The Selection of Native and Invasive Plants by Frugivorous Birds in Maine

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Abstract - Frugivores and fruit-producing plants often have a mutualistic relationship in which plants provide animals with nutritious fleshy pulp in return for the dispersal of seeds within the fruit. Although the selection and dispersal of invasive plant species by birds has major implications for native animals, plants, and communities, few studies have focused on whether birds select invasive versus native fruits. I compared fruit removal and fruit choice by birds, and fruit energy content of two invasive plant species, *Lonicera tatarica* and *Rosa multiflora*, and two native plant species, *Cornus amomum* and *Viburnum opulus*, in central Maine. Frugivores preferentially consumed fruit from *L. tatarica* and *C. amomum*, and they did not discriminate between *R. multiflora* and *V. opulus* during choice trials. Although the two native plant species had significantly higher caloric content than the two invasive species, higher energy density of native plants was not directly correlated with more rapid fruit removal or fruit preference.

Introduction

Plants that produce fleshy fruits depend on mutualistic relationships with frugivorous animals for seed dispersal (e.g., Howe 1977, 1984; Snow 1971; Thompson and Willson 1979). Fruit provides an important food source for many birds and mammals, and consumption of fruit often serves to disperse the plant's propagules far from the parent plant. Frugivores consume both native and invasive fruit and therefore may facilitate the rapid spread of fruiting invasive species (e.g., Lavorel et al. 1999, Richardson et al. 2000, Simberloff and Von Holle 1999). Birds are particularly efficient dispersers of invasive fruit because they are mobile and tend to move between similar habitats; therefore, birds can spread seeds faster and farther than dispersal from physical vectors (Moody and Mack 1988) and seeds are likely to be deposited in favorable habitats (Schiffman 1997). Nearly half of Cronk and Fuller's (1995) list of representative invasive plants are spread by animals (Richardson et al. 2000), and many of the most aggressive invasive species in Maine produce bird-disseminated fleshy fruit (Maine Department of Conservation 1999).

Fruiting plants in the north temperate zone exhibit four major patterns of fruit production and seed dispersal: summer large-seeded fruit, summer small-seeded fruit, fall high-quality fruit, and fall low-quality fruit (Stiles 1980). Plants that produce fruit during the summer attract

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both mammals and summer resident birds, and typically have very small or very large seeds to reduce seed predation by mammals. Fall high-quality fruit ripens during fall migration of birds when abundance of avian dispersers is high. Such fruits have a high energy content and are highly palatable to birds (Stiles 1980, White and Stiles 1992), but their abundant nutrients and lack of secondary compounds cause such fruit to rot quickly (Herrera 1982, Janzen 1977). In contrast, fall low-quality fruit has fewer nutrients and more secondary compounds, so they are less palatable to frugivores (Cipollini and Levey 1997, Herrera 1982, Jones and Wheelwright 1987, Stiles 1980) and more resistant to damage from microbes and invertebrates; hence,they persist longer than other fruit (Herrera 1982, Janzen 1977). Frugivores avoid these low-quality fruits in the fall when other high-quality, palatable fruit is prevalent, and eat low-quality, persistent fruit during winter when other fruit is gone (Jones and Wheelwright 1987, Stiles 1980).

The introduction of invasive fruiting plants can provide important food for birds in some temperate regions (Baird 1980, Ingold and Craycraft 1983, McDonnell and Stiles 1983, Stapanian 1982). White and Stiles (1992) suggest that fleshy fruits provided by invasive plants may affect migration, range, and survival of frugivorous birds. For example, avail-ability of fruit from invasive plants during winter has changed the winter range of the Northern Mockingbird (*Mimus polyglottos* (L.)) in the north-eastern United States (Stiles 1982). Distribution and abundance of inva-sive fruiting plants can therefore alter patterns of frugivory (Simberloff and Von Holle 1999).

The selection and dispersal of invasive plant species by birds there-fore has major implications for native animals, plants, and communities. However, little is known about whether birds select native fruits over invasive fruits in a plant community. To better understand the dynamics of invasive and native fruit selection by frugivorous birds, I compared fruit removal and fruit choice by birds, and fruit quality of two invasive species, *Lonicera tatarica* L. (Tatarian honeysuckle) and *Rosa multi-flora* Thunb. ex Murr. (multiflora rose), and two native species, *Cornus amomum* P. Mill. (silky dogwood) and *Viburnum opulus* L. (highbush cranberry), in central Maine. I predicted that frugivores would prefer the invasive species (*L. tatarica* and *R. multiflora*) over the native species (*C. amomum* and *V. opulus*) as indicated by faster rates of fruit removal and greater selection by frugivores in choice trials.

