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Original Article

Songbird Use of Native and Invasive Fruit in the Northeastern USA

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ABSTRACT Fruit is consumed by songbirds, yet whether or not it comprises an important component of habitat quality depends on the extent to which it is used by birds. In addition, there is evidence fruits of exotic invasive species may be nutritionally inferior to fruits of native species, so the influence of plant invasion on bird body condition is of interest to managers. Birds that consume invasive fruits may also serve as seed vectors, and consumption of fruits of invasive species may exacerbate invasion. Thus, the extent to which songbirds consume fruits of native versus invasive plant species, influence of plant invasion on bird body condition, and extent to which birds exhibit foraging behaviors that elevate their potential to act as dispersers of invasive species have important implications for habitat management. To understand bird use of native and invasive fruits and the potential role of birds in dispersing invasive plants, we observed bird foraging, measured body condition indices of birds captured in mist nets, measured available fruits of native and invasive plants, and calculated indices of seed dispersal for bird species based on fruit handling and consumption, within 16 shrubland sites in western Massachusetts, USA. Our findings indicate that birds use fruit extensively (57% of foraging events), use varied among species, and frugivorous species at our sites generally chose the fruit of native species, especially *Prunus,* over fruits of invasive species. Body condition indices were negatively related to the proportion of invasive fruit in most cases. In general, birds were better dispersers for native fruits than for invasive fruits. Our findings support the value of native fruit resources as a component of habitat quality, and, conversely, suggest that nonnative plant invasion may lead to reduced habitat quality for songbirds. © 2020 The Wildlife Society.

KEY WORDS avian, frugivory, habitat quality, northeast, selection, shrublands.

Exotic plant invasions can have substantial effects on native biodiversity and ecosystem functions (Vitousek 1990, D'Antonio and Vitousek 1992, Wilcove et al. 1998). Invasive plants can be detrimental to populations of native vertebrates by altering vegetation characteristics and food availability in native landscapes (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, Rodewald et al. 2010). However, in some cases, invasive plants have been shown to provide important resources for native wildlife (Sax et al. 2005, Schlossberg and King 2010, Meyer et al. 2015). Fruit crops produced by invasive species may be an important resource for birds during lifecycle periods when energy demand is high (Vega Rivera et al. 1998, Suthers et al. 2000, Gleditsch and Carlo 2014). The potential for both negative and positive influences from the presence of invasive plant species presents challenges for the management and conservation of native landscapes and associated wildlife populations.

Many of the invasive species that are problematic in the northeastern United States were originally planted for the benefit of wildlife, and the abundant fruit produced by these species is readily consumed by birds (Gill and Healy 1974, Baird 1980, Stiles 1982, White and Stiles 1992, Suthers et al. 2000, Renne et al. 2002). Despite its widespread consumption, however, the value of invasive fruit has come under scrutiny by some managers who question whether the fruit produced by invasive plants is comparable in quality to that of native plants or, alternatively, whether invasive fruit is essentially an avian junk food (e.g., Ingold and Craycraft 1983, Oehler 2006). The value of invasive fruit as a component of habitat quality for birds has been difficult to assess because previous studies that have examined the relationships among use, selection, and nutritional components of native and invasive fruit have revealed few consistent patterns (Vilà and D'Antonio 1998, Drummond 2005, Greenberg and Walter 2010, Smith et al. 2013).

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Moreover, suites of native and invasive fruits do not appear to differ in regard to their nutritional qualities (i.e., sugar, lipids, fiber, protein, minerals; White and Stiles 1992, Smith et al. 2007, Kueffer et al. 2009, Gosper and Vivian-Smith 2010, Jordaan and Downs 2012).

Seasonal differences in the availability of food resources and energetic requirements of birds may be an important influence on fruit choice and observed patterns of use and the season in which studies were conducted may have contributed to the variation in previous findings (e.g., Stiles 1980, Jones and Wheelwright 1987, Smith et al. 2013). For example, Smith et al. (2013) reported greater removal rates of native fruit compared with invasive fruit by migratory birds in New York, USA, during the autumn. Whereas Drummond (2005) reported no difference in removal rates or fruit preference between native and nonnative fruits during the winter in Maine, USA. Thus far, most studies of avian frugivory have focused on the winter and autumn migration periods when fruits of many species are no longer available, thus examinations of patterns in fruit selection during different seasons are needed to better understand the relative importance and potential value of invasive fruit resources to birds across seasons and lifecycle periods.

