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FRUIT QUALITY AND CONSUMPTION BY SONGBIRDS DURING AUTUMN MIGRATION

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ABSTRACT.—Seasonal fruits are an important food resource for small songbirds during autumn migration in southern New England. Therefore, conservation and management of important stopover sites used by migrating birds requires knowledge about nutritional requirements of songbirds and nutritional composition of commonly consumed fruits. We measured nutrient composition and energy density of nine common fruits on Block Island, Rhode Island, and conducted a field experiment to estimate consumption rates of three of these fruits by birds during autumn migration. Most common fruits on Block Island contained primarily carbohydrates (41.3–91.2% dry weight), and little protein (2.6–8.6%) and fat (0.9–3.7%), although three contained more fat: *Myrica pennsylvanica* (50.3%), *Viburnum dentatum* (41.3%), and *Parthenocissus quinquefolia* (23.6%). Bird consumption of high-fat, high-energy *V. dentatum* fruit and high-carbohydrate, low-energy *Phytolacca americana* fruit was greater than consumption of *Aronia melanocarpa*, a high-carbohydrate, low-energy fruit. We estimated that migratory birds on Block Island must eat up to four times their body mass in fruit wet weight each day to satisfy their energy requirements when eating low-energy fruits such as *P. americana*, and they cannot satisfy their protein requirements when eating only certain high-energy fruits such as *V. dentatum*. Our results suggest that many migratory birds must eat both fruits and insects to meet their dietary needs. Thus, shrubland habitat at important migratory stopover sites such as Block Island should be managed so that it contains a variety of preferred fruit-bearing shrubs and an adequate abundance of insects. *Received 30 May 2006. Accepted 24 September 2006.*

Many species of migratory songbirds that are primarily insectivorous during the breeding season consume large amounts of fruit during autumn migration (Thompson and Willson 1979, Herrera 1984, Parrish 1997), even though many common fruits may contain less protein and fat than is likely needed to fuel migratory flight (Berthold 1976, Herrera 1982, Bairlein and Gwinner 1994). The concentration of fat and carbohydrate in fruit varies considerably among plant species but the amount of protein in fruit is consistently low (Johnson et al. 1985, White 1989, Witmer 1996, Izhaki 1998). Given that birds must rebuild expended energy and protein stores at stopover sites during migration (Bauchinger and Biebach 1998, Piersma 2002), birds that eat fruits may satisfy their energy needs but have limited protein intake (Levey and Martínez del Rio 2001). The low protein content of fruits may explain why some birds are unable to maintain body mass when fed only fruit (Berthold 1976, Levey and Karasov 1989, Sedinger 1990, Izhaki 1992), although other characteristics of fruit pulp, such as secondary compounds or amino acid content, may also contribute to protein limitation (Parrish and Martin 1977, Izhaki and Safriel 1989, Mack 1990). Facultative frugivores, such as omnivorous migrating songbirds, typically have higher protein requirements than more specialized frugivores and, therefore, may be protein limited when feeding exclusively on low-protein fruits (Robbins 1993, Witmer 1998, Tsahar et al. 2006). Lack of sufficient protein in the diet of migratory songbirds can hinder their ability to regain body mass and result in an increased amount of time refueling at stopover sites (Berthold 1976, Bairlein and Gwinner 1994, Pierce and McWilliams 2004).

The ability of a fruit to satisfy protein requirements of a bird depends in part on the ratio of energy to protein in the fruit. This is because birds usually eat to satisfy their energy requirements rather than particular nutrient requirements (Robbins 1993). Therefore,

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birds will eat less of a fruit with a high energy to protein ratio, thus ingesting less protein, compared to a fruit with a relatively low energy to protein ratio. We can make predictions about which fruits can satisfy a bird's protein requirements by measuring the ratio of energy to protein in fruits eaten by selected migratory songbirds, and estimating the protein requirements of these same birds (Bosque and Pacheco 2000). However, relatively few studies have investigated how nutritional requirements of migratory birds relate to nutritional composition of fruits available at temperate stopover sites (Sorenson 1984, Johnson et al. 1985, Witmer 1998).

