RESEARCH ARTICLE

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Fleshy Fruit Removal and Nutritional Composition of Winter-fruiting Plants: a Comparison of Non-native Invasive and Native Species

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ABSTRACT: Invasive, non-native plants threaten forest ecosystems by reducing native plant species richness and potentially altering ecosystem processes. Seed dispersal is critical for successful invasion and range expansion by non-native plants; dispersal is likely to be enhanced if they can successfully compete with native plants for disperser services. Fruit production by non-native plants during winter (or dormant season), when native fruits and arthropods are scarce, might enhance chances of fruit consumption and seed dispersal by vertebrates. We compared the proportion and rate of fruit removal among five invasive, non-native and two native plant species that retain fruit during winter to test whether non-native fruits are readily removed and their seeds dispersed by vertebrates–even where native fruit is available. We also assessed whether the nutritional content of fruit pulp affects fruit removal rates, and collected bird droppings from fecal traps to examine species and rates of seed dispersal. Most (83% to 93%) fruit was removed from all species except native *Smilax rotundifolia* L. (55%). Most (92%) seeds collected from bird droppings were from non-native plants (six species); only 8% were from native plants (four species). Mean fruit survival time (across species) was positively correlated with total sugar and negatively correlated with lipid. Total fruit consumed was not correlated with nutrient content. Our results indicate most fruits of tested winter-fruiting, non-native invasive plants are removed, and their seeds are dispersed. In the southern Appalachian Mountains, only a few native plant species, notably greenbriar (*Smilax* spp.), American holly (*Ilex opaca* Aiton), and sumac (*Rhus* spp.) retain abundant, ripe fruit during winter months, and these species tend to be patchy in their distribution. Therefore, winter fruit availability by non-native invasive plants offers an important opportunity for dispersal and range expansion, and is likely key in their successful invasion of ecosystems.

Index terms: exotic plant, fruit, invasive plant, non-native plant, nutrition, seed dispersal

INTRODUCTION

Invasive, non-native plant species pose a major threat to the conservation and management of forest ecosystems by reducing native plant species richness and potentially altering ecosystem functions (e.g., Vitousek 1990; Greenberg et al. 2004). In the United States, damage and control costs are estimated at $138 billion annually (Pimentel et al. 2005). Identifying mechanisms of range expansion and successful invasion by non-native plant species is an important step in developing strategies for invasive species control and ecosystem restoration (Knight et al. 2007).

Seed dispersal is critical for successful invasion and range expansion by non-native plants (LaFleur et al. 2007). Vertebrates are important seed dispersal agents for plants that produce fleshy fruits. Birds disperse more seeds than any other vertebrate group (Stiles 2000), including seeds of non-native invasive plants (e.g., White and Stiles 1992; Richardson et al. 2000; Deckers et al. 2008). Fruit preference of birds is affected by both nutritional quality and physical characteristics of fruits, such as size, color, and lipid or sugar content (Gautier-Hion et al. 1985).

The timing and quantity of fruit production may affect consumption rates by vertebrates, and thereby influence the abundance and rate of spread of plant species that produce fleshy fruit (Willson and Whelan 1993; Lonsdale 1999). The range expansion and successful invasion by non-native plant species is likely to be enhanced if they can successfully compete with native plants for disperser services (Sallabanks 1993).

Several studies have shown that native fruits produced in winter are readily consumed by wildlife (McCarty et al. 2002) and can influence the local abundance and distribution of birds (Skeate 1987; Borgmann et al. 2004). White and Stiles (1992) found that absolute fruit use was lower in winter (when less fruit was available) than in fall, but the relative use of non-native species increased to up to half of winter fruit biomass consumed. They suggested that fruits of non-native plant species that are consumed primarily during winter are "missing" a key dispersal opportunity by fall migrant birds. Alternatively, non-native species that produce fruit when native fruit production is low may enhance their chances of consumption and dispersal by birds and mammals (Gosper 2004; Gosper et al. 2005).

Fruit choice by birds is a complex interplay between the nutritional composition of fruit, avian digestive specializations,

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changing nutritional needs, availability of alternative food sources, and seasonal patterns of fruit and frugivore abundance (Levey and Martinez del Rio 2001). Some studies suggest that high-lipid fruits are consumed and dispersed more rapidly than "low quality" (low-lipid) fruits in fall (White and Stiles 1992). Others indicate that frugivores frequently do not discriminate among fruits on the basis of nutritional quality, or that their selection is inconsistent (Borowicz 1988; Fuentes 1994; Whelan and Willson 1994; Jordano 2000). Further, digestive abilities may differ among species (Martinez del Rio and Restrepo 1993; Fuentes 1994). For example, Cedar Waxwings (*Bombycilla cedrorum* Vieillot) specialize in sugary fruits (and may require less dietary protein), whereas thrushes specialize in lipid-rich fruits (Witmer and Van Soest 1998). American Robins (*Turdus migratorius* L.) produce low levels of the enzyme sucrase and, thus, cannot digest high-sucrose fruits (Martinez del Rio and Restrepo 1993). Factors contributing to fruit selection, and particularly selection of co-occurring, non-native versus native fruits, have important implications for seed dispersal rates and geographic spread of non-native, invasive plant species.