Methods

Study species and sites

I studied two invasive species, *L. tatarica* and *R. multiflora*, that are both among the most aggressive invasive species in Maine (Maine

Department of Conservation 1999). Both species originate from Eurasia; *L. tatarica* was introduced primarily for ornamental use (Nyboer 1992) and *R. multiflora* for wildlife cover and food (Szafoni 1991). *Lonicera tatarica* and *R. multiflora* threaten native habitats because they grow quickly to form dense, impenetrable mats that shade or smother competitors (Nyboer 1992, Szafoni 1991). Both have red fruit that is dispersed by birds and mammals (Nyboer 1992, Szafoni 1991, Vellend 2002, Williams 1999,). The two native species, *C. amomum* and *V. opulus,* are also dispersed by animals (Borowicz and Stephenson 1985, Jones and Wheelwright 1987, Martin et al. 1968). *Cornus amomum* produces pale to dark blue fruit (Borowicz and Stephenson 1985) and *V. opulus* has clusters of bright red fruit (Jones and Wheelwright 1987).

The fruit removal study was conducted at three sites in Kennebec County, ME, where the four plant species occur together: the Perkins Arboretum at Colby College in Waterville, the Oxbow Nature Trail on the Messalonskee Stream in Waterville, and the Pine Tree State Arboretum in Augusta. All three sites are primarily mixed deciduous and coniferous forests. The fruit choice experiment was conducted at four stations in the Perkins Arboretum.

Fruit removal

I estimated the rate of fruit removal from individual *C. amomum, L. tatarica, R. multiflora,* and *V. opulus* plants by recording the number of fruits on one netted and one unnetted branch on each plant each week from 19 September 2002 to 24 February 2003, excluding seven weeks during December 2002 and January 2003 (Table 1). Two branches on each plant were randomly selected and one branch was labeled with plastic ribbon while the other branch was labeled and enclosed with bird netting to exclude frugivores and provide a control for fruit loss from disease or abiotic factors. As an index of frugivore impact, I divided the proportion of fruits remaining on unnetted branches by that on netted branches. I calculated the arcsine transformed proportion of fruits remaining each week and then analyzed trends over time using repeated measures ANOVA.

Table 1. Number of plants monitored during weekly fruit counts between 19 September 2002 and 24 February 2003 at three sites: Perkins Arboretum at Colby College in Waterville, ME; Oxbow Nature Trail in Waterville, ME; and Pine Tree State Arboretum in Augusta, ME.

Species	Perkins	Oxbow	Pine Tree	Total
Cornus amomum	10	12	0	22
Lonicera tatarica	6	12	14	32
Rosa multiflora	7	12	0	19
Viburnum opulus	5	0	7	12

I used video and digital cameras to document the identity of nocturnal and diurnal frugivores, and the rate of fruit removal at night versus the day. I haphazardly chose one plant from each species at each site and video cameras recorded three hours of frugivore activity at each chosen plant. In addition, I haphazardly chose two plants of each species at the Perkins Arboretum, two plants of each species at the Oxbow Nature Trail, and one plant of each species at the Pine Tree State Arboretum. Digital pictures were taken at dawn and dusk at each chosen plant and removal rates were estimated by counting number of fruits in each picture. I calculated the arcsine transformed percentage of fruits remaining for each plant species at each location and then used one-way ANOVA to determine if fruit removal differed by plant species.

Fruit choice

To determine bird choice of fruits, I placed equal amounts of fruit from the four plant species on four 56- x 56-cm platform feeders erected one meter off the ground. Fresh fruits were collected, removed from branches, and displayed in equal number and random positions on feeders for one-hour trials. During the trial, I recorded the number and species of frugivores choosing each fruit. Frugivores did not visit the platform feeders until February, when only fruit from *R. multiflora* and *V. opulus* remained available. Thus, I report fruit choice for only these two plant species. Fruit choice by frugivores was calculated as the number of fruits removed from one plant species divided by the total number of fruits removed during a trial. Proportions were arcsine-transformed and differences in fruit choice were analyzed using one-way ANOVA.

