condition and invasive fruit. Confidence intervals also indicated positive relationships with *Rosa* and *Lonicera* (marginal).

The single supported model for the condition of Scarlet Tanagers combined was the model containing sex, which indicated that the condition of males was greater than

females; however this relationship was not strongly supported (95% confidence interval included 0).

Dispersal

Focal frugivore species with sufficient observation for analysis of disperser importance were American Robin, Baltimore Oriole, Cedar Waxwing, and Gray Catbird. Combined, these species comprised 82% of all foraging observations for fruit (N = 62). Two of these species, Cedar Waxwing and Gray Catbird, had a sufficient number of observations for individual analyses. Fruit handling success was high across species, and I observed only two instances of a bird dropping a fruit; both of which were Gray Catbirds foraging on *Prunus*. “Biting” was the principal feeding technique used for *Rubus* (86%), while “swallowing whole” was used for all other fruits (Table 3.1). Although birds were observed biting off smaller pieces of *Rubus* fruit, this fruit is a composite of smaller drupelets, which each contains a seed. Thus, ‘biting’ *Rubus* was assumed to result in consumption of the seed and observations of this event were included in the analyses. No birds were observed carrying unswallowed fruit away from the foraging location.

Overall, focal frugivores differed significantly in measures of FDI and ODI (FDI, $F_{(2, 25)} = 3.6$, $P = 0.04$; ODI, $F_{(2, 25)} = 3.67$, $P = 0.04$), while differences in the average number of individuals per flock (AvgFlock) were marginally significant ($F_{(2, 25)} = 3.6$, $P = 0.08$). In most cases Cedar Waxwings ranked higher than other frugivores, significantly so for ODI (CEDW > GRCA, $P = 0.05$) and marginally for both FDI (CEDW > GRCA

and CEDW > AMRO, both $P = 0.08$) and AvgFlock (CEDW > AMRO, $P = 0.17$ and CEDW > GRCA, $P = 0.11$).

There were no differences among fruit bearing plants in the average number of individuals per flock of Cedar Waxwings ($F_{(3, 7)} = 3.00$, $P = 0.10$), Grey Catbirds ($F_{(4, 7)} = 0.58$, $P = 0.68$), or all frugivores combined ($F_{(6, 11)} = 2.11$, $P = 0.10$). The FDI and ODI for all frugivores combined differed among species of fruit bearing plants ($F_{(6, 11)} = 3.41$, $P = 0.04$, $F_{(6, 11)} = 14.8$, $P = <0.001$, respectively) and in each case a post-hoc comparison indicated that the dispersal indices of *Prunus* (FDI, ODI) were greater than most other fruit-bearing plants species (Table 3.3). While the FDI of Cedar Waxwings ($F_{(3, 7)} = 2.03$, $P = 0.20$) and Grey Catbirds ($F_{(4, 7)} = 2.64$, $P = 0.12$) did not differ among species of fruit-bearing plant, the ODI of Cedar Waxwing ($F_{(2, 7)} = 8.7$, $P = 0.008$) and Gray Catbird ($F_{(4, 7)} = 4.75$, $P = 0.04$) did differ among fruit-bearing plants. A post-hoc analysis indicated that for both frugivore species, the ODI of *Prunus* was higher than other fruit-bearing plants. For waxwings, the ODI of *Prunus* was greater than *Lonicera* ($P = 0.06$) and *Vaccinium* ($P = 0.009$), while for catbirds, the ODI of *Prunus* was greater than *Rubus* ($P = 0.05$) and *Rhamnus* ($P = 0.08$).

There was no difference between native and invasive fruit-bearing plants in the average number of individuals per a flock ($P = 0.62$) or FDI for frugivores combined ($P = 0.21$) (Table 3.4). However, the ODI of frugivores combined was greater for natives than for invasives ($P = 0.005$). The dispersal indices of Cedar Waxwing and Gray Catbirds did not differ between native and invasive fruit-bearing plant species, in terms of AvgFlock, FDI or ODI (all P -values > 0.05).

Frugivore species did not differ in importance as dispersers of invasive plant seed in regards to AvgFlock ($F_{(2, 5)} = 0.28, P = 0.77$), FDI ($F_{(2, 5)} = 0.37, P = 0.71$), and ODI ($F_{(2, 5)} = 1.25, P = 0.36$). However for the dispersal of native plants, frugivore species differed in terms of AvgFlock ($F_{(2, 13)} = 3.72, P = 0.05$), and ODI ($F_{(2, 13)} = 3.89, P = 0.05$), but not FDI ($F_{(2, 13)} = 1.62, P = 0.24$). Cedar Waxwings averaged more individuals per flock than other frugivores but these differences were marginal; Gray Catbirds ($P = 0.10$), American Robins ($P = 0.09$). Lastly, the ODI of Cedar Waxing was significantly greater than the ODI of American Robin ($P = 0.04$).

Discussion

I observed a diverse assemblage of birds consume fruits from a variety of species of plants. Yet, despite their extensive use of fruits, patterns in fruit selection indicated that these birds chose the fruit of native species over those of invasive species. Consequently, native plants received greater dispersal services from frugivores than invasive plants. Dispersal was not limited by fruit preference, however, and frugivores consumed the fruits of many species other than those they preferred, including those of invasive plants. While there are some purported benefits of invasive fruit resources for wildlife habitat, my findings indicate the contrary. Not only did many of the most important dispersers prefer native fruits, but also the condition of these birds decreased in sites with a higher prevalence of invasive species.

A comparison of my findings to previous studies of fruit preference between native and invasive fruit is difficult due to variable results that have been reported for captive birds (Jung 1992, LaFleur et al. 2007), removal experiments with free-living birds (Sallabanks 1993, Drummond 2005), and observational field-studies (Whelan and Willson 1994). However, while these studies did not find strong patterns in selection between native and invasive plants, their results do show that frugivores prefer some fruits to others. Similarly, while I observed the strongest selection for native fruits, all native fruit were not preferred more than all invasive fruits; in fact some invasive fruits were highly preferred.

In large part, the greater selection of native fruit by frugivores can be attributed to their use of *Prunus*. The extensive use of *Prunus* sp. fruit is consistent with previous studies that have examined avian fruit use in the eastern United States (Wheelwright 1986, White and Stiles 1992, Witmer 1996, McCarty et al. 2002). Second to the native *Prunus*, however, frugivores consumed fruits of the invasive plant *Lonicera*, an observation that is also consistent with the reports of several previous studies (Ingold and Craycraft 1983, Witmer and Van Soest 1998, Drummond 2005). In North America, fruits that ripen early in the season, like *Prunus*, are typically high in sugar and low in secondary compounds, and these characteristics make fruit highly palatable to birds (Stiles 1980, Cipollini and Levey 1997a). The preference of birds for fruits high in sugar is widely documented (Moermond and Denslow 1985, Jordano 1988, Loiselle and Blake 1990, Cipollini and Levey 1993, Witmer 1996) and it is suggested that sugar-rich fruits are a high quality energy source for birds, due to digestive adaptations that allow them to efficiently assimilate sugars (Cipollini and Stiles 1993, Lepczyk et al. 2000). Indeed,

among those fruits that I examined the most frequently consumed (*Prunus* and *Lonicera*) were also among the highest in sugar content (Table 3.6). Secondary compounds in fruit pulp, which enhance the persistence of fruit, can also have a strong influence on fruit selection because these chemicals make fruit less palatable to birds (Janzen 1977, Cipollini and Stiles 1992, Levey and Martínez del Río 1999). The presence of unpalatable secondary compounds in *Lonicera* fruit, which unlike the fruits of *Prunus* are persistent, may explain why frugivores preferred *Prunus* fruit over *Lonicera* fruit, despite their equally high levels of sugar.

The role of fruit secondary compounds in mediating fruit persistence and palatability (Herrera 1982), may also explain the patterns of avoidance that I observed. Specifically, I found that birds strongly avoided the fruit of *Rosa* – the most persistent of the fruits that occurred in my study sites. The extreme persistence of *Rosa* fruit suggests it may have particularly high levels of unpalatable, secondary compounds (Witmer 2001). Given the unpalatability of these compounds, birds likely avoided *Rosa* because more of their preferred early-season fruits were available (Baird 1980, Loiselle and Blake 1990). Seasonal changes in the availability of these preferred, but less persistent fruits, may explain the contrast between my observations and those of studies that were conducted during fall (Suthers et al. 2000) and winter (Baird 1980, Stiles 1992, Drummond 2005), in which birds were found to readily consume the fruits of *Rosa*.