In the southern Appalachians, only a few native plant species, notably greenbriar (*Smilax* L. spp.), American holly (*Ilex opaca* Aiton), and sumac (*Rhus* L. spp.) retain abundant, ripe fruit during winter months, and these species tend to be patchy in their distribution (Greenberg et al. 2007). These plants may be critical to winter survival of potential seed dispersers, including birds and mammals. In contrast, several invasive non-native species, including multiflora rose (*Rosa multiflora* Thunb. Ex Murr.), English ivy (*Hedera helix* L.), Chinese privet (*Ligustrum sinense* Lour.), oriental bittersweet (*Celastrus orbiculatus* Thunb.), and Japanese honeysuckle (*Lonicera japonica* Thunb.) produce prolific quantities of fruit that persist well into winter or early spring (Miller 2003). We suggest that fruit availability during winter, when other wildlife food resources such as native fruit (Greenberg et al. 2007) and arthropods (Greenberg and Forrest 2003; Whitehead 2003) are scarce, is an important seed dispersal strategy and a major factor influencing the successful invasion of many non-native plant species.

We compared fruit removal rates between native and non-native plant species that retain fruit in winter to test the hypothesis that non-native fruits are readily removed (and presumably consumed) by vertebrates and the seeds are dispersed, even when native fruit is available. We also hypothesized that (1) fruit removal rates and timing differ among winter fruit-producing plant species, but do not differ between native versus non-native plants; and (2) removal rates correlate with the nutritional content (lipid, sugar, or protein) of fruits. To test these hypotheses we compared the rates, temporal patterns, and proportions of fruit removed by vertebrates among several invasive, non-native plant species and native plant species that retain fruit during late fall and winter months. We also collected bird droppings from fecal traps within our study area, and identified the seeds they contained to assess the relative proportions of native and non-native species they contained. Finally, we analyzed the nutritional content of fruit pulp of native and non-native study species, and assessed whether their average lipid, sugar, or protein content was correlated with rates and patterns of fruit removal by vertebrates.

METHODS

Study Area

Our study was conducted within an approximately 50 km^2 area within the Asheville Basin in Asheville, North Carolina, and included the Bent Creek Experimental Forest, the Biltmore Estate, the North Carolina Arboretum, the University of North Carolina at Asheville campus, and nearby locations. Annual precipitation within the study area averages 800 mm and is evenly distributed year-round. Elevation ranges from 700 to 1070 m. Winters are short and mild, and summers are long and warm. Common tree species include scarlet oak (*Quercus coccinea* Muenchh), chestnut oak (*Q. prinus* L.), black oak (*Q. velutina* Lam.), blackgum (*Nyssa sylvatica* Marshall), sourwood (*Oxydendrum arboretum* (L.) DC), and occasional shortleaf pine (*Pinus echinata* Miller). Tulip poplar (*Liriodendron tulipifera* L.) and northern red oak (*Q. rubra* L.) dominate on moist slopes and coves. Red maple (*Acer rubrum* L.), hickory (*Carya* Nutt. spp.), dogwood (*Cornus florida* L,) and white oak (*Q. alba* L.) are common throughout (McNab 1996).

Fruit Removal Rates

We marked fruits of five species of invasive, non-native plants, *Rosa multiflora*, *Hedera helix*, *Ligustrum sinense*, *Celastrus orbiculatus*, and *Lonicera japonica*, and two species of native plants, *Ilex opaca* and *Smilax rotundifolia* L., that produce fleshy fruit during late fall and retain fruit during winter. Fruiting study plants were located along roadside or agricultural edges where they tended to be most abundant. In most cases, only a subset of our study species co-occurred, and the number of fruiting individuals per study species also varied within any given location; we were unable to find multiple locations where most study species were present. Therefore, although we attempted to maximize the spatial distribution of our individual study plants, we considered study plants as our sampling unit and location (areas $\geq$ 0.7 km apart) as a random variable in our experimental design.

Following the methodology of McCarty et al. (2002), we marked 10 fully developed, unripe fruits widely distributed across each plant. For clonal shrubs (e.g., *R. multiflora*) or multi-stemmed vines (e.g., *C. orbiculatus*), a "plant" was considered a single stem. Fruits were marked with a small, inconspicuous dot (< 1 mm diameter) of paint near the pedicel and another dot on the branch where its pedicel attached. We then cleared leaf litter in an approximately 0.3-m diameter, circular patch beneath marked fruits to facilitate searches for marked fallen fruits.

Fruit marking began in mid-August 2005 and was complete for most species by the first week of October 2005. *Hedera helix* fruits were not fully developed until December, and we completed marking fruits on that species in early January. To reduce bias associated with adding new plants (with 100% of their marked fruit present) over the course of several weeks, we considered 3 to 9 October to be our "start" week for the study (9 to 15 January for *H. helix*). The number of marked fruits that remained on each plant during our "start" week was considered to be the initial number marked (100%) even if some of the originally marked 10 fruits were gone; if < 5 marked fruits remained, we did not include that individual in our analyses. To assure that our comparisons included only those species with peak fruit production during winter, we included in our analyses only species having > 50% unripe fruits during our first sample week (3 to 9 October 2005).