Fruit quality

Bomb calorimetry was used to determine total caloric content per gram of dried fruit (Shoemaker et al. 1981). Fruits from each species were dried in a drying oven at 75 °C for one day. Dried fruit was then pelleted with a hydraulic press at four metric tons of pressure. Fruit pellets were incinerated in an adiabatic jacket bomb calorimeter (20 atm. oxygen) with an iron fuse wire. Solid benzoic acid was used as a standard to calculate the heat capacity of the system. Bomb calorimetry was repeated on each fruit species until values were within 5% (Shoemaker et al. 1981). Internal energies of combustion per gram of dry weight were square root-transformed and analyzed using a posthoc multiple comparisons test in ANOVA.

Results

Fruit removal

All netted fruit of *L. tatarica* and *C. amomum* had rotted by November 21, whereas netted fruit of *R. multiflora* and *V. opulus* persisted

through the end of the study in late February ($F_{3,71} = 46.251$, $P < 0.0001$; Figs. 1, 2). Netted branches had significantly more total fruit remaining than unnetted branches throughout the study ($F_{1,139} = 6.619$, $P = 0.0111$). Fruit removal on unnetted and netted branches was significantly differ-ent within the first month for *C. amomum* ($F_{1,42} = 5.454$, $P = 0.0244$) and
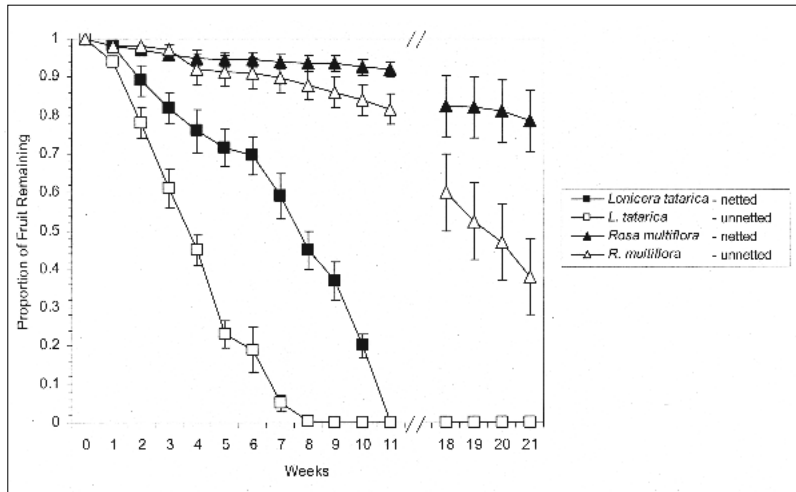

Figure 1. Proportion of fruit remaining (mean ± SE) on unnetted and netted branches during fall and winter (Week 0 is 19–26 Sept. 2002) for two invasive plant species, *Lonicera tatarica* and *Rosa multiflora*.
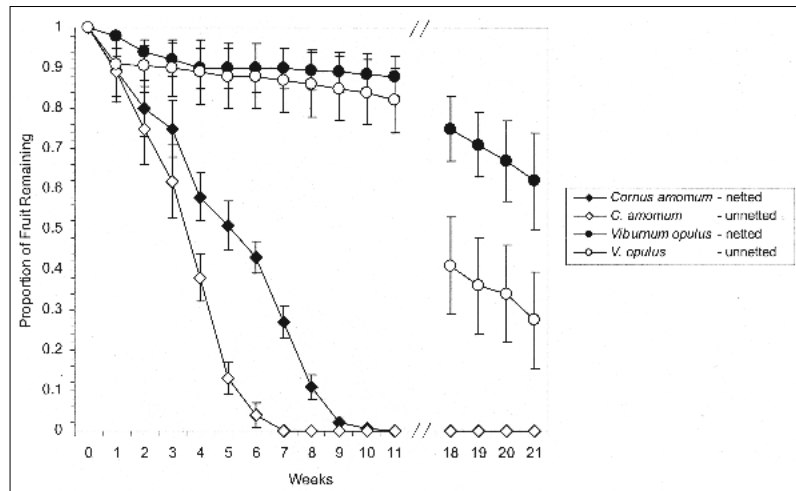

Figure 2. Proportion of fruit remaining (mean ± SE) on unnetted and netted branches during fall and winter (Week 0 is 19–26 Sept. 2002) for two native plant species, *Cornus amomum* and *Viburnum opulus*.