Our objectives were to: (1) measure the nutrient composition and energy density of fruits from nine common plant species that are abundant in southern New England's maritime shrublands, (2) identify which fruits can satisfy the energy and protein requirements of migratory songbirds, (3) estimate the rate at which migratory birds consume fruits from three plant species that differ in nutrient composition and energy density, and (4) provide suggestions for management of coastal shrubland that would improve habitat quality at stopover sites such as Block Island, Rhode Island.

METHODS

Study Site.—We estimated fruit quality during September–November 2001 and bird consumption of wild fruits during October 2004 at Clay Head Preserve (~190 ha) on Block Island, Rhode Island (41° 10′ N, 71° 34′ W). This island is an important stopover site for migratory songbirds during autumn migration (Baird and Nisbet 1960, Able 1977, Parrish 1997, Reinert et al. 2002). The maritime shrub community nearest the coast is dominated by stands of short northern bayberry (*Myrica pennsylvanica*) intermixed with *Rubus* spp. and poison ivy (*Toxicodendron radicans*). The more inland maritime shrub community consists of tall *M. pennsylvanica* mixed with northern arrowwood viburnum (*Viburnum dentatum*), black chokeberry (*Aronia melanocarpa*), shadbush (*Amelanchier* spp.), winterberry (*Ilex verticillata*), wild rose (*Rosa* spp.), and *Rubus* spp. Pokeweed (*Phytolacca americana*), a tall herbaceous plant, grows in scattered clumps in clearings and in the understory, and poison ivy and Virginia creeper (*Parthenocissus quinquefolia*) are found among the taller shrubs. Oriental bittersweet (*Celastrus orbiculatus*), autumn olive (*Elaeagnus umbellata*), and multiflora rose (*Rosa multiflora*) are common invasive species on Block Island.

Fruit Quality.—Fruit was collected on 4 days (9 Sep, 10 and 23 Oct, 3 Nov) during autumn 2001 within Clay Head Preserve. Species collected included *V. dentatum*, *A. melanocarpa*, *M. pennsylvanica*, *I. verticillata*, *P. quinquefolia*, *P. americana*, *C. orbiculatus*, wild rose hips, and *E. umbellata*. These are the most common fruits available to birds on Block Island during their autumn migration. Fruit samples were frozen in the field and stored frozen at −20° C at the University of Rhode Island until processed for nutrient composition. Processing in the laboratory involved thawing the fruits and then manually removing the seeds and stems. The seedless fruit was freeze-dried and ground in a small Waring blender.

Total energy content of fruit was measured by bomb calorimetry using a Parr 1266 Isoperibol Oxygen Bomb Calorimeter. Fat content was directly measured using a 2-g subsample of each fruit placed in separate ceramic thimbles (30 × 80 mm, medium porosity) and refluxed with petroleum ether for 6 hrs in a Soxhlet apparatus (Dobush et al. 1985). Nitrogen content was measured using a 3–4 mg sample of each fruit, which was then loaded and sealed into a clean tin capsule and placed in the autosampler of a Carlo-Erba NA 1500 Series II Elemental Analyzer attached to a continuous flow isotope ratio Micromass Optima Spectrometer (CF-IRMS). We estimated crude protein content by multiplying nitrogen content by 4.4 (Witmer 1998). Samples were then placed in a 550° C muffle furnace for ~3 hrs to obtain ash content. Total carbohydrate content was calculated as 100% minus percent fat, protein, and ash and included structural carbohydrates (e.g., plant fiber) and soluble carbohydrates (e.g., plant sugars). Mann-Whitney *U*-tests were used to compare fat and energy content of fruits picked in early (9 Sep, 10 Oct) versus late (23 Oct, 3 Nov) migration.