During weekly surveys (October 2005 to April 2006), we counted the number of marked fruits remaining on each plant, and recorded each as unripe, ripe, or damaged. The type of damage (e.g., by insects, animals, rot, microbes, or desiccation) was also recorded. When a fruit was missing, we searched the cleared patch below its former location. If missing fruits were not found within approximately 15 seconds of searching within and near the cleared patch, we assumed that the fruit had been removed by a vertebrate. If the fallen fruit was found, we tossed it to avoid counting the same fallen fruits on return visits. Thus, our estimates of fruit removal are likely conservative since we could not document whether fallen fruits were removed later by vertebrates. Conversely, it is possible that we occasionally missed fallen fruits in our searches and mistakenly considered them as consumed. We also estimated the entire proportion of unripe, ripe, or damaged fruit on each study plant once per month.

Fruit Nutrition

We collected several ripe fruits of each study species from multiple (≥ 12) individual plants within multiple (≥ 5) locations within our study area. Fruits were placed in a plastic bag, labeled (date, location, species), placed on an icepack in a cooler for transport, and stored in a freezer. In the lab we separated seeds and pulp, dried the pulp at 65 °C to a constant mass, and then weighed the sample. For a given species, equal amounts of dry pulp from different individual plants were mixed so that samples for nutritional analyses were composed of fruit pulp of multiple individuals from several locations (> 10 g dry pulp from 216 to 1260 fruits, depending on the species). Nutritional content of fruits was analyzed using Association of Analytical Communities analytic methods (AOAC 1990) by Minnesota Valley Testing Labs (1126 North Front St., New Ulm, MN 560730-1176), and analyses for each species included lipid, soluble carbohydrate (glucose, sucrose, lactose, maltose, fructose, and total sugar), and protein.

Seed Traps for Bird Fecal Droppings

We erected 3 traps at each of 11 study locations (33 traps total) that were designed to capture bird droppings. Traps consisted of 2 perches (wooden dowels) at 2 heights (1.3 and 1.6 m above the ground) fastened to stakes, with a square, screen wire "basket" positioned below the perches to capture fecal droppings. Traps were positioned approximately 10 m from agricultural or woodland edges to reduce accumulation of falling leaves and other debris in the traps and to enhance the likelihood of birds using the perches (as opposed to shrub or tree limbs along the edges) (Holl 2002).

Bird droppings were collected from traps weekly during October 2005 to April 2006. Droppings were scooped individually (or if inseparable, collected together and an estimate of the number of droppings was recorded) into vials, labeled, and stored dry (no alcohol or other preservatives) at room temperature in the lab. Bird droppings were examined to determine fruit and arthropod components and the relative abundance of native versus non-native fruit seeds during fall and winter months. Seeds were identified to species in the lab using an established seed collection in the Bent Creek herbarium, or other seed samples gathered as needed from fruits within our study area.

Statistical Analyses

We used one-way ANOVA to determine whether the total proportion of fruit consumed, fallen, or remaining on the plant differed among species, or between invasive non-native and native plant categories. Post-hoc tests were performed using the Tukey multiple comparison procedure (Zar 1984). Proportion data were square-root arcsine transformed prior to analysis to meet normality assumptions of ANOVA and back-transformed for tabular and graphical presentation. Because only a subset of species, and often few individual plants of any given species as well, occurred within any general area, we considered location (areas ≥ 0.7 km apart) to be a random variable, and considered individual plants to be our sampling unit for all statistical analyses.

Fruit removal rates and rate of disappearance (including consumed and fallen fruit) were estimated using Kaplan-Meier survival estimates (e.g., McCarty et al. 2002) for each species (Lifetest procedure in SAS). Fruits remaining on plants on the last sampling date (censored) were assigned a survival time of one week after the study terminated. Therefore, survival times and standard errors are only estimates for all species. Estimates for most species are acceptable, as there was little censoring; however, survival time estimates for *Smilax* was likely significantly underestimated, as that species had substantial amounts of fruit remaining on the plant at the end of the study.

We used a non-parametric Wilcoxon sign-rank test to determine whether fruit survival time differed among species. We used linear regression to examine the trend between lipid (%), total sugar (g/100 g), and protein (N x 6.25) content of fruit and the mean survival time of each species (each species represented a data point). We also examined the trend between nutrient content and mean total percent of fruit consumed using linear regression. For all statistical analyses, significance was accepted at $P \leq 0.05$.

RESULTS

Patterns of Fruit Availability and Removal

Most fruit on most study species was unripe in September, but > 50% of fruits were ripe by October (when counts of marked fruit began) (Table 1). Exceptions were *H. helix*, which did not develop fruits until November (when 17% were ripe) or December (when 60% were ripe). *Ilex opaca* fruits were fully developed in September (or before), but did not ripen until November (Table 1). Most fruit damage was due to desiccation. The proportion of damaged fruit was low on all species with fruit through November, but increased each month beginning in December. By the end of April, few fruits remained on plants of all non-native species, and 50% to 92% of those were damaged. In contrast, little damage was evident on fruits of both native species with fruit at that time (*I. opaca* and *S. rotundifolia*) (Table 1).