In addition to these principal patterns in fruit selection, species exhibited different patterns in fruit use. In some cases these patterns appear to reflect an interaction between a preference for early-season (sugar-rich) fruit, and another species-specific trait that could affect the availability and selection of fruit, namely foraging strata (Malmberg and

Willson 1988). For example, my observations found that catbirds, which are understory foragers, would use fruits from lower shrubs, like *Rubus*, while Cedar Waxwings, which rarely forage outside of the subcanopy strata, may avoid *Rubus* but consume fruits from taller species, such as *Lonicera*. Another trait that can underlie species-specific patterns in fruit selection is the digestive adaptations of a species (Johnson et al. 1985, Witmer and Van Soest 1998, Levey and Martínez del Rio 2001). For example, the digestive adaptations of Cedar Waxwings allow them to specialize on simple sugars, but they can only poorly digest lipids. Consequently, their diet is characterized by fruits high in sugar and a lack of fruit that are lipid-rich (Witmer 1996). Indeed the fruit preferences of Cedar Waxwings that I observed are consistent with this explanation; waxwings foraged almost exclusively on sugar-dominated fruits (Witmer and Van Soest 1998, Martínez del Rio et al 1996, Witmer 1996).

Body condition

The general patterns I observed in fruit selection were paralleled by the patterns in the relationships between fruit abundance and condition, further highlighting the importance of native fruit as a component of habitat quality. The consistency of these patterns was most evident in the relationship between fruit abundance and Cedar Waxwing condition, which was positively related to their preferred sugar-rich fruits, and negatively related to the abundance of *Rosa*, which they avoided. However, while all native sugar rich fruits had positive effects on Cedar Waxwing condition, the one sugar-rich invasive fruit, *Lonicera*, which was preferred by waxwings, had no effect on the body condition of waxwings. This appeared to be a general pattern for the effects of

invasives on condition, where invasive fruit abundance either had no effect on condition, as in the case of *Lonicera*, or had negative consequences. My finding that native fruits were both preferred by birds and had a positive effect on their body condition, is evidence for the benefits of native fruit resources for native habitat quality (Strong and Sherry 2000, Johnson and Sherry 2001). In contrast, the negative relationship I observed between condition and invasive fruit is further indications that exotic plant invasions may lead to reduced habitat quality for populations of native birds.

The notion that invasive fruit is nutritionally poor (junk food) is likely based in part on the original models of dispersal in which lipid-rich fruit were deemed, “high-quality” while carbohydrate-rich fruit was deemed, “low-quality” (Snow 1971, McKey 1975, Herrera 1984). It has since been demonstrated, however, that most small-bodied North American birds can digest sugars significantly better than lipids (Lepczyk et al. 2000). Furthermore, there is no strong evidence that native and invasive fruit have consistent differences in their nutrient content (Hall 1977, Ingold and Craycraft 1983, Johnson et al 1985, White 1989, Drummond 2005, Witmer 1996, Smith et al. 2007, Keuffer et al. 2009). However, another contribution to the “junk food” notion may have been the work of Stiles (1980) who used these traditional models, which were developed in Europe, to categorize the fruits of the eastern United States. Based on the criteria outlined by Stiles (1980), the traits of fruit persistence and low-lipid content, qualified all invasive fruits in this study as “low-quality,” and this distinguished them from native fruit. While my observation that consumption of invasive fruit was negatively correlated with condition does appear to be consistent with the notion that invasive fruit is the

equivalent of avian “junk food,” this link is purely correlative, as I have no information on the effects of fruit consumption on survival.

Invasive plants could also have affected frugivore condition indirectly, by altering habitat structure and/or the availability of other food resources (e.g., Ortega et al 2006, Burke and Nol 1998). For example, invasive plants may have a negative impact on the abundance and diversity of arthropod prey, because native insects may be unable to overcome the chemical defenses of exotic plant species (Tallamy 2004). Invasive plants may also have a negative effect on the abundance and diversity of fruit resources in a habitat, by out-competing other fruit-bearing native plants. Alterations in the diversity or availability of food resources may be particularly detrimental to frugivorous birds, which require a diverse diet of insect food and fruits in order to meet their nutritional needs (Bairlein 1990) and avoid the toxic effects of secondary compounds (Cipollini and Levey 1997a, 1997b; Levey and Cipollini 1998).

In contrast to the general, negative effects of invasives on the body condition of most frugivores, invasive fruit had a positive effect on the condition of adult male Gray Catbirds. Although I observed only a few instances of Gray Catbirds consuming invasive fruit during the course of my study, this finding is consistent with the reports of previous studies, which have reported that the persistent fruits of invasive plants are important food resource for catbirds during the fall and winter months (White and Stiles 1992, Suthers et al. 2000). Specifically, I observed this relationship between male catbird condition and *Lonicera* and *Rosa*, which is similar to Schlossberg and King (2009), who found that *Lonicera* and *Rosa* were preferred nesting substrates of catbirds, and that catbird nests in invasive plants were more successful than those in native plants.

Similarly, Mazzei (2009) reported that breeding abundance of Gray Catbirds was positively correlated to the cover of invasive species in wildlife openings in Connecticut. Together, these findings provide several measures of support indicating that for catbirds, invasive plants may enhance habitat quality (Johnson 2006). This relationship may not be true of invasive shrubs in general, however, as evidence is currently limited to the genera *Lonicera* and *Rosa*. Indeed, the fruit abundance of another common invasive, *Rhamnus*, had a negative effect on the condition of catbirds combined.

Dispersal

American Robin, Cedar Waxwing, and Gray Catbird were the major agents of dispersal of both native and invasive plants in this study system. These species are among the most abundant, and the most frugivorous birds in North America (Wheelwright 1986, Witmer 1996), and their importance as seed dispersers is widely recognized (Thompson and Willson 1979, Ramirez and Slack 1994, Malmberg and Willson 1988, Parish 1997, Renne 2000, Drummond 2005). Consistent with previous accounts, the major disperser species swallowed fruits (and seeds) whole (Johnson et al 1985, Malmberg and Willson 1988), suggesting that fruit selection by these species would result in the dispersal of a seed away from its parent plant – a required condition for a species to be considered an effective disperser (Schupp 1993). Because the fruit-handling techniques were similar among the major frugivores, the trait that was most important in determining a species' importance as a disperser was its flocking behavior. Cedar Waxwing, which had the strongest flocking tendencies of the major dispersers, was thus the most important disperser species overall. Cedar Waxwing is the most frugivorous bird species in North

America (Martin et al. 1951), and is well known for its propensity to forage on fruit in large flocks (Witmer 1996). Similarly to this study, Ramirez and Slack (1994) identified Cedar Waxwing as the most important disperser species of Ashe Juniper trees (*Juniperus ashei*), based on flocking behavior and overall abundance. The preference for fruit by Cedar Waxwings therefore has important implications for the dispersal of native and invasive plants, as I observed waxwings remove most of the seeds from the plants for which they exhibited repeated preference, which included both native and invasive species.

In this study, I examined frugivore traits that determine the quantity of seed dispersal (Schupp 1993) services provided to a plant species including; fruit preference, foraging behavior, and overall abundance (Ramirez and Slack 1994, Renne et al 2000; 2002). While these behavioral characteristics may be necessary conditions for a species to be an effective seed disperser, they are not necessarily sufficient. For example, other aspects of dispersal quality, which were beyond the scope of this study, can determine the fate of seed dispersal by affecting the success of germination. Dispersal quality can differ among frugivores due to species-specific differences in post-foraging movement patterns that can affect the location of seed deposition, and influence the likelihood of seed germination (Hererra 1985, Hoppes 1987, Schupp 1993). For example, in the study by Chavez-Ramirez and Slack (1994), the flocking behavior of waxwings led to greater quantities of seeds removal, the tendency of these flocks to use communal perches between forage bouts resulted in clumped seed deposition and consequently, low germination success due to density-dependant seed mortality. The effects of gut processing can influence seed germination. *Lonicera tartarica* benefited from earlier

dates of germinations when seeds were ingested by American Robins (Krefting and Roe 1949). In addition, morphology can determine the relative importance of a species as a disperser. For example, American Robins may be important disperser for the native *Vitis*, which has a large fruit, and thus requires a bird with a large gape size to consume its fruits (Johnson et al 1985, Malborg and Willson 1988).

Conclusions

This study provides the first community-based examination of avian fruit selection between co-occurring native and invasive plants, and may offer a unique insight to fruit preferences relative to a wide array of species, as it was conducted at a peak time in fruit availability in the northeastern United States. While fruit selection and potential seed dispersal was greater for native plants than invasive plants, birds consumed the fruit of a variety of species and they were also effective potential dispersers for invasive plants. Thus, the interactions I observed between avian dispersers and fruit-bearing plants are consistent with a large body of literature that describes these relationships as generalized or “diffuse” mutualisms (Howe 1986, Jordano 1988, Malmborg and Willson 1988, Loiselle and Blake 1990, Fuentes 1994). In addition, my observations support the suggestion that successful fleshy-fruited invasive species are often participants in generalized dispersal system (Richardson et al 2000, Renne et al. 2002).