Nutrient Requirements.—We used published allometric equations to estimate energy and protein requirements of two bird species of different body mass that are common omnivorous fall migrants on Block Island: Hermit Thrush (*Catharus guttatus*) and Yellow-rumped Warbler (*Dendroica coronata*). Daily nitrogen requirement (DNR, mg N/day) of the Hermit Thrush was estimated using an equation for the Wood Thrush (*Hylocichla mustelina*): DNR = (911.2 mg N) × (body mass, kg)$^{-0.75}$/day (Witmer 1998). DNR of the Yellow-rumped Warbler was estimated using an allometric equation based on 10 species of omnivorous birds: DNR = (575.4 mg N) × (body mass, kg)$^{-0.76}$/day (Tsahar et al. 2006). We used this interspecific allometric equation because (a) there is no published single-species equation for a small migratory passerine with feeding habits similar to Yellow-rumped Warblers, and (b) this interspecific equation along with that for Wood Thrush provides a range of estimated nitrogen requirements that is useful for evaluating nutritional adequacy of fruits. Field metabolic rate (FMR, kJ/day) for free living, non-reproducing birds was estimated using: log FMR = 1.145 + (0.53 × log body mass, g) (Koteja 1991). Daily energy requirement (DER, kJ/day) was estimated using DER = FMR/0.64 assuming a 64% efficiency of conversion of dietary energy (Karasov 1990). Data on the observed diets of Hermit Thrushes and Yellow-rumped Warblers during autumn stopover on Block Island were available from earlier work (Parrish 1997).

We used estimated DER and the energy density of each fruit (kJ/g dry mass) to calculate dry food intake required to meet daily energy requirements. Wet food intake was then calculated based on the measured percent mass loss between wet fruit mass with seed and dry fruit mass without seed. We assumed 75% mass loss between wet with seed to dry without seed for *M. pennsylvanica* because this fruit contains waxy pulp. We plotted the percent protein required in fruit to meet daily protein requirements if birds ate sufficient fruit to satisfy their energy requirements. We then plotted measured protein and energy densities in wild fruits to identify which fruits would satisfy protein requirements of birds. We expanded our analysis of fruit quality in relation to protein requirements of birds beyond fruits for which we measured nutrient composition by including nutrient composition of other fruits present on Block Island that were published by White (1989).

Fruit Removal.—We randomly selected and marked one branch on five separate *V. dentatum*, *P. americana*, and *A. melanocarpa* plants within the inland maritime shrubland community on 9 Oct 2004. We selected a companion branch and enclosed the fruiting portion of this branch with translucent netting ensuring the netted branches were still exposed to environmental conditions while preventing birds from accessing the fruits. We counted the total number of fruits on each branch when it was initially selected and weekly thereafter for three weeks to estimate the rate of fruit removal and consumption at Clay Head Preserve during autumn migration. We recounted fruits on a given branch until we arrived at the same number of fruits at least twice to obtain an accurate measurement of the number of fruits on each branch. We counted separately the unripe fruits (defined as those fruits that were more than 50% green) and ripe fruits on each branch of *P. americana*.

We compared the initial number of fruits per branch among the three plant species with two-way ANOVA with species and branch type (enclosed, unenclosed) as grouping variables. We calculated the percent of fruits remaining each week on each enclosed (*V. dentatum*, n = 5; *P. americana*, n = 4; *A. melanocarpa* n = 5) and unenclosed (*V. dentatum*, n = 5; *P. americana*, n = 4; *A. melanocarpa* n = 5) branch to estimate changes in fruit numbers over time (Drummond 2005). The arcsine transformed values were analyzed using repeated measures ANOVA. We also developed a fruit consumption index by dividing the percent of fruits remaining on unenclosed branches by the percent of fruits remaining on companion enclosed branches (*V. dentatum*, n = 5; *P. americana*, n = 3; *A. melanocarpa*, n = 5). This ratio was subtracted from one to yield an index in which greater values reflect higher cumulative consumption over time. We used repeated measures ANOVA to analyze changes in the arcsine transformed fruit consumption index over time. Two pairs of *P. americana* branches were eliminated from the analysis because one branch in each pair died before the end of the study.