Overall, the proportion of marked fruit removed by vertebrates ($F_{1,189} = 0.79$, $P = 0.3741$) remaining on plants ($F_{1,189} = 2.22$, $P = 0.14$), and falling from plants ($F_{1,189} = 0.85$, $P = 0.36$), did not differ significantly between non-native and native plants (species combined) (Table 2). However, differences among species were apparent. The total proportion of fruit removed was high (> 82% for most species); fewer *S. rotundifolia* fruits (55%) were removed than fruits of other study species ($F_{6,184} = 6.18$, $P < 0.0001$) (Table 2). The proportion of fruit remaining on plants (e.g., not removed or fallen) showed similar trends, with more fruit remaining on *S. rotundifolia* (44%) than on the other species (< 13%) ($F_{6,184} = 10.55$, $P < 0.0001$) (Table 2). The proportion of fruit falling from plants also differed among species ($F_{6,184} = 3.72$; $P = 0.0016$), and was highest for *C. orbiculatus* (9%), lowest for *L. japonica* (1%), and did not differ among the other species (Table 2).

Fruit survival time differed among species (Wilcoxon $\chi^2 = 420.0$, df = 6, $P < 0.0001$) (range 7.3 to 25.4 weeks) (Figure 1). Overall, mean survival time was higher for native plants (20.2 ± 0.4 weeks) than for non-native plants (14.1 ± 0.2 weeks) (Wilcoxon $\chi^2 = 131.8$, df = 1, $P < 0.0001$). Mean fruit survival time before removal by vertebrates differed among tested species (Wilcoxon $\chi^2 = 379.6$, df = 6, $P < 0.0001$) (range 7.3 to 19.6 weeks) (Table 2). Mean survival time until removal of *H. helix* was lower than other species (7.3 ± 0.3 SE weeks), whereas *I. opaca* (18.5 ± 0.3 SE weeks) and *S. rotundifolia* (19.6 ± 0.8 weeks) fruits had relatively longer mean survival times until removal (Table 2). Despite having different survival times, *H. helix* and *I. opaca* fruits were removed rapidly in February and March, whereas fruits of other species were removed at a slower but more consistent rate (Figure 1). Mean survival until removal by vertebrates was higher for native (18.7 ± 0.3 SE weeks) than non-native (13.7 ± 0.2 SE weeks) fruits (Wilcoxon $\chi^2 = 121.8$, df = 1, $P < 0.0001$).

Seeds in Fecal Traps

We collected 497 bird droppings containing 1493 seeds during October 2005 to April 2006. Of 1455 identified seeds, 92.4% were from 6 species of non-native plants, and 7.6% were from 4 species of native plants (Table 3). The majority of seeds were from *C. orbiculatus* (45.4%; minimum 132 fruits), *R. multiflora* (38.1%; minimum 85.2 fruits) and *L. sinense* (8.6%; minimum 125 fruits) (Table 3). Arthropod remains were identified from only 18 (3.6%) bird droppings, although traces of arthropods were observed in several droppings without seeds (pers. observation). The number of droppings collected from fecal traps and the number and species of seeds within the droppings varied among months and species (Figure 2). The number of droppings and seeds collected from fecal traps also varied among locations, with 64% of droppings and 86% of seeds collected from just one of our 11 locations.

Nutritional Content and Survival Time of Fruits

Fruit weight (with seeds and pulp intact) and dry pulp weight were similar among study species (Table 4). However, the average number of seeds per fruit ranged from 1.0 to 6.5 among species (Table 4). Fruits of most analyzed species contained low lipid levels (< 4.8%) with the exception of two invasive non-native species, *H. helix* (27%) and *L. sinense* (11.4%) (Table 4). Total sugar also was similar among species, with *H. helix* having the lowest (14.2 g/100 g) followed by *L. sinense* (22.7 g/100 g) (Table 4). Protein (N x 6.25) content ranged from 4.2% to 9.3% (Table 4). Mean fruit survival time was positively correlated with total sugar (g/100 g) ($F_{1,5} = 7.12$, $P = 0.04$, $r^2 = 0.59$, RMSE = 2.83), negatively correlated with percent lipid ($F_{1,5} = 14.36$, $P = 0.01$, $r^2 = 0.74$, RMSE = 2.24), and not correlated with percent protein ($P = 0.54$) (Figure 3). There was no significant relationship between the mean percent of

Table 1. Mean percentage of unripe/ripe/damaged fruit on study plants (marked + unmarked fruit counts) from September 2005 to April 2006, Asheville, NC.

Species	Status	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Celastrus orbiculatus	Non-native	80/13/7	38/53/9	0/81/19	0/62/38	0/29/71	0/18/83	0/12/88	0/22/78
Hedera helix	Non-native	---	---	83/17/0	40/60/0	0/95/5	0/69/31	0/53/47	0/50/50
Ligustrum sinense	Non-native	92/5/2	46/49/5	7/88/5	0/98/2	0/97/3	0/79/21	0/75/25	0/32/68
Lonicera japonica	Non-native	87/9/4	26/64/10	1/80/19	1/64/36	0/38/62	0/7/93	0/4/96	0/8/92
Rosa multiflora	Non-native	44/50/6	10/82/8	0/87/13	0/76/24	0/69/31	0/49/51	0/46/54	0/38/62
Ilex opaca	Native	97/0/3	94/3/3	1/96/3	0/97/3	0/98/2	0/98/2	0/91/9	0/92/8
Smilax rotundifolia	Native	99/0/1	40/58/2	0/98/2	0/97/3	0/100/0	0/98/2	0/98/2	0/95/5

total fruit consumed and sugar, lipid, or protein content of fruits ($P \geq 0.40$).