Selection of fruit by birds has implications for the reproductive success of their food plants. Birds are the major dispersal agents of many invasive plant species (Glyphis et al. 1981, Buchanan 1989, Renne et al. 2002); including nearly all the fruit-bearing invasives in the northeastern United States (Silander and Klepeis 1999). Birds are highly vagile and move among habitats that are by definition available for invasive species, so they have the potential to facilitate new introductions and rapid spread of invasive species. This potential depends in part on the extent to which they select fruits of invasive plants. If birds select fruit of invasive plants over the fruits of native plants, natives may be outcompeted for dispersal services, which could have serious consequences for native plant communities. Not all bird species that consume fruit are necessarily seed dispersers and species vary in effectiveness as dispersers as a result of differences in foraging behaviors and relative abundances (Schupp 1993, Chavez-Ramirez and Slack 1994). Despite the important role of avian frugivores in the dispersal of fruit-bearing plants, relatively few studies have examined how fruit selection by birds may contribute to the spread of invasive plants (Gosper et al. 2005, Buckley et al. 2006, Aslan and Rejmánek 2012). In addition, for many bird-dispersed plants in the northeastern United States, species-specific data about the foraging behaviors of major avian dispersers are currently lacking, which limits our ability to understand dispersal ecology of invasive plants in this region.

Therefore, to increase knowledge of the ecology of bird-dispersed invasive plants, we undertook a study of avian frugivory in managed shrubland habitats in the northeastern United States with the following objectives: 1) determine whether birds selected fruits of either native or invasive species, 2) examine the relationship between fruit abundance and body condition indices for bird species that exhibited frugivory, and 3) evaluate the importance of individual bird species and bird species combined as potential dispersers of invasive plants.

STUDY AREA

Our study was conducted from mid-July through early September of 2006–2008 at 16 shrubland sites in Berkshire, Hamden, Hampshire, Franklin, and Worcester counties in western Massachusetts, USA. Study sites consisted of wildlife openings ($n = 12$) and regenerating clearcuts ($n = 4$) on private and public land. Wildlife openings were maintained by mechanical treatment approximately every 10 years and had been treated within 7–8 years prior to our study. Regenerating clearcuts were between 6 and 7 years post-harvest. Sites ranged in size from 5 to 19 ha and were a minimum distance of 2.5 km apart.

Study sites were characterized by shrubs and saplings, herbaceous vegetation and scattered trees. Common shrubs included native species of dogwood (*Cornus* spp.), raspberry and blackberry (*Rubus* spp.), sumac (*Rhus* spp.), blueberry (*Vaccinium* spp.), and spirea (*Spirea* spp.), as well as invasive species such as honeysuckle (*Lonicera* spp.), common buckthorn (*Rhamnus cathartica*), glossy buckthorn (*Rhamnus frangula*), autumn olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*). Common saplings included red maple (*Acer rubrum*), birches (*Betula* spp.), white ash (*Fraxinus americana*), black cherry (*Prunus serotina*), white pine (*Pinus strobus*), red oak (*Quercus rubra*), and pin cherry (*Prunus pensylvanica*) and residual trees were typically apple (*Malus* spp.), black cherry, and white ash.

METHODS

Field Sampling

Foraging observations.—To determine whether birds selected fruits of either native or invasive species, we conducted foraging observations from July through early September at 10 sites during 2007 and 5 sites during 2008 (4 of which were also surveyed in 2007). This period coincided with the peak diversity and abundance of native and nonnative fruits in the region (Stiles 1980), as well as the peak in the abundance and diversity of birds in shrubland habitats, which are utilized by both shrubland and forest bird species (Labbe and King 2014). The study period also coincided with the postfledging or postbreeding seasonal lifecycle phase that occurs after nesting and before the onset of migration (Faaborg et al. 1996; Vega Rivera et al. 1998, 1999) and associated deposition of subcutaneous fat (Rappole and Ballard 1987). We recorded all observations along transects spaced 25 m apart across a 200 × 150-m sampling grid established within each study plot. Following the protocol of Hejl et al. (1990), observers walked slowly along transects and recorded observations of the first foraging attempt after a bird was initially encountered. Although use of initial foraging observations theoretically may bias results toward conspicuous foraging maneuvers, biases appear to be minor in most cases