Invasive species are a major concern of land managers, and this has strong empirical basis (Rejmanek 2000, Buckley et al. 2006). My finding that birds more often chose native fruit over invasive fruit, and that invasive fruit negatively affected their condition, supports this concern. Understanding the mechanisms that underlie the dispersal ecology

of invasive plants has important implications for conservation and if the traits of invasive species that make them attractive to birds can be identified, this information may be utilized for restoration efforts (Gosper 2004). Thus, the consistency between my observations and previous studies in the characteristics associated with fruit selection is promising, as it suggests that preference patterns could reach a level of predictability to be used a tool for conservation.

Table 3.1. Observations of frugivory for all species that were observed consuming fruit and the fruit handling methods used by birds. Foraging data was collected during July and Aug., 2007-2008 in 15 shrubland habitats in Berkshire, Franklin, Hamden, Hampshire and Worcester counties in western Massachusetts.

Species	<i>Cornus</i>	<i>Elaeagnus</i>	<i>Lonicera</i>	<i>Prunus</i>	<i>Rhamnus</i>	<i>Rubus</i>	<i>Vaccinium</i>	swallow	bite	drop	N fruit Obsv	Total Obsv
Focal frugivores												
Cedar Waxwing	0	2	4	18	0	0	3	27	0	0	27	58
Gray Catbird	1	0	3	16	2	3	0	21	2	2	25	50
American Robin	0	0	1	9	0	0	0	10	0	0	10	13
Baltimore Oriole	0	0	0	2	0	1	0	1	2	0	3	7
Northern Cardinal	0	0	0	0	0	2	0	0	2	0	2	2
Scarlet Tanager	0	0	0	1	0	1	0	1	1	0	2	3
Other species												
Black-throated Blue Warbler	0	0	0	0	0	2	0	0	2	0	2	6
Brown-headed Cowbird	0	0	0	0	0	1	0	0	1	0	1	1
Eastern Tufted-titmouse	0	0	0	1	0	0	0	0	1	0	1	1
Rose-breasted Grosbeak	0	0	0	0	0	1	0	0	1	0	1	1
Song Sparrow	0	0	0	0	0	1	0	0	1	0	1	2
White-throated Sparrow	0	0	0	0	0	1	0	0	1	0	1	1

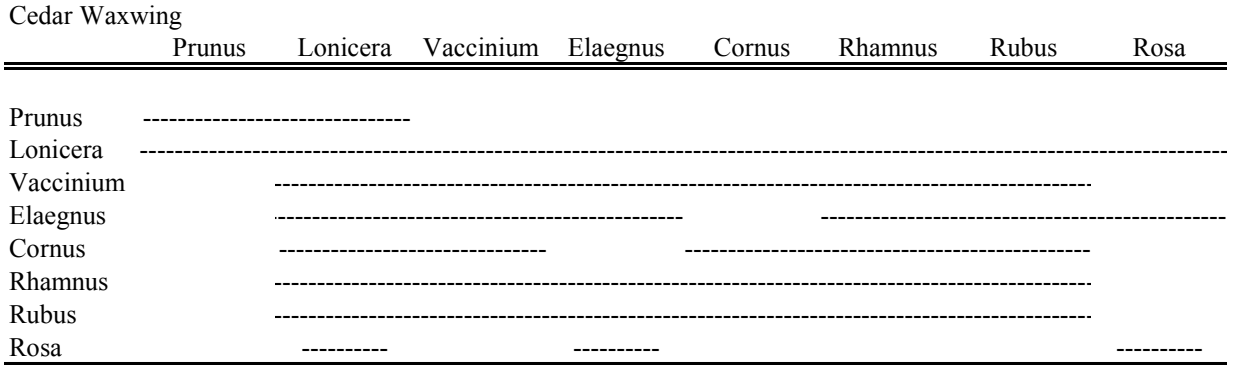


Figure 3.1a

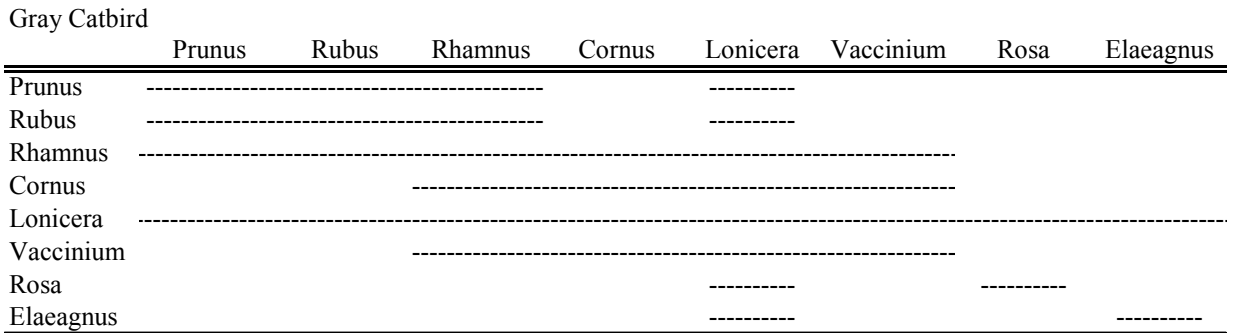


Figure 3.1b

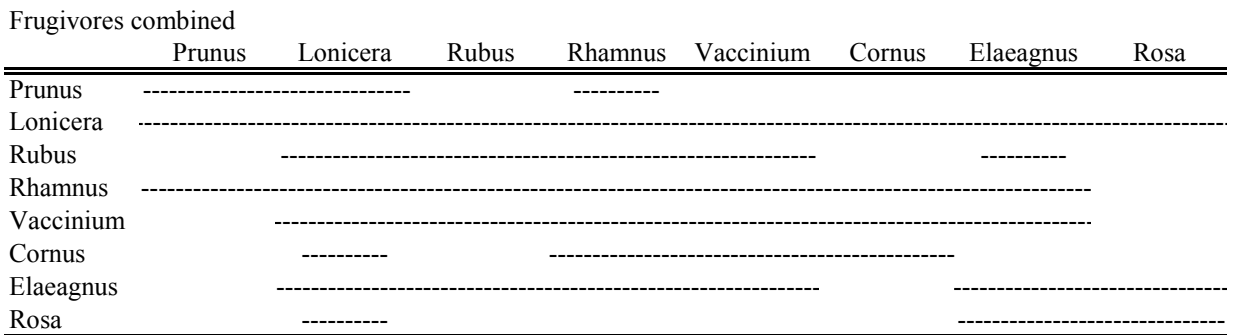


Figure 3.1c

Figures 3.1a-c.

Profile of fruit preference for two common frugivores and frugivores combined depicting results from a compositional analysis of fruit use versus availability. Fruits are sorted from left to right from the most preferred to the most avoided. Fruits classes underscored by the same line indicate there was no difference in selection between classes, whereas the lack of an underscore indicates the fruit of one class was selected more/less than the other. Foraging data was collected during July and August, 2007 -2008 in western MA.

	<i>Cornus</i>	<i>Elaeagnus</i>	<i>Lonicera</i>	<i>Prunus</i>	<i>Rhamnus</i>	<i>Rosa</i>	<i>Rubus</i>	<i>Vaccinium</i>	Rank
<i>Cornus</i>		+++	-	---	+	+++	-	-	5
<i>Elaeagnus</i>	---		+	---	+	+	+	-	4
<i>Lonicera</i>	+	-		-	+	+	+	+	2
<i>Prunus</i>	+++	+++	+		+++	+++	+++	+++	1
<i>Rhamnus</i>	-	-	-	---		+++	+	-	6
<i>Rosa</i>	---	-	-	---	---		---	---	8
<i>Rubus</i>	+	-	-	---	-	+++		-	7
<i>Vaccinium</i>	+	+	-	---	+	+++	+		3

Figure 3.2. A simplified ranking matrix for Cedar Waxwings summarizing fruit use relative to availability. Symbols in the matrix represent results from significance tests comparing the proportions of a fruit selected by a bird with the proportions of fruit available. A positive signs indicate a fruit was used more than expected based on its availability; a negative sign represents the opposite. A triple sign indicated selection was significantly different than random at $P < 0.05$. Foraging data was collected in July and August, 2007 and 2008 in western Massachusetts.