DISCUSSION

Our results indicate that non-native plants that produce fleshy fruit during winter have a high likelihood of having their fruits consumed and their seeds dispersed by vertebrates, most likely birds. In our study $\geq$ 82% of fruits of five invasive, non-native plant species were consumed, and high numbers of seeds of three of those species (*C. orbiculatus*, *L. sinense*, and *R. multiflora*) were collected from fecal traps designed to collect droppings from perching birds. Greenberg et al. (2001) also found high removal rates of both *C. orbiculatus* and *I. opaca*.

In the southern Appalachians, very few native plants produce or retain substantial amounts of fruit in winter (Greenberg et al. 2007). We sampled only two native species (*I. opaca* and *S. rotundifolia*) because we were unable to find others (e.g., *Rhus* spp.) in sufficient numbers or with sufficient amounts of fruit within in our study area. Most *I. opaca* fruits and nearly half of *S. rotundifolia* fruits were consumed during the study period, and relatively few seeds of those or other native fruits were collected from fecal traps. We cannot make generalizations regarding removal rates of native versus non-native species as a group. However, it is clear that rates of non-native fruit removal are similar to or greater than rates of native fruit removal.

Because fruits of most native plant species are generally not available during winter, the likelihood of fruit consumption and seed dispersal of non-native plants relative to native plants is high. In the southern Appalachians, winter fruit production by non-native plants results in less competition for animal-mediated dispersal services with native plant species, the majority of which produce fleshy fruit during summer and fall (Greenberg et al. 2007). Fruit availability by some non-native plant species during winter when other wildlife food resources are scarce is likely a key factor in their successful invasion.

The fruit survival curves of most species

Table 2. Mean (± 1 SE) percentage of fruits of select native and invasive non-native plants that were removed by vertebrates, remained on plants, or fell off of plants as of the final sampling date, and mean and median fruit survival time (weeks) of marked fruits counted beginning in October 2005 (or January 2006 for *H. helix*) through April 2006. Different letters among rows within columns indicate significant differences among species, or between native and non-native plants (species combined). Percentage data are presented as actual means, but were square-root arcsine transformed for ANOVAs.

								Survival (wks)		Survival (wks)	
Species	Category	No. plants	No. loctns	No. fruits	Removed	Remained	Fallen	Until Removed	Total	Until Removed	Total
Celastrus orbiculatus	Non-native	39	11	373	88.5±1.9^{A}	2.4±0.8^{A}	9.1±1.8^{A}	15.8±0.5	13.3±0.4	15	15
Hedera helix	Non-native	17	5	166	93.4±2.1^{A}	3.7±1.9^{A}	2.9±1.4^{AB}	7.3±0.3	7.0±0.3	7	7
Ligustrum sinense	Non-native	32	9	272	90.0±2.3^{A}	6.2±2.1^{A}	3.8±1.3^{AB}	13.6±0.5	14.6 0.6	13	12
Lonicera japonica	Non-native	29	10	278	90.3±2.4^{A}	8.3±2.4^{A}	1.4±0.8^{B}	13.5±0.4	14.6±0.5	13	13
Rosa multiflora	Non-native	36	10	333	82.1±3.1^{A}	13.0±2.7^{A}	4.9±1.3^{AB}	14.7±0.4	16.5±0.5	16	15
Ilex opaca	Native	31	7	308	91.2±2.0^{A}	4.6±1.7^{A}	4.2±1.5^{AB}	18.5±0.3	19.1±0.4	19	20
Smilax rotundifolia	Native	7	4	65	54.7±8.5^{B}	43.7±8.6^{B}	1.6±1.6^{B}	19.6±0.8	25.4±1.0	17	28
Non-native	All species	153	16	1422	88.2±1.2	7.0±1.0	4.9±0.7	13.7±0.2	14.1±0.2	13	13
Native	All species	38	7	373	84.5±3.2	11.8±3.2	3.7±1.2	18.7±0.3	20.2±0.4	19	20

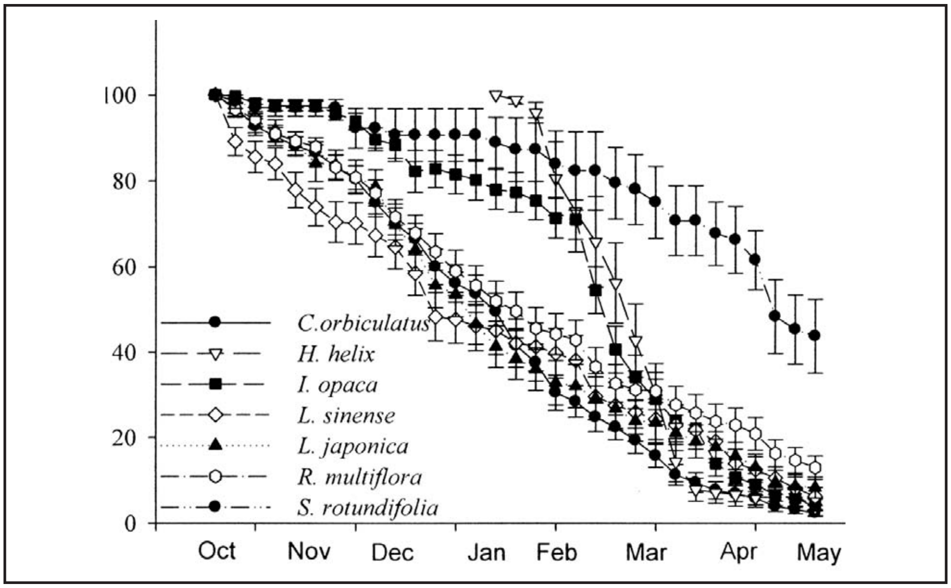

Figure 1. Mean (+ 1 SE) percent of marked fruits remaining on non-native and native plants, October 2005 to April 2006, Asheville, NC.