(Wagner 1981, Morrison 1984, Hejl et al. 1990). We recorded foraging behaviors including food type (insect or fruit), fruit species or genus, substrate from which the food was obtained, foraging maneuver used to obtain and consume the food, and the number and species of other birds in the foraging flock (Remsen and Robinson 1990). We adapted classifications of foraging observations for fruit from Remsen and Robinson (1990) and recorded these as either bite, drop (uneaten), swallow whole, or taken in flight. These foraging behaviors and characteristics are known to influence bird species' effectiveness as seed dispersers (Renne et al. 2002). We focused foraging observations on the common bird species, but observations were recorded for other species opportunistically in accordance with the methods described above. We conducted transects between 1 and 5 times/week during the survey period and collected all foraging observations during the first 5 hours after sunrise. To minimize dependence between foraging events, after each foraging observation the observer proceeded along the transect line for a minimum distance of 25 m before conducting subsequent observations. We did not conduct foraging observations during periods of high winds or rain.

Condition indices.—We measured attributes used to derive body condition indices from birds captured using 12-m mist nets (32-mm denier) spaced 50 m apart on the same 200 × 150-m grids on which foraging observations were collected. We sampled each site twice between mid-July and late August during 2006 and 2007. We sampled sites in a fixed order such that each site was sampled both early and late in the season. We 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). We did not collect wing measurements for birds with wing molt because such measurements would yield inaccurate wing length. During the postfledging or postbreeding lifecycle period, birds have not yet begun to accumulate subcutaneous fat deposits for migration (Rappole and Ballard 1987), nevertheless, we recorded subcutaneous fat scores as well as evidence of brood patches because each are factors that could potentially influence measures of condition. We conducted bird capture and handling under a protocol approved by the Institutional Animal Care and Use Committee of the University of Massachusetts (Permit #26-02-05).

We calculated indices of condition by first performing a principal component analysis (PCA) on 2 morphometric measurements, tarsus and wing length, to derive a single measurement for body structure. We then regressed the resulting body structure variable (PC1) on body mass (mass) using linear regression, and used residuals from the regression as an index of body condition (Schulte-Hostedde et al. 2005). We tested data for deviations from normality and log-transformed them as needed to meet assumptions of the regression analysis. We classified birds by sex and age (hatch-year or after-hatch-year) based on one or more of the following characteristics: degree of skull ossification, plumage, molt patterns, and evidence of cloacal protuberance or brood patch (Pyle 1997). Demographic factors such as age and sex can influence condition because of age-related differences in foraging efficiency and fat deposition (Heise and Moore 2003, Vanderhoff and Eason 2007), and competition (Gauthreaux 1978, Grubb and Woodrey 1990, Marra et al. 1993). Therefore, we derived condition indices separately by sex and age class for each bird species when sample sizes were sufficiently large (Freeman and Jackson 1990, Milenkaya et al. 2013). We included only initial captures of individuals in the analyses. We banded all captured birds (except ruby-throated hummingbird [*Archilochus colubris*]) with a U.S. Geological Survey, Bird Banding Lab aluminum band.

Fruit availability.—We measured fruit availability at 100 points/site. We established 10 sample points at a random bearing and random distance up to 25 m from the center of each mist net location. We counted all fruits within a 1-m-diameter circle centered on the sample point. We tallied fruit by species and categorized as unripe, ripe, or desiccated to account for availability over time. We conducted counts once per a site at the end of the sampling period.

Statistical Analyses

We analyzed fruit selection for bird species with ≥10 foraging observations that were also observed foraging in ≥8 sites, as well as for all species combined. We determined proportions of used and available fruit for each bird species for each site. We calculated the proportion of used fruit as the total number of foraging events per plant species divided by the total number of foraging observations at that site. The proportion of available fruit was the total fruit count per plant species divided by the total fruit count over all fruit species combined. We used compositional analysis to examine whether fruit was selected disproportionately to its availability (Aebischer et al. 1993), and evaluated deviations from random use of fruit using Wilk's lambda test in a multivariate analysis of variance. If overall use was found to differ from random, we then determined differences among fruit genera using randomization tests (50,000 iterations) to compare the log-odds ratios of ranked used and available fruit (Aebischer et al. 1993). Tests were 2-tailed and $\alpha = 0.05$. We performed analyses using Program R v. 2.10.1 (R Development Core Team 2009) with the function compana() in the library adehabitat (Calenge 2006).