L. tatarica ($F_{1,50}$ = 4.379, P = 0.0415). Proportion of fruit remaining on unnetted and netted branches of *R. multiflora* and *V. opulus* did not differ until the final four weeks in February, when netted branches had significantly more fruit remaining than unnetted branches (*R. multiflora*, $F_{1,24}$ = 11.549, P = 0.0024; *V. opulus*, $F_{1,17}$ = 4.589, P = 0.0469).
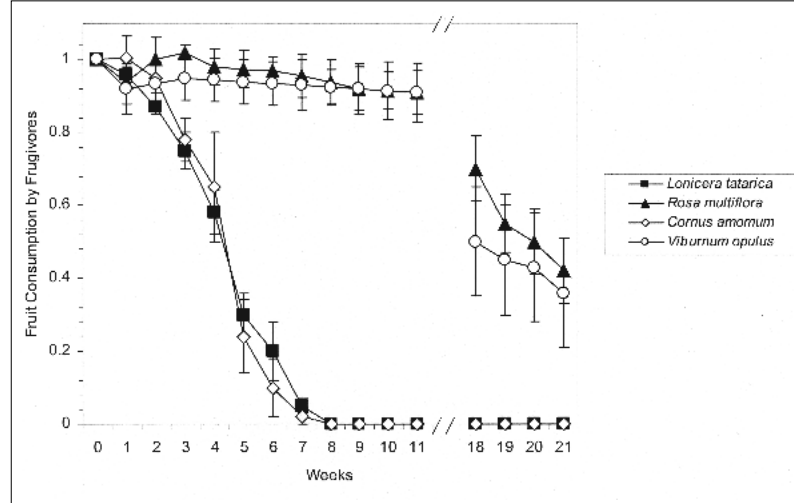

Figure 3. Fruit consumption by frugivores during fall and winter (week 0 is 19–26 Sept. 2002) for two invasive plant species, *Lonicera tatarica* and *Rosa multiflora* and two native plant species, *Cornus amomum* and *Viburnum opulus*. Fruit consumption was estimated each week by dividing the proportion of fruits remaining (mean ± SE) on unnetted branches by that of respective netted branches.

Table 2. Number and percent of diurnal visits by bird and mammal frugivores to four plant species in Maine during November and December 2002 as documented by videotape sampling at twelve plants (3 per plant species).

Plant species	Mammals		Birds	
	Visits	Percent of total	Visits	Percent of total
Cornus amomum	0	0.0	6	10.0
Lonicera tatarica	1	14.3	6	85.7
Rosa multiflora	0	0.0	0	0.0
Viburnum opulus	0	0.0	0	0.0

Table 3. Energy density (mean ± SE, n = 2) of four species of dried fruit collected during fall in Maine. Energy densities with different letters are significantly different (P < 0.05) based on a posthoc multiple comparisons test.

Plant species	Internal heat/gram (kJ/g dry)
Cornus amomum	19.986 ± 0.193 A
Lonicera tatarica	17.811 ± 0.070 B
Rosa multiflora	15.814 ± 0.302 C
Viburnum opulus	19.475 ± 0.204 A

Rate of fruit removal from netted and unnetted branches did not differ between invasive and native fruiting plants ($F_{1,61} = 0.062$, $P = 0.8040$) (Figs. 1 and 2).

Frugivores removed fruits from *L. tatarica* and *C. amomum* early in the fall, whereas frugivores did not remove fruits of *R. multiflora* and *V. opulus* until February ($F_{2,64} = 78.087$, $P < 0.0001$; Fig. 3). Frugivore consumption was not significantly different between *L. tatarica* and *C. amomum* ($F_{1,40} = 0.990$, $P = 0.3258$), or between *R. multiflora* and *V. opulus* ($F_{1,25} = 0.123$, $P = 0.7283$). There was no significant effect of site on fruit removal ($F_{2,60} = 0.033$, $P = 0.9680$).

I observed a total of 13 visits by frugivores to focal plants during thirty-six hours of diurnal videotape recording at three plants from each of the four plant species (Table 2). Cedar Waxwings (*Bombycilla cedrorum* Vieillot) and an eastern gray squirrel (*Sciurus carolinensis* Gmelin) were the only species of bird and mammal observed visiting the focal plants. Cedar Waxwings only visited *L. tatarica* and *C. amomum* plants while one eastern gray squirrel visited a *L. tatarica* plant (Table 2).

Fruit removal at night was estimated by counting fruits from 20 focal plants on digital pictures taken at dusk and the following dawn. Fruit was removed at night from only *L. tatarica* and *C. amomum* plants. Proportion of fruit removed at night from the five focal plants of each species was low (1.54% for *L. tatarica,* 1.11% for *C. amomum*, 0.00% for *V. opulus* and *R. multiflora*) and not significantly different between plant species ($F_{3,16} = 0.684$, $P = 0.5750$).