indicated that they were consumed at a relatively constant rate for the duration of the study. *Smilax rotundifolia* fruits, however, were removed at a much lower rate than most other species. Both *I. opaca* and *H. helix* were removed rapidly, with most removal occurring during February and March. *Ilex opaca* fruits were fully developed by September and mostly ripe by November, but relatively few were taken until mid-February when fruits were removed rapidly. *Hedera helix* fruits generally were not fully developed until late November or December, ripened in December and January, and survived for a very short time thereafter. Overall, these results indicate fruit phenology patterns of some winter-fruiting plants may affect the timing and rate of removal by vertebrates, but do not appear to affect the total amounts of fruit removed.

Seeds collected from fecal traps did not correspond with peak removal periods of marked fruits of any species. For example, *R. multiflora* seeds in fecal traps peaked in December and April, and *C. orbiculatus* seeds peaked in December and March, yet marked fruits of both species showed a relatively constant rate of removal throughout the 7-month study period. In contrast, we found relatively few seeds of *I. opaca* or *H. helix* in fecal traps although most marked fruit of both species was removed during February and March. Relatively fewer seeds of *L. sinense* were found in fecal traps during most months, which corresponded with the relatively constant removal rates of marked fruits. Most droppings and seeds were collected from one of the 11 study locations with fecal traps. This, and the high monthly variation in both the number of bird droppings and seeds in fecal traps, may be due to an erratic use of perches above our fecal traps and, thus, a seed collection that did not correspond with fruit consumption patterns by birds. Further, seed composition in fecal traps could be biased by differences in the diets, behavior, and habitat use of bird species that regularly use isolated perches. Conversely, our results may be indicative of winter bird behavior, where large flocks of birds target specific areas with high abundance of fruit, and birds may be virtually absent from much of the landscape for long periods of time.

The discrepancy between the proportion of fruit removed and the number of seeds collected from bird droppings indicates that fruit removal is not necessarily an accurate indicator of seed dispersal by birds. Mammals also consume fruit during winter and may be important vectors of seed dispersal; our results could be due to a higher consumption of fruits by mammals than we assumed. Fruit and seed size, the number of seeds within different species of fruits, as well as gape size, gut passage time, fruit preference, mobility, and habitat use by fruit-eating birds all may influence the number and distance of seeds dispersed by birds (Jordano 2000). Birds may consume pulp but discard seeds, or regurgitate seeds near the mother plant, limiting the seed

Table 3. Total number and proportion of seeds (by species), and minimum number of fruits consumed (based on mean number of seeds per fruit), identified from droppings collected from fecal traps during October 2005-April 2006 near agricultural and roadside edge, Asheville, NC.

		Seeds			
Species	**Category**	**Total**	**Percent**	**Min Fruits**	**% Fruits**
Celastrus orbiculatus	Non-native	660	45.4	132	36
Eleagnus umbellata	Non-native	1	0.1	1	0.3
Hedera helix	Non-native	3	0.2	1.7	0.5
Ligustrum sinense	Non-native	125	8.6	125	34.1
Lonicera japonica	Non-native	1	0.1	0.2	0.1
Rosa multiflora	Non-native	554	38.1	85.2	23.3
Ilex opaca	Native	5	0.3	1.3	0.4
Phytolacca Native	Native	77	5.3	8.9	2.4
Rhus toxicodendron	Native	1	0.1	1	0
Vitis sp.	Native	28	1.9	10.8	2.9
Total Non-native	All species	1344	92.4	345.1	94.2
Total Native	All species	111	7.6	21.1	5.8