Tables 3.2a-d. Model selection results for univariate mixed- model regression analysis of avian body condition (mass-length residuals). Independent variables were Year, Age, Sex, total fruit abundance (totalFruit) and abundance of the common fruits, pooled by genera Fruit and demographic variables with sufficient observations (>5% occurrence) were included in the analysis. Data was collected during July-Aug. in 2006 through 2008 in Berkshire, Franklin, Hamden, Hampshire and Worcester counties in Massachusetts.

Table 3.2a

	Model	AICc	Δ AICc	ω
Baltimore Oriole	Age	115.71	0	0.560
	Sex	117.02	1.31	0.290
	Null	120.63	4.92	0.050
	PrpInv	121.50	5.79	0.030
	Year	121.86	6.15	0.030
	totalFrt	122.61	6.90	0.020
	Vaccinium	122.75	7.04	0.020
	Rubus	125.17	9.46	0.005
	Prunus	125.29	9.58	0.005
	Rosa	125.92	10.21	0.003
Baltimore Oriole <i>Females</i>	Null	47.88	0	0.350
	prpInv	49.59	1.71	0.150
	Age	49.84	1.95	0.130
	Year	50.10	2.22	0.110
	totalFrt	50.47	2.59	0.100
	Rubus	51.30	3.42	0.060
	Prunus	52.04	4.16	0.040
	Vaccinium	52.66	4.77	0.030
	Rosa	52.69	4.80	0.030
Baltimore Oriole <i>Males</i>	Age	54.40	0	0.750
	Null	59.11	4.71	0.070
	PrpInv	59.69	5.29	0.050
	Year	60.13	5.72	0.040
	totalFrt	61.54	7.14	0.020
	Vaccinium	61.80	7.40	0.020
	Prunus	61.92	7.52	0.020
	Rosa	62.38	7.97	0.010
	Elaeagnus	63.23	8.83	0.009
	Rubus	63.39	8.99	0.008

* 'prpInv' was arcsine transformed for the analysis of male Baltimore Orioles

Table 3.2b

	Model	AICc	Δ AICc	ω
Cedar Waxwing	prpInv	-163.74	0	0.880
	Null	-158.95	4.79	0.080
	Prunus	-154.78	8.96	0.010
	Rosa	-154.07	9.67	0.007
	Rubus	-153.94	9.80	0.007
	Rhamnus	-153.39	10.35	0.005
	Sex	-153.36	10.38	0.005
	Year	-152.3	11.44	0.003
	totalFrt	-151.1	12.64	0.002
	Cornus	-150.29	13.45	0.001
	Elaeagnus	-150.06	13.68	0.001
	Lonicera	-149.45	14.29	0.001
	Age	-149.1	14.64	0.001
	Vaccinium	-149.04	14.70	0.001
Cedar Waxwing <i>Females</i>	prpInv	122.28	0	0.580
	Rosa	124.22	1.94	0.220
	Prunus	126.29	4.01	0.080
	Null	128.34	6.06	0.030
	Year	128.36	6.08	0.030
	Vaccinium	129.24	6.96	0.020
	totalFrt	129.81	7.53	0.010
	Rhamnus	130.42	8.14	0.010
	Cornus	130.69	8.41	0.009
	Rubus	131.73	9.45	0.005
	Lonicera	132.3	10.02	0.004
	Elaeagnus	132.46	10.18	0.004

Table 3.2c

	Model	AICc	Δ AICc	ω	
Gray Catbird	Sex	848.27	0	0.480	
	Rhamnus	849.37	1.10	0.280	
	Null	852.80	4.53	0.050	
	Elaeagnus	853.15	4.88	0.040	
	prpInv	853.33	5.06	0.040	
	Age	853.74	5.47	0.030	
	Prunus	853.89	5.62	0.030	
	Year	854.96	6.69	0.020	
	totalFruit	856.05	7.78	0.010	
	Cornus	856.41	8.14	0.008	
	Vaccinium	856.82	8.55	0.007	
	Lonicera	857.52	9.25	0.005	
	Rubus	858.32	10.05	0.003	
	Rosa	858.65	10.38	0.002	
Gray Catbird	Null	-87.29	0	0.890	
<i>Females</i>	Year	-81.66	5.63	0.050	
	prpInv	-79.32	7.97	0.020	
	totalFruit	-78.30	8.99	0.009	
	Rhamnus	-77.58	9.71	0.007	
	Rubus	-77.27	10.02	0.006	
	Elaeagnus	-76.44	10.85	0.004	
	Prunus	-76.42	10.87	0.004	
	Vaccinium	-76.36	10.93	0.004	
	Cornus	-76.02	11.27	0.003	
	Rosa	-75.24	12.05	0.002	
	Lonicera	-74.95	12.34	0.002	
	Gray Catbird	prpInv	40.00	0	0.902
	<i>Males</i>	Rosa	44.67	4.68	0.087
Null		51.76	11.76	0.003	
Lonicera		52.10	12.10	0.002	
Year		52.59	12.59	0.002	
Prunus		53.07	13.08	0.001	
totalFruit		53.82	13.82	0.001	
Elaeagnus		54.80	14.81	0.001	
Vaccinium		55.04	15.27	<0.001	
Rubus		55.41	15.64	<0.001	
Rhamnus		56.38	16.61	<0.001	
Cornus		56.74	16.96	<0.001	

* 'prpInv' was arcsine transformed for the analysis of male Gray Catbirds

Table 3.2d

		AICc	Δ AICc	ω
Scarlet Tanager	Sex	47.03	0	0.520
	Null	49.21	2.18	0.180
	prpInv	49.64	2.61	0.140
	Age	52.04	5.01	0.040
	totalFruit	52.04	5.01	0.040
	Rosa	53.22	6.20	0.020
	Cornus	53.80	6.77	0.020
	Vaccinium	53.89	6.86	0.020
	Rubus	54.16	7.13	0.020

Tables 3.3a-d. Estimates and 95% Highest Posterior Density (HPD) confidence intervals constructed from a Markov Chain Monte-Carlo sample (MCMC) from univariate mixed-model regression analysis of avian body condition (mass-length residuals). Predictor variables included in body condition models were year, demographic parameters (Age, Sex), the total abundance of fruit (totalFruit) and the abundance of the most common fruits, pooled by genera (N = 8). Variables with sufficient observations were included in the analysis. Data was collected during July-Aug., 2006-2008 in Berkshire, Franklin and Hampshire counties in Massachusetts.

Table 3.3a

		Est	SE	lowerCI	upperCI	P
Baltimore Oriole N = 28	prpInv	0.210	0.760	-1.784	2.252	0.966
	Prunus	-0.030	0.140	-0.322	0.313	0.991
	Rosa	-0.020	0.100	-0.355	0.195	0.855
	Rubus	0.040	0.140	-0.233	0.362	0.918
	totalFruit	-0.300	0.390	-1.319	0.606	0.702
	Vaccinium	-0.220	0.140	-0.573	0.091	0.303
Baltimore Oriole <i>Females</i> N = 12	prpInv	-0.360	0.760	-2.739	2.097	0.943
	Prunus	0.150	0.270	-0.457	0.796	0.828
	Rosa	-0.140	0.150	-0.535	0.226	0.642
	Rubus	0.270	0.250	-0.294	0.844	0.550
	totalFruit	0.030	0.700	-1.826	1.943	0.999
	Vaccinium	0.050	0.230	-0.574	0.662	0.984
Baltimore Oriole <i>Males</i> N = 13	Elaeagnus	0.110	0.270	-0.493	0.738	0.912
	prpInv	0.990	0.830	-1.231	2.951	0.627
	Prunus	-0.340	0.340	-1.224	0.567	0.702
	Rosa	0.250	0.180	-0.227	0.728	0.522
	Rubus	0.060	0.270	-0.508	0.695	0.927
	totalFruit	0.350	0.550	-1.016	1.709	0.848
	Vaccinium	-0.310	0.490	-1.415	0.838	0.824

Table 3.3b

		Est	SE	lowerCI	upperCI	P
Cedar Waxwing N = 84	Cornus	-0.009	0.007	-0.023	0.005	0.459
	Elaeagnus	-0.007	0.005	-0.015	0.003	0.363
	Lonicera	-0.005	0.003	-0.013	0.002	0.305
	prpInv	-0.074	0.019	-0.116	-0.035	0.004
	Prunus	0.017	0.006	0.004	0.029	0.048
	Rhamnus	-0.014	0.006	-0.024	-0.001	0.086
	Rosa	-0.010	0.004	-0.017	-0.003	0.035
	Rubus	0.011	0.004	0.002	0.019	0.045
	totalFruit	-0.014	0.015	-0.045	0.017	0.622
Vaccinium	0.007	0.007	-0.009	0.020	0.745	
Cedar Waxwing <i>Female</i> N = 25	Cornus	-0.266	0.227	-0.725	0.208	0.494
	Elaeagnus	-0.065	0.175	-0.452	0.280	0.909
	Lonicera	-0.111	0.158	-0.478	0.244	0.796
	prpInv	-3.057	1.134	-5.450	-0.630	0.048
	Prunus	0.557	0.221	0.110	1.061	0.061
	Rhamnus	-0.313	0.297	-0.952	0.275	0.568
	Rosa	-0.400	0.123	-0.659	-0.144	0.015
	Rubus	0.163	0.164	-0.161	0.514	0.584
	totalFruit	-0.039	0.708	-1.674	1.648	0.998
Vaccinium	-0.469	0.317	-1.149	0.173	0.338	

Table 3.3c.