RESULTS

Fruit Quality.—Most fruits on Block Island contained primarily carbohydrates (41.3–91.2% dry weight) and little fat (0.9–3.7%; Table 1), except for *M. pennsylvanica*, *V. dentatum*, and *P. quinquefolia* which had appreciably higher fat content (50.3, 41.3, and 23.6%, respectively). These three higher-fat fruits had energy densities almost twice as great as other fruits such as *P. americana* and *E. umbellata* (Table 1). We found no significant seasonal change in energy density (U = 93, P = 0.82) or fat content (U = 118, P = 0.97) of fruits throughout the autumn period. We estimated that migratory birds must eat approximately three to four times their body mass in *P. americana* berries to satisfy their energy requirements (Table 2). In contrast, songbirds that eat *V. dentatum* fruit must eat less than or up to their own body mass in fruit each day because of its higher energy density (Table 2). If birds eat only enough to satisfy their energy requirements, we estimated that omnivorous birds such as Yellow-rumped Warblers could not satisfy their daily protein requirements by eating high-energy fruits like *M. pennsylvanica* and *V. dentatum* (Fig. 1). Many more fruits would not satisfy daily protein requirements if minimum nitrogen requirements were as high as those estimated for the Hermit Thrush. However, most birds would likely meet their daily protein requirements if feeding exclusively on lower energy fruits such as *P. americana*, although low-energy fruits with less protein such as *V. corymbosum* would likely be protein deficient (Fig. 1).

Fruit Removal.—When we first counted fruits on 9 October, *A. melanocarpa* had significantly more fruits per branch than both *V. dentatum* and *P. americana* (species: $F_{2,20}$ = 11.2, P = 0.001). There were no significant differences in number of fruits on enclosed and unenclosed branches on 9 October (branch type: $F_{1,20}$ = 2.7, P = 0.11; species × branch type: $F_{2,20}$ = 0.4, P = 0.68). The percent fruit remaining on unenclosed branches during the next 3 weeks decreased with *V. dentatum* losing the greatest percent of its fruit most rapidly (time: $F_{2,22}$ = 18.9, P < 0.001; species: $F_{2,11}$ = 17.9, P < 0.001; time × species: $F_{4,22}$ = 0.3, P = 0.86; Fig. 2). The per-

TABLE 1. Nutrient composition (% dry weight ± SE) and energy density (kJ/g dry weight ± SE) of common fruit species on Block Island, Rhode Island collected during September–November 2001. Numbers associated with each species are used to identify species in Fig. 1.

Species	Common name	Fat	Protein	Carbohydrate	Ash	Energy density
1 *Myrica pennsylvanica*	Bayberry	50.3 ± 1.4	3.0 ± 0.0	41.3 ± 0.2	3.4 ± 1.3	28.7 ± 0.5
2 *Viburnum dentatum*	Viburnum	41.3 ± 5.8	2.6 ± 0.0	50.0 ± 5.5	3.7 ± 1.0	27.4 ± 0.6
3 *P. quinquefolia*	Virginia creeper	23.6 ± 4.8	6.0 ± 0.0	67.7 ± 5.3	3.7 ± 0.4	22.3 ± 0.0
4 *Ilex verticillata*	Winterberry	3.7 ± 0.7	2.9 ± 0.0	88.1 ± 0.7	3.3 ± 0.3	19.9 ± 0.7
5 *Celastrus orbiculatus*	Bittersweet	2.6 ± 1.1	8.6 ± 0.1	89.1 ± 1.4	3.3 ± 0.5	18.8 ± 0.9
6 *Aronia melanocarpa*	Chokeberry	0.9 ± 0.6	3.5 ± 0.0	91.2 ± 0.8	2.9 ± 0.4	18.1 ± 0.6
7 *Rosa* spp.	Rose	2.2 ± 1.7	5.6 ± 0.0	87.5 ± 1.6	5.4 ± 0.2	17.3 ± 0.8
8 *Phytolacca americana*	Pokeweed	2.9 ± 0.1	5.8 ± 0.0	79.8 ± 0.5	12.4 ± 0.4	16.5 ± 1.0
9 *Elaeagnus umbellata*	Autumn olive	2.1 ± 0.2	6.0 ± 0.0	89.9 ± 0.7	3.0 ± 0.7	15.8 ± 0.3

TABLE 2. Estimated required fruit intake for two migratory bird species based on measured energy density of the fruits (Table 1) and predicted daily energy requirements of the birds[a].