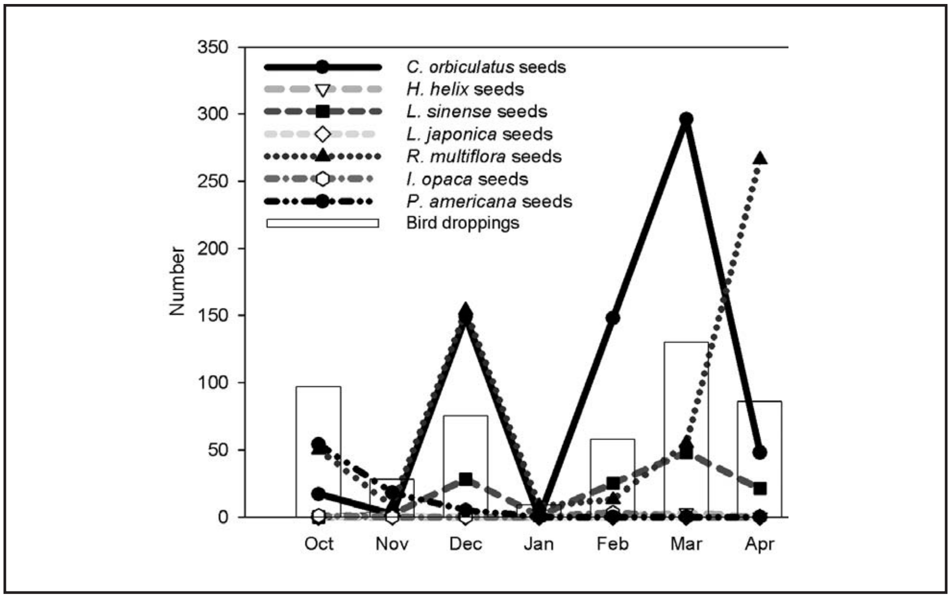

Figure 2. Total number of bird droppings and seeds contained in droppings collected from fecal traps placed in 11 study locations, October 2005 to April 2006, Asheville NC.

dispersal distance (Levey 1987). Similarly, seeds of fruits that are digested rapidly may be defecated close to their source. Fruits of some species may be selected more frequently by specific bird species whose subsequent movement and habitat use influence seed dispersal patterns (Levin et al. 2003; Kwit et al. 2004). We were unable to test seed dispersal distances because we did not track fruit sources or frugivores. Further, some birds or mammals likely destroy seeds during consumption and are, therefore, not effective dispersal agents. Clearly, further study of fruit-frugivore interactions would enhance understanding of seed dispersal dynamics and how rates of range expansion differ among non-native plant species.

We found a strong negative correlation between lipid content of fruit pulp and mean fruit survival time and a positive relationship between total sugar content and mean fruit survival time. These relationships were heavily influenced by rapid removal rates of high-lipid, low-total sugar *H. helix* fruits soon after they were fully developed (February and March). The heavy influence of one species (*H. helix*) on our correlations indicates that these results should be interpreted cautiously.

Ilex opaca fruits were relatively lower in lipid than *H. helix* fruits, and similar in total sugar content to other study species that were removed at a relatively constant rate for the duration of the study period. Yet, in our study, *I. opaca* fruits also were removed rapidly during the same time period as *H. helix* fruits (February and March) despite their being available for several months prior. Witmer (2001) observed the same pattern of guelder rose (*Viburnum opulus* Aiton; a non-native species) fruit consumption by Cedar Waxwings, and demonstrated that waxwings only consumed *V. opulus* fruits when eastern cottonwood (*Populus deltoides* Marshall) catkins were simultaneously available and intermittently consumed (in the spring), in order to maintain a positive protein balance. This was due to the low protein content and high levels of secondary compounds within *V. opulus* fruits that made them acidic, but were buffered by the high protein pollen within *P. deltoides* catkins. Thus, reasons for differences in temporal patterns and rates of removal of different fruits and among different species of birds may be more complex than simple fruit availability or ripening patterns (Levey and Martinez del Rio 2001; Witmer 2001).

These two distinct temporal patterns of removal rates–rapid removal within a 6-week period vs. relatively constant removal over a 7-month period–suggests that flocks of birds targeted *I. opaca* and *H. helix* during a relatively short time period, whereas other species were removed occasionally and at a relatively constant rate by individual birds or mammals. These patterns are corroborated by our observations of *H. helix* fruits being consumed by large flocks of American Robins and *I. opaca* fruits being consumed by flocks of both American Robins and Cedar Waxwings (also see Witmer 1996).

CONCLUSIONS

Our results indicate most fruits of tested winter-fruiting, non-native invasive plants are removed, and their seeds are dispersed. Despite distinct differences in the temporal patterns of fruit removal among both native and non-native species, the total proportion of fruit removed was very high for nearly all study species. Generally, fruit nutritional characteristics did not affect fruit choice or modify removal rates based on abundance, with the possible exception of high-lipid, low-sugar *H. helix* fruits, which were removed rapidly after ripening. Clearly, non-native plant species that retain abundant fruit during winter, when fruits of native plants and other food resources are scarce, capture an important opportunity for dispersal and range expansion that is likely key in their successful invasion of ecosystems.

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Table 4. Sample size, nutritional content of fruit pulp, and individual fruit characteristics of invasive, non-native, and native plant species1 collected from western North Carolina.

	Invasive Non-native Species					Native Species	
	CELORB	**HEDHEL**	**LIGSIN**	**LONJAP**	**ROSMUL**	**ILEOPA**	**SMIROT**
Fruit Samples for Nutrient Analyses							
No. locations	7	5	5	6	5	5	5
No. plants	21	17	20	12	18	21	16
No. fruits	642	255	1260	648	360	252	493
Total dry pulp weight (g)	10.9	11.2	10.6	11.1	11.1	10.3	11.3
Nutrients							
Lipid (%)	4.3	27	11.4	4.8	1.7	3.1	3.3
Total sugar (g/100g)	34.7	14.2	22.7	26.7	30.3	32.3	26.6
Glucose (g/100g)	12.2	6.2	11.8	11.1	13.3	14.8	12.6
Sucrose (g/100g)	7.1	<0.2	0.3	5.9	<0.2	<0.2	<0.2
Lactose (g/100g)	<0.2	<0.2	<0.2	<0.2	<0.2	<0.2	<0.2
Maltose (g/100g)	0.2	0.4	<0.2	0.3	<0.2	0.3	0.6
Fructose (g/100g)	15.2	7.6	10.6	9.4	17	17.2	13.4
Protein (N x 6.25)	9.3	7.7	6.1	7.4	7.8	4.2	7.4
Individual Fruit Characteristics							
Wet weight (g) (mean±SE)	0.18±0.01	0.24±0.01	0.07±0.00	0.15±0.02	0.13± 0.00	0.26±0.00	0.14±0.01
Dry pulp weight (g) (mean±SE)	0.02±0.00	0.04±0.00	0.01±0.00	0.02±0.00	0.03±0.00	0.05±0.00	0.02±0.00
Number of seeds per fruit (mean±SE)	5.0±0.2	1.8±0.2	1.0±0.0	4.3±0.8	6.5±0.6	4.0±0.0	1.7±0.2