		Est	SE	lowerCI	upperCI	P
Gray Catbird N = 195	Cornus	-0.060	0.030	-0.110	0.001	0.133
	Elaeagnus	-0.200	0.080	-0.350	-0.030	0.064
	Lonicera	0.070	0.060	-0.050	0.190	0.475
	prpInv	0.530	0.400	-0.290	1.340	0.410
	Prunus	0.200	0.100	-0.010	0.400	0.154
	Rhamnus	-0.270	0.090	-0.430	-0.080	0.024
	Rosa	-0.010	0.060	-0.130	0.110	0.975
	Rubus	-0.002	0.070	-0.170	0.130	0.959
	totalFruit	0.030	0.230	-0.430	0.480	0.966
	Vaccinium	-0.090	0.110	-0.300	0.120	0.668
Gray Catbird <i>Females</i> N = 36	Cornus	-0.002	0.004	-0.011	0.005	0.825
	Elaeagnus	-0.004	0.004	-0.011	0.004	0.335
	Lonicera	0.000	0.003	-0.006	0.006	0.335
	prpInv	0.004	0.024	-0.046	0.054	0.793
	Prunus	0.003	0.004	-0.005	0.012	0.436
	Rhamnus	-0.006	0.005	-0.015	0.003	0.350
	Rosa	0.002	0.003	-0.004	0.007	0.594
	Rubus	-0.004	0.003	-0.010	0.002	0.688
	totalFruit	0.008	0.012	-0.016	0.034	0.702
	Vaccinium	0.003	0.004	-0.005	0.012	0.792
Gray Catbird <i>Males</i> N = 12	Cornus	-0.238	0.156	-0.437	0.395	0.992
	Elaeagnus	0.689	0.275	-0.378	0.568	0.925
	Lonicera	0.370	0.146	0.049	0.690	0.085
	prpInv	2.834	0.421	1.235	3.369	0.002
	Prunus	-0.598	0.208	-0.952	0.381	0.681
	Rhamnus	0.070	0.242	-0.456	0.600	0.950
	Rosa	0.462	0.084	0.224	0.638	0.003
	Rubus	0.230	0.301	-0.457	0.890	0.780
	totalFruit	0.615	0.579	-0.620	1.645	0.629
	Vaccinium	-0.247	0.165	-0.619	0.126	0.371

Table 3.3d.

		Est	SE	lowerCI	upperCI	<i>P</i>
Scarlet Tanager	Cornus	0.010	0.290	-0.724	0.728	0.998
N = 11	prpInv	-1.380	1.540	-4.933	2.442	0.710
	Rosa	-0.230	0.260	-0.869	0.408	0.728
	Rubus	-0.100	0.220	-0.593	0.407	0.885
	totalFruit	-0.420	0.380	-1.395	0.537	0.616
	Vaccinium	-0.120	0.250	-0.713	0.524	0.943

Table 3.4. Dispersal importance indices for common frugivore species (>10 obsv.) and frugivores combined. AvgFlock is the average number of individuals within in a foraging group. FDI is an index of flock disperser importance representing quantity of seed removal and average individuals per flock ($FDI = \sum OBS_{site} * AvgFlock$), ODI is an index of overall dispersal importance and further incorporates frequency of occurrence ($ODI = FDI * N_{obsv}$). Indices were calculated for plant species pooled by genera. Foraging data was collected during July and Aug. in 15 shrubland habitat in Berkshire, Franklin, Hamden, Hampshire and Worcester counties in western Massachusetts.

	Average individuals per visit	Flock Dispersal importance (FDI)	Overall dispersal importance (ODI)
American Robin (N = 10)			
Lonicera	2.80 (NA)	2.80 (NA)	2.80 (NA)
Prunus	0.70 (0.23)	2.08 (1.09)	18.74 (9.76)
Cedar Waxwing (N = 27)			
Elaeagnus	6.00 (NA)	12.00 (NA)	24.00 (NA)
Lonicera	2.10 (1.10)	5.30 (4.30)	21.20 (17.20) b b
Prunus	2.37 (0.60)	6.93 (1.87)	124.71 (33.60) a
Vaccinium	1.00 (0.00)	1.50 (0.50)	4.50 (1.50) b
Gray Catbird (N = 23)			
Cornus	2.00 (NA)	2.00 (NA)	2.00 (NA)
Lonicera	2.25 (0.75)	3.00 (0.00)	9.00 (0.00)
Prunus	1.50 (0.50)	1.50 (0.50)	3.00 (1.00) a
Rhamnus	0.78 (0.23)	3.69 (1.90)	59.00 (30.38) b
Rubus	1.00 (0.19)	1.00 (0.19)	3.00 (0.57) b
Frugivores Combined (N = 69)			
Cornus	2.00 (NA)	2.00 (NA)	2.00 (NA)
Elaeagnus	6.00 (NA)	12.00 (NA)	24.00 (NA)
Lonicera	3.83 (2.59)	16.33 (14.35)	130.67 (114.76) b
Prunus	3.54 (0.39)	26.48 (7.52)	1217.93 (345.68) a
Rhamnus	1.50 (0.50)	1.50 (0.50)	3.00 (1.00) b
Rubus	1.83 (0.28)	3.98 (1.46)	25.33 (11.53) b
Vaccinium	1.00 (0.00)	1.50 (0.50)	4.50 (1.50) b

Letters are arranged in sequential order a>b etc. and fruits with different letters indicate a significant difference between them at $P < 0.05$ (Tukey test). Values are means \pm 1 SE.

Table 3.5. Dispersal indices for native and invasive plants and results of t-test. Differences that were significant at $P < 0.05$ are indicated by *.

	Mean(SE)		<i>t</i>	<i>df</i>	p-value
	Invasive	Native			
American Robin (N = 10)					
avgFlock	2.80 (NA)	0.65 (0.20)	--	--	--
FDI	2.80 (NA)	1.85 (1.04)	--	--	--
ODI	2.80 (NA)	16.61 (9.34)	--	--	--
Cedar Waxwing (N = 27)					
avgFlock	3.23 (1.59)	1.89 (0.56)	-1.75	3.85	0.10
FDI	7.37 (3.50)	6.16 (2.09)	0.10	6.35	0.35
ODI	44.20 (21.02)	129.39 (43.87)	1.69	5.44	0.14
Gray Catbird (N = 23)					
avgFlock	1.63 (0.43)	0.74 (0.18)	0.64	2.49	0.58
FDI	2.00 (0.58)	3.11 (0.95)	-0.30	3.53	0.78
ODI	10.00 (2.89)	55.94 (17.06)	1.75	7.83	0.12
Other (N = 7)					
avgFlock	--	0.42 (0.10)	--	--	--
FDI	--	0.84 (0.42)	--	--	--
ODI	--	5.85 (2.97)	--	--	--
Frugivores Combined (N = 69)					
avgFlock	3.80 (1.59)	2.94 (0.49)	0.52	4.80	0.62
FDI	12.80 (8.27)	25.41 (6.97)	-1.35	8.07	0.21
ODI	153.60 (99.27)	1448.21 (397.45)	-3.68	9.36	<0.01 *