Species	Common name	Dry food intake (g/day)		Wet food intake (g/day)	
		HETH	YRWA	HETH	YRWA
Myrica pennsylvanica	Bayberry	4.71	2.97	18.83	11.89
Viburnum dentatum	Viburnum	4.97	3.13	21.68	13.69
P. quinquefolia	Virginia creeper	6.04	3.81	34.04	21.49
Ilex verticillata	Winterberry	6.80	4.29	22.34	14.10
Celastrus orbiculatus	Bittersweet	7.20	4.55	66.07	41.71
Aronia melanocarpa	Chokeberry	7.39	4.66	25.87	16.33
Rosa spp.	Rose	7.65	4.83	35.72	22.55
Phytolacca americana	Pokeweed	8.06	5.09	90.71	57.26
Elaeagnus umbellata	Autumn olive	8.67	5.47	68.16	43.03

[a] Daily energy requirements were estimated using the average body mass of each species: Hermit Thrush = 31.2 g (HETH; Jones and Donovan 1996); Yellow-rumped Warbler = 13.1 g (YRWA; Hunt and Flaspohler 1998), an allometric equation: Log FMR = 1.145 + 0.53 log mass (g) (Koteja 1991), and assuming a 64% efficiency of conversion of dietary energy: DER = FMR/0.64 (Karasov 1990).

cent fruit remaining on enclosed branches also decreased over time (time: $F_{2,22} = 5.9$, $P = 0.009$) although at a much slower rate than it did on unenclosed branches (Fig. 2). Enclosed *A. melanocarpa* and *P. americana* branches lost a greater percent of their fruit than *V. dentatum* during the 3 weeks (species: $F_{2,11} = 5.5$, $P = 0.022$; time × species: $F_{4,22} = 0.5$, $P = 0.73$; Fig. 2). Rate of consumption was higher earlier in the season than later with consumption of *V. dentatum* fruit greater than consumption of either *P. americana* or *A. melanocarpa* fruit (time: $F_{2,20} = 11.4$, $P < 0.001$; species: $F_{2,10} = 35.3$, $P < 0.001$; time × species: $F_{2,10} = 1.7$, $P = 0.20$; Fig. 3).

DISCUSSION

Birds Eat Certain Fruits During Migration.—Our results show that fruits were readily consumed by birds during autumn migration although consumption rates differed by plant species. Fruit removal in excess of loss due to natural abscission can be attributed to bird consumption because birds are the most important vertebrate consumers of fruit on Block Island. There are only nine terrestrial mammal species on the island and none of these species eats primarily fruits (Lang and Comings 2001).

Birds on Block Island ate more high-energy *V. dentatum* fruit than the lower energy fruits of *P. americana* and *A. melanocarpa*. Parrish (1997) also found that *V. dentatum* was the most prevalent fruit in the diet of fall migrants on Block Island. *P. americana* and *M. pennsylvanica* were also readily consumed by birds, although consumption of *M. pennsylvanica* was almost exclusively by Yellow-rumped Warblers (Parrish 1997). This is most likely because the fat in this fruit is primarily composed of wax esters that can only be efficiently digested by a few species including the Yellow-rumped Warbler (Place and Stiles 1992). *V. dentatum* fruits are more energy dense because of their high fat content compared to the high-carbohydrate fruits *P. americana* and *A. melanocarpa*. Total carbohydrate content of fruits includes structural carbohydrates, such as cellulose, that most passerines cannot digest, and more readily digestible soluble carbohydrates, such as hexose sugars (Karasov 1990, Martínez del Rio and Karasov 1990). We were unable to ascertain if birds ate less high-carbohydrate fruits such as *A. melanocarpa* because the carbohydrate was mostly structural carbohydrates as we only measured total carbohydrates of fruits. Patterns of fruit consumption were also not simply related to dietary protein because *P. americana* had more protein than *V. dentatum* and most other fruits sampled in our study. These results suggest that fruit selection by birds on Block Island was not simply related to differences in macronutrient composition between fruits.