*CELORB = *C. orbiculatus* ; HEDHEL = *H. helix* ; LIGSIN = *L. sinense* ; LONJAP = *L. japonica* ; ROSUML = *R. multiflora* ; ILEOPA = *I. opaca;* SMIROT = S. rotundifolia

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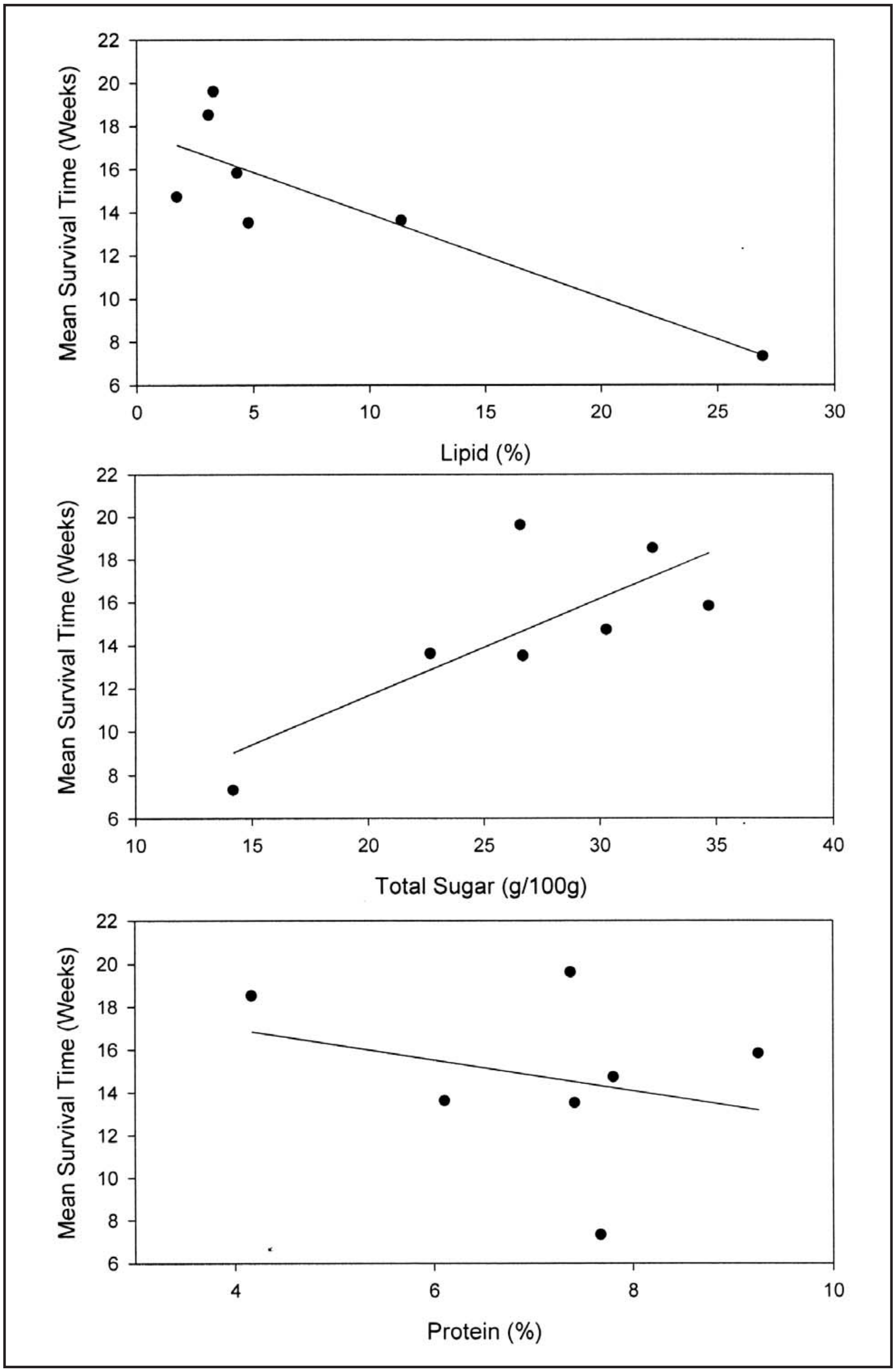

Figure 3. Relationship between lipid (%), total sugar (g/100g), and protein (N x 6.25) content of fruit pulp and mean survival time of marked fruits on 5 non-native and 2 native species of plants that retain fruit in winter.

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