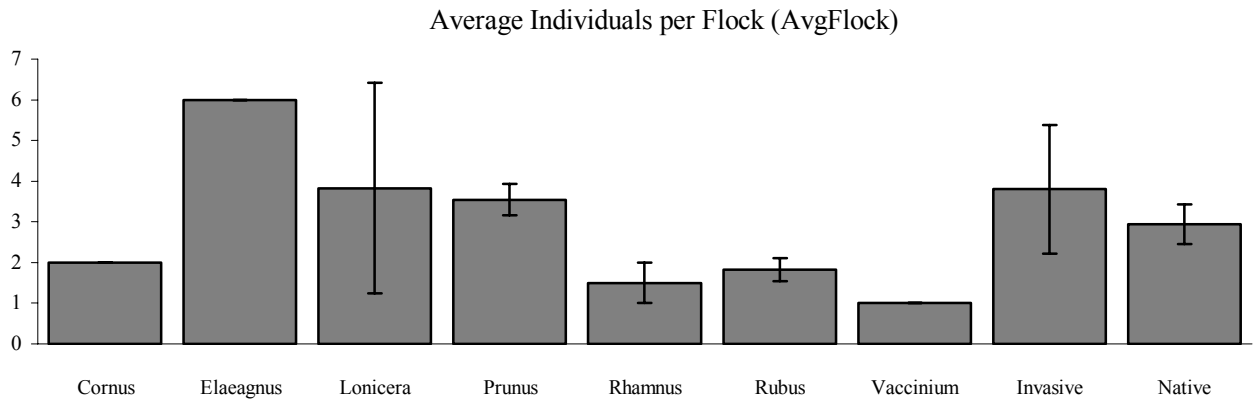


Figure 3.3a. Average number of individuals per a flock (AvgFlock) ($\pm 1SE$) of frugivores foraging on the fruit of common native and invasive bird-disperse plants co-occurring in managed shrubland habitats. Values are shown for plant species pooled by genera, and combined by native/invasive status. Frugivores are represented by the common species: American Robin, Baltimore Oriole, Cedar Waxwing, Gray Catbird, Northern Cardinal, and Scarlet Tanager. Indices were calculated for native and invasive plants, and for plant species pooled by genera. Foraging data was collected during July and Aug. in 15 shrubland habitats in Berkshire, Franklin, Hamden, Hampshire and Worcester counties in western Massachusetts.

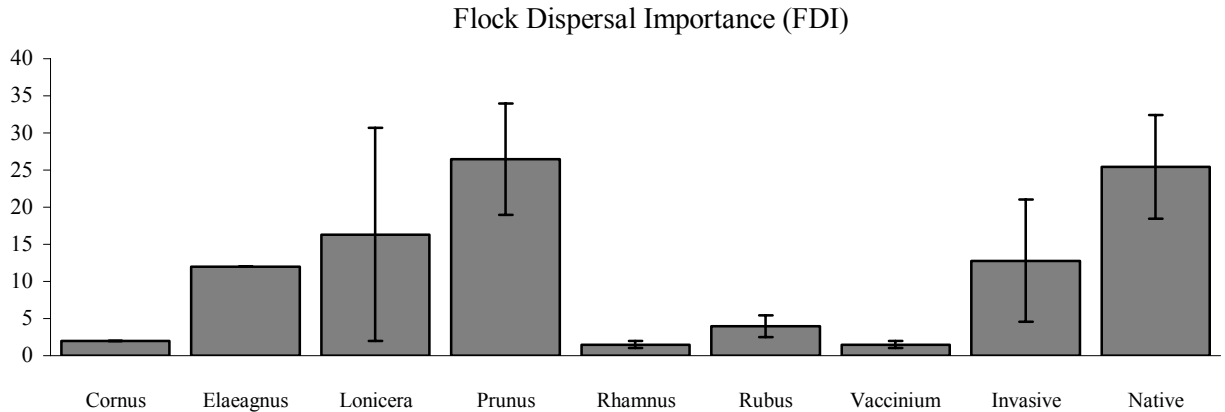


Figure 3.3b. Relative contribution of the frugivore community to the dispersal of common native and invasive bird-dispersed-plants co-occurring in shrubland habitats, as represented the index “flock dispersal importance” (FDI) and is based on quantity of seed removal and average individuals per flock ($FDI = \sum OBS_{site} * AvgFlock$). Values are shown for plant species pooled by genera, and combined by native/invasive status. The frugivore community is represented by the common species: American Robin, Baltimore Oriole, Cedar Waxwing, Gray Catbird, Northern Cardinal, and Scarlet Tanager. Indices were calculated for native and invasive plants, and for plant species pooled by genera. Foraging data was collected during July and Aug. in 15 shrubland habitat in Berkshire, Franklin, Hamden, Hampshire, and Worcester counties in western Massachusetts.

Table 3.6. Nutritional composition of focal fruit genera examined in this study. Nutrient composition of fruit genera examined in this study compiled from literature (Hall 1977, Johnson et al 1985, White 1989, Witmer 1996; 1999; 2000, Drummond 2005, Smith et al 2007). Only the species observed in the study were used. Fruits with more than one record were averaged.

	Rank			Composition (%)			N obsv	N species
	Lipid	Protein	Sugar	Protien	Lipid	Sugar		
<i>Cornus</i>	1	5	7	3.3	41	19	5	3
<i>Elaeagnus</i>	6	4	4	4.7	1.4	62.7	1	1
<i>Lonicera</i>	4	--	1	--	2	74	1	1
<i>Prunus</i>	2	2	2	7.4	3.2	73.4	4	3
<i>Rhamnus</i>	3	3	6	6.5	2.8	45.3	1	1
<i>Rosa</i>	5	1	5	7.6	1.5	55.1	1	1
<i>Rubus</i>	8	--	3	--	<1	71	1	1
<i>Vaccinium</i>	7	6	3	1.7	0.9	71	2	2

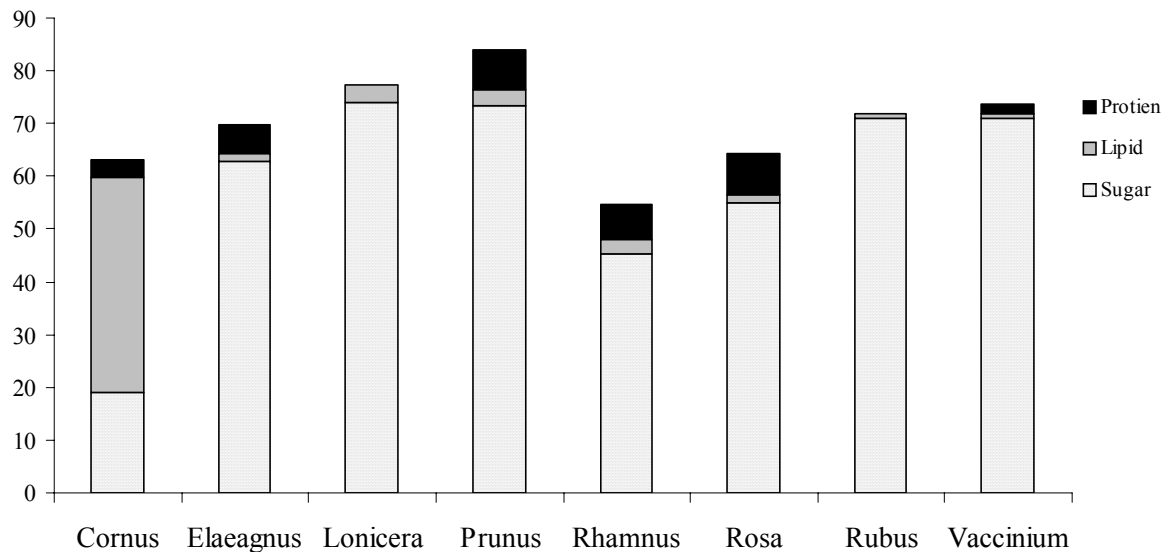


Figure 3.4. Nutritional composition of focal fruit genera examined in this study. Nutrient composition of fruit genera examined in this study compiled from literature (Hall 1977, Johnson et al 1985, White 1989, Witmer 1996; 1999; 2000, Drummond 2005, Smith et al 2007). Only the species observed in the study were used. Fruits with more than one record were averaged.