We examined the relationship between fruit abundance and body condition indices for bird species that exhibited frugivory and for which we had >10 captures and a complete record of measurements (mass, tarsus, and wing length) using restricted maximum likelihood (REML) linear mixed models fitted with the lmer() function in R v. 2.10.1 with site included as a random effect. Explanatory variables included the abundance of fruit genera, the proportion of invasive fruit (prpInv), and a site-level measurement of total fruit abundance (totalFruit). As before, we included age and sex in these models and conducted separate analysis by sex and age classes when sample sizes were sufficiently large. Prior to all analyses, we tested for a year effect by examining differences in deviance between the null model and a model including a term for year. No effects of year were found for any species or sex category; therefore, we pooled data across years within each study site for all analyses.

We constructed univariate models with explanatory variables and used Akaike's Information Criterion adjusted for small sample size (AIC_c) to rank each model in the set of candidate models and we considered models with an AIC_c score ≤ 2 AIC_c units of the top model to be supported (Burnham and Anderson 2002). We further evaluated models based on AIC_c weights (Burnham and Anderson 2002). To determine the precision of parameter estimates, we constructed 95% Highest Posterior Density (HPD) confidence intervals from a Markov Chain Monte-Carlo sample generated from 50,000 iterations of fitted models. The HPD intervals return the shortest interval with a 95% probability content in the empirical distribution. We considered model terms with 95% confidence intervals that did not include zero to be strongly supported. We determined significance of fixed effects from P-values calculated for each of HPD intervals using $\alpha = 0.05$. For each bird species, we conducted a separate analysis for males and females and for all birds combined (all birds included male, female, and birds of unknown sex). We assessed model fit by graphical inspection of residual plots; we performed Shapiro–Wilk normality tests on residuals. We log-transformed fruit abundance variables prior to analysis to reduce the extremity of variation and we included only fruits that occurred in >5% of observations in the condition analysis.

We restricted analyses of potential disperser importance to bird species with ≥10 observations that were observed foraging on ≥2 fruit species in ≥2 sites; we pooled the remaining species into the category other. To examine how the bird community as a whole contributed to the potential seed dispersal of native and invasive plants, we pooled observations of all birds into a single additional category, birds combined.

To evaluate the importance of individual bird species and bird species combined as potential dispersers, we developed 2 indices based on Renne et al. (2000) that incorporate foraging behavior traits, overall abundance (of species and species combined), and fruit selection. These characteristics determine the quantity of seed dispersal services provided to a plant species and are key conditions for a bird species to be an effective seed disperser (Schupp 1993, Chavez-Ramirez and Slack 1994). During the time frame of this study, territories have generally broken down and birds have begun to forage in flocks. Species still exhibit different tendencies to forage in flocks, however, and these indices aim to capture the flocking behavior of species that forage in these study sites. Foraging observations that we used to calculate these indices were the number of seed-swallowing events (OBS; excludes observations where food item was dropped, or seed was not ingested), and the average number of individuals of a given species within a foraging group (AvgFlock). The first index, Flock Disperser Importance (FDI), estimates the importance of an average foraging event by a species and was calculated as the product of OBS and AvgFlock (Renne et al. 2000).

$$\mathrm{FDI} = \sum \mathrm{OBS}_{\mathrm{site}} \times \mathrm{AvgFlock}$$

The second index, Overall Dispersal Importance (ODI), incorporates the species-specific frequency of occurrence (e.g., how common observations [OBS] were across study sites per a given species) and was calculated as FDI times OBS across all sites.

$$\mathrm{ODI} = \mathrm{FDI} \times \sum \mathrm{OBS}$$

We calculated indices by site for each frugivore species that had sufficient data, and assumed that all birds in the flock were foraging. To evaluate the extent of dispersal services received by fruiting plants and whether foraging behaviors of birds differed among plants, we also calculated each index for each plant genera and for native and invasive plants as a group.