Many mechanisms have been proposed to explain the characteristics of fruits and other foods that birds may use to choose their diets. For example, studies of wild and captive songbirds have shown that some species preferentially select high-fat fruits (Stiles 1993, Fuentes 1994), or high-sugar fruits (Levey

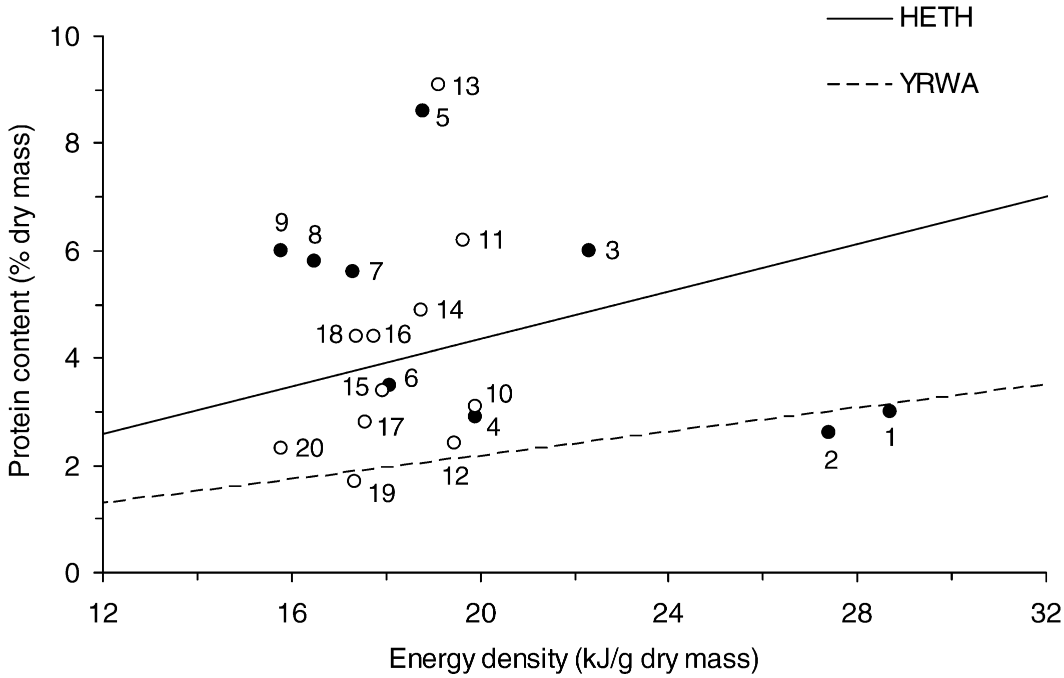

FIG. 1. Estimated dietary protein content required to meet the daily protein requirements for two representative migratory species: Hermit Thrush (HETH) and Yellow-rumped Warbler (YRWA). Energy density and protein content of 20 fruit species on Block Island are represented by circles; fruits below the lines do not contain sufficient protein to satisfy a bird's daily requirements. Solid circles denote fruiting plant species (Table 1). Open circles denote fruiting plant species for which nutrient composition was provided by White (1989): 10 = *Viburnum acerifolium*; 11 = *Smilax rotundifloria*; 12 = *Aronia prunifolia*; 13 = *Sambucus canadensis;* 14 = *Vitis labrusca*; 15 = *Prunus virginiana*; 16 = *Lonicera japonicum*; 17 = *Rosa virginiana*; 18 = *Aronia arbutifolia*; 19 = *Vaccinium corymbosum*; 20 = *Rubus occidentalis.*