APPENDIX 1

VEGETATION MEASUREMENTS

Habitat structure measurements are the mean (SE) number of vegetation contacts in height classifications 0-0.25m, 0.25-0.5m, 0.5-1.0m, 1.0-2.0m, 2.0-3.0m, and >3m; BLSH, broadleaved shrubs (>2m); FRNFRB cover of ferns and forbs; GRAM, cover of grasses sedges, rushes; LBLSH, low broadleaved shrubs (<2m); TREE, density of broadleaved trees (>5m) and INV, cover of invasives

	Fox Den	Green River River	Herman Covey	Leyden North	Leyden South	Muddy Brook	Natty Pond	Poland Brook	Stafford Hill	Taconic Trail S.F.
BLSH	0.12 (0.05)	0.27 (0.08)	0.07 (0.04)	0.08 (0.02)	0.19 (0.04)	0.22 (0.07)	0.34 (0.07)	0.27 (0.05)	0.37 (0.10)	0.06 (0.03)
TREE	0.01 (0.01)	0.10 (0.09)	0.03 (0.02)	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	0.12 (0.04)	0.10 (0.04)	0.02 (0.01)	0.00 (0.00)
FRNFRB	0.37 (0.04)	0.35 (0.06)	0.22 (0.07)	0.38 (0.03)	0.42 (0.06)	0.44 (0.08)	0.36 (0.08)	0.32 (0.05)	0.37 (0.08)	0.54 (0.06)
GRAM	0.21 (0.04)	0.13 (0.07)	0.38 (0.07)	0.26 (0.05)	0.15 (0.04)	0.26 (0.09)	0.00 (0.00)	0.06 (0.04)	0.03 (0.01)	0.12 (0.04)
LBLSH	0.26 (0.04)	0.15 (0.05)	0.30 (0.06)	0.27 (0.03)	0.22 (0.05)	0.07 (0.04)	0.18 (0.03)	0.25 (0.02)	0.21 (0.07)	0.28 (0.04)
INV	0.02 (0.02)	0.56 (0.11)	0.36 (0.14)	0.79 (0.08)	0.34 (0.09)	0.47 (0.15)	0.64 (0.07)	0.40 (0.09)	0.16 (0.07)	0.05 (0.03)
0-0.25m	33.4 (4.07)	18.0 (2.96)	30.6 (6.67)	40.9 (5.40)	38.8 (4.46)	22.8 (5.97)	14.8 (4.65)	20.2 (1.80)	17.0 (3.39)	30.0 (6.60)
0.25-0.5m	39.7 (6.49)	35.4 (5.52)	38.3 (6.11)	42.8 (5.52)	30.2 (3.65)	17.4 (2.40)	16.3 (2.21)	29.4 (2.12)	24.4 (2.47)	20.7 (1.70)
0.5-1.0m	26.8 (5.15)	57.1 (10.5)	32.5 (5.55)	29.4 (4.94)	37.1 (6.14)	28.7 (4.92)	33.2 (4.03)	32.4 (4.50)	26.6 (2.65)	23.6 (5.82)
1.0-2.0m	3.80 (1.47)	38.3 (7.35)	14.6 (8.17)	10.6 (3.60)	19.7 (6.63)	26.6 (7.46)	30.1 (3.89)	16.8 (3.57)	31.1 (5.32)	13.0 (10.3)
2.0-3.0m	2.00 (0.91)	16.8 (5.43)	4.60 (2.91)	1.10 (0.90)	10.6 (4.40)	20.5 (6.26)	12.9 (4.06)	5.90 (2.25)	22.6 (8.40)	0.80 (0.55)
>3.0m	1.80 (0.83)	3.30 (1.60)	0.60 (0.31)	1.00 (1.00)	2.40 (1.03)	1.10 (0.43)	3.10 (0.81)	1.80 (0.55)	2.00 (0.68)	0.30 (0.15)

APPENDIX 2

CAPTURE RATES

Mean capture rates (per 100 hrs.) for species caught in wildlife openings during the postfledging season in western MA., 2007.

	Fox Den Den	Green River River	Herman Covey	Leyden North	Leyden South	Muddy Brook	Natty Pond	Poland Brook	Stafford Hill	Taconic Trail
<i>Early-successional species</i>										
Alder Flycatcher (<i>Empidonax alnorum</i>)	0.00 (0.00)	0.11 (0.04)	0.00 (0.00)	0.03 (0.02)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.07(0.03)	0.09 (0.03)	0.00 (0.00)
American Goldfinch (<i>Carduelis tristis</i>)	0.03 (0.03)	0.04 (0.02)	0.08 (0.02)	0.05 (0.03)	0.05 (0.02)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.08 (0.03)	0.03 (0.02)
Blue-winged Warbler (<i>Vermivora pinus</i>)	0.00 (0.00)	0.00 (0.00)	0.04 (0.02)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)	0.03 (0.02)	0.01 (0.01)
Cedar Waxwing (<i>Bombycilla cedrorum</i>)	0.00 (0.00)	0.07 (0.03)	0.04 (0.03)	0.04 (0.02)	0.16 (0.07)	0.01 (0.01)	0.11 (0.06)	0.11 (0.06)	0.08 (0.04)	0.05 (0.02)
Chestnut-sided Warbler ^a (<i>Dendroica pensylvanica</i>)	0.08 (0.04)	0.03 (0.02)	0.00 (0.00)	0.02 (0.01)	0.04 (0.03)	0.04 (0.02)	0.08 (0.04)	0.15 (0.07)	0.24 (0.07)	0.00 (0.00)
Common Yellowthroat ^a (<i>Geothlypis trichas</i>)	0.12 (0.04)	0.14 (0.05)	0.16 (0.06)	0.17 (0.04)	0.14 (0.04)	0.19 (0.07)	0.20 (0.07)	0.24 (0.07)	0.26 (0.06)	0.20 (0.05)
Eastern Towhee ^a (<i>Pipilo erythrophthalmus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
Field Sparrow (<i>Spizella pusilla</i>)	0.07 (0.03)	0.00 (0.00)	0.02 (0.01)	0.09 (0.05)	0.27 (0.13)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.07 (0.03)	0.11 (0.05)
Gray Catbird (<i>Dumetella carolinensis</i>)	0.00 (0.00)	0.10 (0.03)	0.08 (0.02)	0.07 (0.02)	0.28 (0.06)	0.15 (0.05)	0.39 (0.10)	0.26 (0.11)	0.19 (0.07)	0.06 (0.04)

House Wren (<i>Troglodytes aedon</i>)	0.01 (0.01)	0.01 (0.01)	0.03 (0.02)	0.00 (0.00)	0.05 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.09 (0.04)	0.00 (0.00)
Indigo Bunting (<i>Passerina cyanea</i>)	0.00 (0.00)	0.06 (0.03)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.04 (0.02)	0.00 (0.00)
Mourning Warbler ^c (<i>Oporonis philadelphia</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)
Nashville Warbler (<i>Vermivora ruficapilla</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)
Northern Cardinal (<i>Cardinalis cardinalis</i>)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Prairie Warbler ^b (<i>Dendroica discolor</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.06 (0.20)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Song Sparrow ^a (<i>Melospiza melodia</i>)	0.13 (0.04)	0.26 (0.08)	0.14 (0.05)	0.31 (0.07)	0.18 (0.07)	0.05 (0.03)	0.01 (0.01)	0.08 (0.04)	0.24 (0.06)	0.33 (0.08)
Swamp sparrow (<i>Melospiza georgiana</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.04 (0.03)	0.00 (0.00)	0.00 (0.00)
White-throated Sparrow ^a (<i>Zonotrichia albicollis</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)
Yellow Warbler (<i>Dendroica petechia</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)
Black-and-white Warbler ^a (<i>Mniotilta varia</i>)	0.03 (0.02)	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Mature-forest species American Redstart (<i>Setophaga ruticilla</i>)	0.06 (0.06)	0.04 (0.02)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.02 (0.02)	0.00 (0.00)	0.05 (0.02)	0.03 (0.02)	0.01 (0.01)

Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)
Blackburnian Warbler (<i>Dendroica caerulea</i>)	0.02 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.02 (0.01)
Black-capped Chickadee (<i>Poecile atricapilla</i>)	0.02 (0.01)	0.02 (0.01)	0.00 (0.00)	0.02 (0.01)	0.03 (0.03)	0.00 (0.00)	0.09 (0.04)	0.00 (0.00)	0.09 (0.05)	0.00 (0.00)	0.00 (0.00)
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Black-throated Green Warbler (<i>Dendroica virens</i>)	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)
Canada Warbler (<i>Wilsonia canadensis</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Dark-eyed Junco (<i>Junco hyemalis</i>)	0.10 (0.05)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Downy Woodpecker (<i>Picoides pubescens</i>)	0.03 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Eastern Tufted-Titmouse (<i>Baeolophus bicolor</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Hermit Thrush (<i>Catharus guttatus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Least Flycatcher ^a (<i>Empidonax minimus</i>)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.04 (0.02)	0.01 (0.01)	0.00 (0.00)
Louisiana Waterthrush (<i>Seiurus motacilla</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Magnolia Warbler (<i>Dendroica magnolia</i>)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)