We compared dispersal indices (FDI, ODI) among bird species, plant species, and between native and invasive status using 2-sample t-tests or analysis of variance. We examined homogeneity of variance using Fligner–Killeen tests and normality using Shapiro–Wilk tests; when necessary, we applied square-root transformations to meet assumptions of the analysis. We used Tukey's Honest Significant Difference (HSD) method when multiple comparisons were made. We performed all analyses in R v. 2.10.1.

RESULTS

We recorded 255 foraging events by 31 bird species of which 57% ($n = 145$) were directed at fruit and 43% ($n = 110$) at insects. We observed 12 bird species foraging on 7 species of fruit, of which 2 (cedar waxwing [*Bombycilla cedrorum*] and gray catbird [*Dumetella carolinensis*]) met our criteria for inclusion in the fruit selection analyses and 3 (cedar waxwing, gray catbird, and American robin [*Turdus migratorius*]) met our criteria for inclusion in the fruit dispersal analyses. These species accounted for 47% of all observations of frugivory. Fruiting plants included in the analyses comprised 90% of available fruit overall and consisted of native species from 4 genera (*Cornus, Prunus, Rubus,* and *Vaccinium*) and exotic invasive species from 4 genera (*Lonicera, Elaeagnus, Rhamnus,* and *Rosa*). We captured 1,854 individual birds of 64 species of which 4 (gray catbird, cedar waxwing, Baltimore oriole [*Icterus galbula*], and scarlet tanager [*Piranga olivacea*]) met our criteria for inclusion in the body condition analyses. These species accounted for 20% of all captures. Confirmation that our survey window coincided with the postfledging or postbreeding period was evidenced by the subcutaneous fat scores: 90% of captures had a fat score of 0, 9% had fat score of 1, 1% had fat score ≥2 (Pyle 1997).

Cedar waxwings exhibited selectivity with respect to fruit consumption (Wilk's $\Lambda = 0.001$, $P = 0.02$), with *Prunus* ranked highest and *Rosa* lowest (Table 1). Neither gray

Table 1. A simplified ranking matrix for cedar waxwing, summarizing results from a compositional analysis of fruit use relative to availability. At the intersection of row *i* and column *j*, a "+" indicates that the fruit in *i* was used more than the fruit in *j*, and a "−" indicates it was used less; a triple sign indicates an effect at $P < 0.05$. Data collected during July–early September 2007–2008 in western Massachusetts, USA.

	Cornus	***Elaeagnus***	***Lonicera***	***Prunus***	***Rhamnus***	***Rosa***	***Rubus***	***Vaccinium***	**Rank**
Cornus		+ + +	−	− − −	+	+ + +	−	−	5
Elaeagnus	− − −		+	− − −	+	+	+	−	4
Lonicera	+	−		−	+	+	+	+	2
Prunus	+ + +	+ + +	+		+ + +	+ + +	+ + +	+ + +	1
Rhamnus	−	−	−	− − −		+ + +	+	−	6
Rosa	− − −	−	−	− − −	− − −		− − −	− − −	8
Rubus	+	−	−	− − −	−	+ + +		−	7
Vaccinium	+	+	−	− − −	+	+ + +	+		3

catbirds (Wilk's $\Lambda = 0.02$, $P = 0.17$), nor frugivore species combined (Wilk's $\Lambda = 0.02$, $P = 0.23$) exhibited selectivity with respect to fruit consumption; however, in these analyses, patterns of fruit selection were qualitatively similar to those of cedar waxwing, with *Prunus* ranked high and *Rosa* ranked low (gray catbird: *Prunus* > *Rubus* > *Rhamnus* > *Cornus* > *Lonicera* > *Vaccinium* > *Rosa* > *Elaeagnus;* frugivore species combined: *Prunus* > *Lonicera* > *Rubus* > *Rhamnus* > *Vaccinium* > *Cornus* > *Elaeagnus* > *Rosa*).

Results of linear mixed models indicated that the body condition indices of cedar waxwings of both sexes combined, as well as females considered separately, were negatively related to the proportion of invasive fruit at a site (Table 2). Similarly, the condition of male and female gray catbirds combined were negatively related to the abundance of *Rhamnus*. The condition index of cedar waxwing females was negatively related to the abundance of *Rosa*. In contrast, the condition index of gray catbird males was positively related to invasive abundance.