1987, Lepczyk et al. 2000), or fruits with particular amino acids (Parrish and Martin 1977), fatty acids (McWilliams et al. 2002, Pierce et al. 2004), colors (Willson et al. 1990, Puckey et al. 1996), or certain pulp-to-seed ratios or seed size (Sorenson 1984, Izhaki 1992, Murray et al. 1993, Stanley and Lill 2002). Secondary compounds may also affect fruit choice because birds may eat a diversity of fruits to avoid toxic levels of particular secondary compounds (Barnea et al. 1993; Cipollini and Levey 1997a, 1997b; Levey and Cipollini 1998; Schaefer et al. 2003). Secondary compounds in fruits may also interfere with protein digestion, which may cause birds to switch to a diet of insects before resuming fruit consumption (Izhaki and Safriel 1989).

Fruit selection in free-living birds may also be related to ecological context (Baird 1980, Moermond and Denslow 1983, Sargent 1990, Whelan and Willson 1994). For example, *V. dentatum* is a high-energy, consumed fruit that is also one the most abundant fruiting species in the habitats used by songbirds during stopover on Block Island. In contrast, *P. americana* is a high-carbohydrate fruit that was consumed at a lower rate than *V. dentatum*, and is less abundant and more patchily distributed throughout the habitat. Thus, both ecological and nutritional factors likely interact to affect patterns of fruit consumption by birds during autumn migration.

Nutritional Adequacy of Fruits for Migrating Birds.—Fruits provide an easily accessible resource for birds that requires relatively little energy to acquire compared to foraging on aerial insects (Parrish 1997). In addition, fruit availability may be increasingly important as the autumn season progresses because insect resources become more unpredictable and scarce with decreasing temperatures and inclement weather conditions (Parrish 2000).

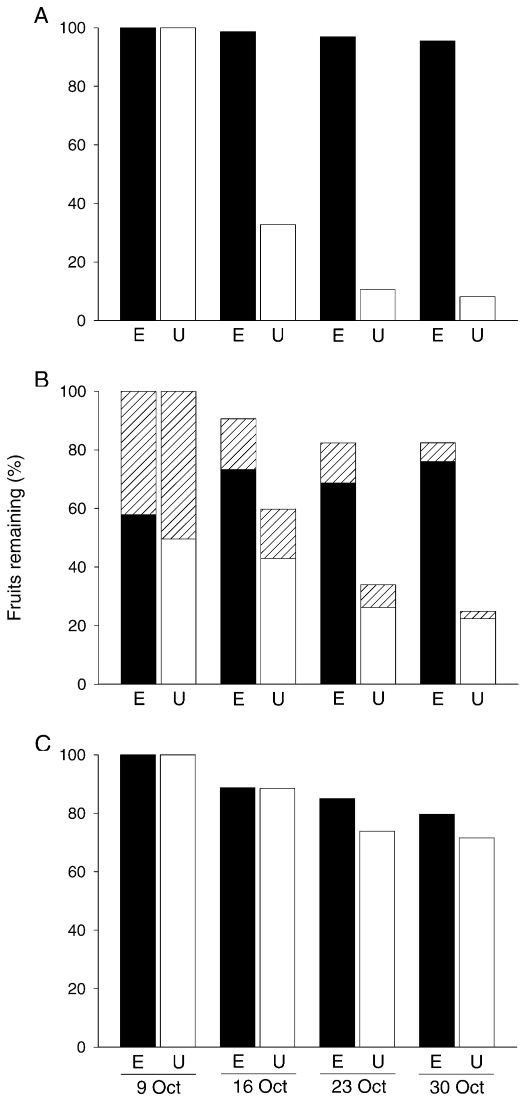

FIG. 2. Mean percent fruit remaining on enclosed (E) and unenclosed (U) branches for *V. dentatum* (A), *P. americana* (B), and *A. melanocarpa* (C). Fruit counts on Block Island were conducted on three sampling dates following initial fruit counts on 9 October 2004. Hatched bars on B denote unripe fruits on enclosed and unenclosed branches.