Olive-sided Flycatcher (<i>Contopus cooperi</i>)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Ovenbird (<i>Seiurus aurocapillus</i>)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.05 (0.02)	0.07 (0.03)	0.03 (0.02)	0.00 (0.00)	0.00 (0.00)
Philadelphia Vireo (<i>Vireo gilvus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
Purple Finch ^a (<i>Carpodacus purpureus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Rose-breasted Grosbeak ^a (<i>Pheucticus ludovicianus</i>)	0.00 (0.00)	0.04 (0.02)	0.00 (0.00)	0.00 (0.00)	0.09 (0.03)	0.00 (0.00)	0.00 (0.00)	0.34 (0.19)	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)
Red-eyed Vireo ^a (<i>Vireo olivaceus</i>)	0.00 (0.00)	0.04 (0.02)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)
Ruby-throated Hummingbird (<i>Archilochus colubris</i>)	0.01 (0.01)	0.06 (0.03)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Scarlet Tanager ^a (<i>Piranga olivacea</i>)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)
Swainson's Thrush (<i>Catharus ustulatus</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
Veery (<i>Catharus fuscescens</i>)	0.00 (0.00)	0.06 (0.02)	0.00 (0.00)	0.02 (0.02)	0.05 (0.02)	0.00 (0.00)	0.06 (0.02)	0.22 (0.08)	0.02 (0.01)	0.02 (0.01)	0.02 (0.01)
Winter Wren (<i>Troglodytes troglodytes</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.09 (0.05)	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)
Wood Thrush ^a (<i>Hylocichla mustelina</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	0.01 (0.01)	0.04 (0.02)	0.02 (0.01)	0.01 (0.01)	0.00 (0.00)	0.01 (0.01)	0.07 (0.03)	0.00 (0.00)	0.11 (0.06)	0.01 (0.01)	0.01 (0.01)

Other Species

American Robin (<i>Turdus migratorius</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	0.03 (0.02)	0.05(0.03)	0.00 (0.00)	0.01 (0.01)
Baltimore Oriole ^a (<i>Icterus galbula</i>)	0.00 (0.00)	0.09 (0.06)	0.00 (0.00)	0.01 (0.01)	0.03 (0.02)	0.00 (0.00)	0.01 (0.01)	0.05(0.03)	0.01 (0.01)	0.09 (0.06)
Brown-headed Cowbird ^a (<i>Molothrus ater</i>)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)	0.00 (0.00)
Eastern Phoebe ^a (<i>Sayornis phoebe</i>)	0.04 (0.03)	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	0.02 (0.01)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)

a. Significant Decline ($P < 0.10$) on BBS (1966-2005)

b. Partners in Flight Watch List

c. Massachusetts Species of Special Concern

APPENDIX 3

FORAGING OBSERVATIONS

Observations were recorded in wildlife openings during July-Aug., 2007-2008 in western MA.

Species	N	%Fruit(#obsv)	%Insect(#obsv)	<i>Cornus</i>	<i>Elaeagnus</i>	<i>Prunus</i>	<i>Rhamnus</i>	<i>Rubus</i>	<i>Vaccinium</i>	Mean Hgt(SE)
American Redstart	5	0 (0)	100 (5)	0	0	0	0	0	0	5.30 (1.36)
American Robin	13	77 (10)	23 (3)	0	0	9	0	0	0	7.70 (2.03)
Baltimore Oriole	7	43 (3)	57 (4)	0	0	2	0	1	0	6.51 (1.76)
Black-capped Chickadee	4	0 (0)	100 (4)	0	0	0	0	0	0	1.45 (0.25)
Brown-headed Cowbird	1	100 (1)	0 (0)	0	0	0	0	1	0	0.50 (NA)
Black-capped Chickadee	2	0 (0)	100 (2)	0	0	0	0	0	0	4.25 (1.75)
Black-throated Blue Warbler	6	33 (2)	66 (4)	0	0	0	0	2	0	3.83 (0.49)
Blackburnian Warbler	2	0 (0)	100 (2)	0	0	0	0	0	0	3.10 (1.90)
Black-throated Green Warbler	6	0 (0)	100 (6)	0	0	0	0	0	0	4.50 (0.76)
Blue-winged warbler	2	0 (0)	100 (2)	0	0	0	0	0	0	3.80 (0.10)
Canada Warbler	1	0 (0)	100 (1)	0	0	0	0	0	0	NA
Cedar Waxwing	58	47 (27)	54 (31)	0	2	18	0	0	3	8.10 (0.80)
Chipping Sparrow	1	0 (0)	100 (1)	0	0	0	0	0	0	1.80 (NA)
Common Yellowthroat	50	0 (0)	100 (50)	0	0	0	0	0	0	1.43 (0.17)
Chestnut-sided Warbler	12	0 (0)	100 (12)	0	0	0	0	0	0	4.90 (1.12)
Dark-eyed Junco	2	0 (0)	100 (2)	0	0	0	0	0	0	5.25 (0.75)
Eastern Tufted Titmouse	1	100 (1)	0 (0)	0	0	1	0	0	0	8.50 (NA)
Gray Catbird	50	50 (25)	50 (25)	1	0	16	2	3	0	4.10 (0.59)
House Wren	1	0 (0)	100 (1)	0	0	0	0	0	0	0.00 (NA)

Magnolia Warbler	1	0 (0)	100 (1)	0	0	0	0	0	0	7.00 (NA)
Nashville Warbler	1	0 (0)	100 (1)	0	0	0	0	0	0	3.00 (NA)
Northern Cardinal	2	100 (2)	0 (0)	0	0	0	0	2	0	1.30 (0.00)
Rose-breasted Grosbeak	1	100 (1)	0 (0)	0	0	0	0	1	0	0.35 (NA)
Red-eyed Vireo	11	0 (0)	100 (11)	0	0	0	0	0	0	6.18 (1.09)
Ruby-throated Hummingbird	2	0 (0)	100 (2)	0	0	0	0	0	0	1.85 (0.15)
Scarlet Tanager	3	67 (2)	33 (1)	0	0	1	0	1	0	7.00 (4.16)
Song Sparrow	3	33 (1)	66 (2)	0	0	0	0	1	0	0.95 (0.68)
Alder Flycatcher	1	0 (0)	100 (1)	0	0	0	0	0	0	8.00 (NA)
Veery	1	0 (0)	100 (1)	0	0	0	0	0	0	3.00 (NA)
White-throated sparrow	1	100 (1)	0 (0)	0	0	0	0	1	0	0.50 (NA)
Yellow Warbler	4	0 (0)	100 (4)	0	0	0	0	0	0	4.63 (2.56)

APPENDIX 4

FRUIT ABUNDANCE

Total fruit counts in managed shrubland habitats where avian foraging observations were collected. Fruit count surveys were based on point intercept survey methods and collected during July-Aug, 2006-2008 in 15 shrubland habitats in western MA. Fruit counts for sites that were surveyed in more than one year were averaged.

Fruit genus	Curtis Road	Eugene Moran	Fox Den	Green River	Haley Farm	Herman Covey	Leyden "north"	Leyden "south"	Muddy Brook	Natty Pond	Poland Brook	Quabbin Gate 8	Quabbin Gate 10	Savoy S.F	Stafford Hill	Taonic Trail S.F
<i>Berberis</i>	0	0	0	0	300	0	0	474	0	0	1572.5	20	0	0	0	0
<i>Celastrus</i>	0	0	0	0	0	57	0	0	0	0	155	0	0	0	65	0
<i>Cornus</i>	0	0	0	0	0	20	0	308	290	1135	982	0	0	0	0	881
<i>Eleagnus</i>	0	0	0	0	1200	1685	50	2992.5	0	0	2192.5	0	0	0	145	0
<i>Ilex</i>	6	0	0	0	0	0	0	160	0	0	0	0	0	0	0	0
<i>Juniperus</i>	0	0	0	0	0	0	175	17	0	0	20	0	0	0	0	0
<i>Lonicera</i>	0	0	0	0	20	5241	0	2480	374	10568	2212.5	0	0	0	88.5	257
<i>Parthenocissus</i>	0	0	0	0	0	1200	0	0	0	0	0	0	0	0	0	0
<i>Phytolacca</i>	0	0	0	0	0	102	0	0	0	0	0	0	0	0	30	0
<i>Prunus</i>	0	365	76	0	0	667	0	28	230	48	117	0	0	1289	89	270
<i>Rhamnus</i>	0	107	0	90	58	0	0	450.5	0	1063	75	0	0	0	78.5	527
<i>Rhus</i>	0	0	0	0	0	0	0	0	0	0	125	0	0	0	0	0
<i>Rosa</i>	0	0	0	7434	0	65	4074	1529	4558	2976	1131.5	0	0	0	0	0
<i>Rubus</i>	705	2438	39	137	150	0	314	1738	111	202	1056.5	1122	458	5136	286.5	1351
<i>Sambucus</i>	0	0	0	0	0	0	0	0	65	0	0	0	0	0	0	0
<i>Similax</i>	0	4808	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Solanum</i>	0	0	0	0	0	31	0	0	108	0	0	0	0	0	0	0
<i>Vaccinium</i>	95	5075	17	0	0	0	0	92	0	0	150.5	222	850	0	0	441
<i>Viburnum</i>	0	41	0	0	0	0	0	0	0	0	0	0	170	68	0	0
<i>Vitis</i>	0	0	0	0	0	0	0	20	0	0	25	15	80	0	0	0

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