Bird species differed in their importance as potential dispersers in terms of Flock Disperser Importance (FDI; $F_{2,25} = 3.6$, $P = 0.04$) and Overall Disperser Importance (ODI; $F_{2,25} = 3.7$, $P = 0.04$). Tukey's HSD test indicated that the importance of cedar waxwing as a potential disperser was greater than the other bird species in terms of ODI ($P = 0.05$) and FDI ($P = 0.08$).

The ODI of cedar waxwings, gray catbirds, and waxwings and catbirds combined differed among plant genera ($P < 0.05$). The FDI for waxwings and catbirds combined also differed among plant genera ($P < 0.05$), but not for waxwings and catbirds separately. In all cases, these indices indicated that potential seed dispersal was greatest for *Prunus* ($P < 0.05$).

Potential seed dispersal of native plants was greater than that of invasive plants as indicated by the ODI of bird species combined ($P = 0.005$), but not FDI, or for bird species considered separately (all $P > 0.05$). Among native plants, bird species differed in their importance as potential

Table 2. Results of AIC_c model selection ranked by ΔAIC_c and parameter estimates ($\beta \pm SE$) for univariate mixed-model regression relating avian condition to the abundance of fruit genera (>5% occurrence), proportion of invasive fruit (prpInv), site-level total fruit abundance, and demographic factors (Age, Sex). 95% Highest Posterior Density confidence intervals are shown with lower (Lower CI) and upper (Upper CI) bounds and *P*-value. Data collected Jul–Aug 2006–2008 in western Massachusetts, USA. Only null model and models with an $AIC_c <$ null model are shown.

	Model[a]	**ΔAIC_c**[b]	w_i	**Dev**	**β**	**SE**	**Lower CI**	**Upper CI**	***P***
Baltimore oriole ($n = 28$)	Age	0 (115.7)	0.573	107.2	−0.69	0.41	−1.69	0.23	0.05
	Sex	1.31	0.298	107.9	1.24	0.70	−0.31	1.84	0.20
	Null	4.92	0.049	113.9	<0.01	0.36	−0.92	0.84	0.77
Baltimore oriole females ($n = 12$)	Null	0 (47.9)	0.390	40.48	<0.01	0.39	−0.98	0.98	0.85
Baltimore oriole males ($n = 13$)	Age	0 (54.4)	0.779	45.67	−1.7	0.75	−3.17	0.10	0.05
	Null	4.71	0.074	52.42	<0.01	0.52	−1.31	1.28	0.79
Cedar waxwing ($n = 84$)	prpInv	0 (−163.7)	0.881	−185.7	−0.07	0.02	−0.12	−0.04	0.004
	Null	4.79	0.080	−172.1	<0.01	0.01	−0.02	0.03	0.56
Cedar waxwing females ($n = 25$)	prpInv	0 (122.3)	0.599	115.6	−3.06	1.13	−5.45	−0.63	0.05
	Rosa	1.94	0.227	113.0	−0.40	0.12	−0.66	−0.14	0.02
	Prunus	4.01	0.081	116.4	0.56	0.22	0.11	1.06	0.06
	Null	6.06	0.029	122.5	<0.01	0.57	−1.34	1.26	0.77
Gray catbird ($n = 195$)	Sex	0 (848.3)	0.489	837.5	−1.49	0.58	−2.63	−0.37	0.02
	Rhamnus	1.10	0.282	837.5	−0.27	0.09	−0.43	−0.08	0.02
	Null	4.53	0.051	845.4	−0.04	0.21	−0.48	0.38	0.34
Gray catbird females ($n = 36$)	Null	0 (−87.3)	0.939	−101.0	<0.01	0.01	−0.02	0.02	0.99
Gray catbird males ($n = 12$)	prpInv	0 (40.0)	0.913	28.49	2.83	0.42	1.24	3.37	0.002
	Rosa	4.68	0.079	30.45	0.46	0.08	0.22	0.64	0.003
	Null	11.76	0.002	44.71	1.00	0.47	−0.11	2.11	0.13
Scarlet tanager ($n = 11$)	Sex	0 (47.0)	0.524	33.81	1.30	0.59	−0.10	2.78	0.07
	Null	2.18	0.176	42.19	<0.01	0.52	−1.29	1.18	0.83

[a] No. of parameters = 1 for all (univariate) models.