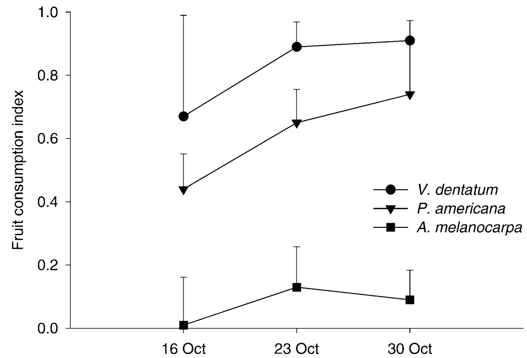

FIG. 3. Mean (± SD) fruit consumption index (1 − [% fruits remaining on unenclosed branches divided by % fruits remaining on companion enclosed branches]) for *V. dentatum*, *P. americana*, and *A. melanocarpa* on Block Island during October 2004. Fruits with index values closer to 1.0 had higher cumulative consumption over time.

We have shown that songbirds that consume only fruits may satisfy their energy requirements but may not satisfy their daily protein requirements because temperate fruits may have too little protein relative to energy content to meet their protein requirements (Witmer 1998). This protein limitation may be particularly difficult for songbirds during migration which must replenish some protein along with fat reserves (McWilliams et al. 2004). Studies with captive birds suggest they can maintain body weight when fed only fruit (Bairlein and Simons 1995, Bairlein 1996), although birds eating mixed fruit and insect diets usually gain mass more rapidly than birds eating either fruit or insects alone (Bairlein and Simons 1995, Parrish 2000). Diet switching or mixing may satisfy the bird's nutrient requirements but may also require time for digestive adaptation, which could increase time spent refueling and delay the overall speed of migration (McWilliams and Karasov 2005). Migratory birds at stopover sites such as Block Island probably must consume a variety of fruits with different energy and protein content, or consume some insects along with fruits to satisfy their protein and energy requirements as observed in some migrating birds (White and Stiles 1990, Parrish 1997). Further studies are needed that measure protein requirements of a variety of birds during migratory and non-migratory periods before we can more accurately predict whether certain fruits provide adequate energy and protein for a given bird species.

CONSERVATION IMPLICATIONS

Many populations of neotropical songbird migrants have declined over the past few decades (Askins et al. 1990). In the past, most emphasis has been placed on conservation of songbird populations in breeding and wintering areas. However, energetically demanding annual migrations can result in mortality rates 15 times higher than during breeding and wintering seasons (Sillett and Holmes 2002). Small songbirds require abundant food resources over the length of their migratory route to successfully complete migration. Thus, availability of suitable stopover habitat is critical for songbird survival and long-term conservation of these populations.

The east coast of the United States is an important migration corridor for many species of landbird migrants. The maritime shrubland habitats that serve as stopover sites receive large numbers of migrants, particularly in areas near significant barriers to migration such as large bodies of water. The superabundant fruits present at these sites are important food resources that are used extensively by migrating birds during autumn stopover. For example, migrant abundance is highest in habitats with greater fruit availability during autumn migration (Blake and Hoppes 1986, Martin and Karr 1986, Suthers et al. 2000, Rodewald and Brittingham 2004). Experimental removal of available fruits decreased local abundance of autumn migrants on Block Island (Parrish 2000) and birds overwintering in the southern United States (Borgmann et al. 2004). Thus, seasonally abundant fruits can be a significant food resource for migrating songbirds in temperate regions of eastern North America (White 1989, Parrish 1997).

Eastern shrubland habitats are becoming rare and more frequently disturbed as development increases (Moore et al. 1995, Askins 2000). In light of the importance of these habitats for migrating birds, the diversity of native fruiting plants in existing shrublands should be maintained to provide the resources needed for efficient migratory refueling. Managers and landowners should focus on creating suitable stopover habitat by cultivating or planting high-energy fruits such as *V. dentatum* along with lower energy, higher-protein fruits such as *P. americana* that are widely consumed by songbirds and that are native to the northeastern United States. More specific management recommendations require additional research and a more comprehensive analysis of fruit consumption across a broader range of habitats and temperate fruit species.

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