[b] Min. values for AIC_c are shown in parentheses.

seed dispersers in terms of ODI ($F_{2,13} = 3.9$, $P = 0.05$), though not FDI ($F_{2,13} = 1.6$, $P = 0.24$). Cedar waxwing had greater disperser potential for native plants than American robin in terms of ODI ($P = 0.04$). Bird species did not differ in their importance as potential dispersers of invasive plants based on FDI ($F_{2,5} = 0.4$, $P = 0.71$), or ODI ($F_{2,5} = 1.3$, $P = 0.36$).

Fruit handling success was high across species, and we observed only 2 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. *Rubus* fruit is a composite of smaller drupelets, each of which contains a seed, thus, for *Rubus,* we assumed biting to result in consumption of the seed and we included observations of this event in the analyses. We observed no birds carrying unswallowed fruit away from the foraging location.

DISCUSSION

Despite the fact that seed dispersal by birds is considered a key component of exotic plant invasion, there is little consensus as to whether birds differentially select native versus invasive fruits. For example, based on a meta-analysis of published studies, Aslan and Rejmánek (2012) concluded that birds tend to select native fruits over nonnative fruit under natural conditions when the full existing suite of fleshy fruited plants are available. However, other studies report no consistent differences in selection by birds between fruits of native and invasive plants (Jung 1992, Whelan and Willson 1994, Drummond 2005, LaFleur et al. 2007). We suggest the strong selection we observed for native fruits was largely driven by the extensive use of *Prunus,* which is consistent with other studies of avian fruit use in the eastern United States (Wheelwright 1986, White and Stiles 1992, Witmer 1996). In contrast, studies reporting heavy use of *Rosa* have been conducted during autumn and winter, after *Prunus* fruits have been depleted (Baird 1980, Stiles 1982, Suthers et al. 2000, Drummond 2005). Observations by White and Stiles (1992) that use of introduced fruits tended to be greatest in late autumn and winter after the heaviest use of native fruits are consistent with this view.

Our finding that bird body condition indices decreased with greater prevalence of invasive fruit supports the notion that fruits of invasive plants are a lower quality food resource compared with fruit of native plants (Ingold and Craycraft 1983, White and Stiles 1992, Drummond 2005, Smith et al. 2013). In apparent contrast with this view, Gleditsch and Carlo (2011) reported that catbirds frequently fed their nestlings *Lonicera* fruit at their sites in Pennsylvania, USA, and body condition indices of catbird nestlings reared in *Lonicera*-dominated habitats were greater than those of nestlings reared in habitats dominated by native shrubs. The absence of an effect of *Lonicera* on body condition indices at our sites could be due to the fact that we were quantifying condition for adults and independent juveniles, not nestlings. Furthermore, Gleditsch and Carlo (2011) did not quantify effects of other invasive species on condition as most of the other species were selected less than *Lonicera,* with one genus (*Rhamnus*) negatively related with catbird body condition. Whether the relationship with condition we observed are direct consequences of fruit consumption or due to indirect effects associated with invasive plants, such as alterations in habitat structure and the availability of insect food resources, is unclear (Tallamy 2004, Ortega et al. 2006, Fickenscher et al. 2014). However, species-specific effects that we observed between invasive fruits and avian condition indicate that habitats dominated by invasive plants may represent lower quality habitats for some species but higher quality habitats for others, and are likely location-specific (Gleditsch and Carlo 2014). A potential limitation of our analysis is that we did not track specific birds and monitor their exact consumption of native and invasive fruits. However, captured birds came from the same population as the birds for which we had fruit selection data, therefore, we feel justified in making inferences about captured birds based on data from observed birds. We also cannot completely account for the influence of other foraging habitat beyond our study sites without tracking individual birds. Given that most study sites were >2.5 km apart, we believe the likelihood of an individual bird foraging at another one of our study sites was very small. Furthermore, there is very little shrubland habitat of the type we studied available in Massachusetts (>3%) because of historical changes in land use and plant succession (Schlossberg and King 2015), thus, the potential for birds to use shrubland habitats other than that within our study sites is limited.

Consistent with previous accounts, American robin, cedar waxwing, and gray catbird swallowed fruits (and seeds) whole, indicating that fruit selection by these species would result in the dispersal of a seed away from its parent plant (Johnson et al. 1985, Katusic-Malmborg and Willson 1988). These species have been widely recognized as important seed dispersers (Wheelwright 1986, Chavez-Ramirez and Slack 1994, Katusic-Malmborg and Willson 1988, Renne et al. 2000, Aslan and Rejmánek 2010) and were the primary potential dispersal agents for both native and invasive plants in our study system based on our criteria and their importance as seed dispersers. Fruit-handling techniques were similar among the major frugivores, so variation in flocking behavior and relative abundance were the most important traits in determining a species' importance as a potential disperser. As such, cedar waxwing, which was abundant in our study system and had the strongest flocking tendencies of the major dispersers, was the most important potential disperser species of those we examined. Cedar waxwing is the most frugivorous bird species in North America, and is well-known for its propensity to forage on fruit in large flocks (Martin et al. 1951, Chavez-Ramirez and Slack 1994, Witmer 1996). Selection for fruit by cedar waxwing therefore has important implications for the dispersal of native and invasive plants.

The behavioral characteristics we have examined in our study are necessary conditions for a species to be an effective seed disperser, but our indices provide an indication only of the quantity of seed dispersed based on species' foraging behavior and relative abundance (Renne et al. 2000). Other factors that we did not measure, such as postforaging behaviors and movement patterns, also contribute to effective seed dispersal by influencing the location of seed deposition, distance from parent plant, and likelihood of germination (Herrera 1985, Hoppes 1988, Schupp 1993, Chavez-Ramirez and Slack 1994). We cannot account for the potential effect of these factors on our measures of disperser importance. However, findings from previous studies indicate that differences in postforaging behaviors and movements do exist among the species we examined (Chavez-Ramirez and Slack 1994). These differences may result in tradeoffs for plants in terms of dispersal efficiency (quantity of seeds dispersed) and efficacy (germination success). For example, the strong flocking behavior of cedar waxwing increases this species' potential to disperse large quantities of seeds away from a parent plant, but it may also result in the deposition of seeds in high densities under postforaging perch sites. For some plant species, this could ultimately reduce germination success as a result of density-dependent seed mortality. In contrast, the loose flock structure of the American robin may result in fewer seeds dispersed per plant, but this species' tendency to forage over wide areas might result in a scattered pattern of seed deposition that is more beneficial for the germination success of some plant species (Chavez-Ramirez and Slack 1994). Nevertheless, our study provides information on several preconditions for birds to serve as dispersers that may serve to inform future efforts to identify links with other aspects of dispersal such as efficiency and efficacy.

Finally, in addition to their value as food, invasive plants are also reported to affect nesting success for birds that use them as nesting substrates. Lower nest success for birds nesting in invasive plants has been reported from Illinois (Schmidt and Whelan 1999), Ohio (Borgmann and Rodewald 2004, Rodewald et al. 2010) and Arizona (Jones and Bock 2005), USA. In contrast, studies from the Northeast indicate that the abundance of gray catbirds and American robins was positively related to the abundance of *Lonicera* fruit (Gleditsch and Carlo 2014), and breeding abundance of gray catbirds was positively correlated to the cover of invasive species in wildlife openings in Connecticut, USA (Mazzei 2009). Furthermore, gray catbirds are reported to select invasive plants as a nesting substrate (Schlossberg and King 2010, Gleditsch and Carlo 2014), and catbird nest success was greater in invasive plants than in native plants in Massachusetts. Given the variability among studies in terms of bird species, plant species, regional predator faunas, and habitat, it is not surprising that results differ among studies.

MANAGEMENT IMPLICATIONS

Our finding that birds select native fruit over invasive fruit, and bird body condition is negatively related to the proportion of invasive fruit at a given site, suggests that control efforts for invasive plant species will enhance habitat quality for songbirds, particularly if it is done in conjunction with practices that encourage the growth of native fruiting species such as *Prunus*. Other native plants that may provide food resources when *Prunus* is not available include *Cornus, Viburnum, Amelanchier, Sambucus,* and *Sassafras*.

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