Fruit choice

When fruits of *V. opulus* and *R. multiflora* were placed on platform feeders for one hour trials during February 2003 (n = 4), the feeders were visited by Cedar Waxwings, ranging from 1 to 15 birds at a time, and one American Robin (*Turdus migratorius* L.), for a total of 19.3 minutes. Birds ate similar proportions of *R. multiflora* and *V. opulus* during these choice trials (mean ± SE: 0.539 ± 0.206 for *V. opulus* and 0.211 ± 0.122 for *R. multiflora*; $F_{1,6} = 0.819$, $P = 0.4003$).

Fruit quality

Energy density of the two native plant species, *C. amomum* and *V. opulus*, was higher than that for the two invasive plant species, *L. tatarica* and then *R. multiflora* ($F_{3,4} = 81.182$, $P = 0.0005$; Table 3).

Discussion

Fruit preferences of frugivores in Maine during fall and winter

Frugivores in this study preferentially consumed fruit from two of the four focal plant species, the invasive *L. tatarica* and the native *C.*

amomum (Fig. 3). Additionally, frugivores did not discriminate between the invasive *R. multiflora* and the native *V. opulus* during choice trials (Table 2). Thus, although the two native plant species had significantly higher caloric content than the two invasive species, higher energy density of native plants was not directly correlated with more rapid fruit removal or fruit preference.

Frugivores quickly removed fruit of *L. tatarica* and *C. amomum* early in the fall, which is typical of high-quality fall-fruiting plants (Stiles 1980), although White (1989) and White and Stiles (1992) classified these two fruits as low-quality because of their low energy and lipid concentration. Frugivores did not consume the persistent winter fruits of *R. multiflora* and *V. opulus* until late winter, which is consistent with the results from other studies (Stiles 1980, Thompson and Willson 1979, Witmer 2001). Fruits of *V. opulus* may persist until late-winter because they contain secondary compounds that make the fruit unpalatable (Jones and Wheelwright 1987, Sorensen 1981, Witmer 2001, Witmer and Van Soest 1998). These fruits are energy rich (Table 3; Witmer 2001) yet persistent, which is contrary to the general hypothesis that persistent fruit must be low in nutrients (Stiles 1980). In contrast, fruit of *R. multiflora* may persist until late-winter because they contain low nutrients (Table 3; White 1989) which may protect the fruit against microbial damage (Janzen 1977) and discourage consumption by frugivores. However, Williams (1999) found no evidence that small mammals avoided eating *R. multiflora* because of secondary compounds in the fruit. Frugivores may eat some fruits only after other more preferred foods are scarce (Williams 1999), and given that secondary metabolites may affect frugivores in different ways, (Cipollini and Levey 1997), the role of secondary compounds in the persistence of *R. multiflora* fruit cannot be completely rejected.

This apparent discrepancy between removal rate and fruit quality of *V. opulus* and *L. tatarica* as predicted by Stiles' (1980) fruiting strategy theory suggests either that nutrient content of fruits may not primarily determine fruit selection (Johnson et al. 1985, Jones and Wheelwright 1987, Sallabanks 1992, Sorensen 1981) or that the quality of fruit depends on the digestive capabilities and nutritional requirements of individual frugivores. I used total energy content of fruit as an index of fruit quality, yet because carbohydrates, lipids, and proteins vary among plant species and because frugivores use these nutrients to varying degrees (Stiles 1980), overall energy content may not be an accurate measure of total fruit quality. Lipid concentration has been used as an index of fruit quality (Stiles 1980,

White and Stiles 1992) because fat produces more energy than carbo-hydrates and is therefore potentially more important to migratory birds (Stiles 1980). However, high-lipid fruits are not always re-moved faster than those with less fat (Borowicz and Stephenson 1985, Witmer and Van Soest 1998). Additionally, given that different species of frugivores differ in their nutritional needs and fruit prefer-ences (Witmer and Van Soest 1998), the same fruit may not satisfy the nutritional requirements of all frugivores.

Consequences of frugivory for native vs. invasive plants

In Maine, invasive plant species with persistent winter fruit are likely to have a significant impact on native frugivory because of the limited number of species of plants and birds there. Persistent winter fruit in Maine is consumed primarily by just two bird species, Cedar Waxwings and American Robins. Although specialized interactions between frugivores and plants are rare (Wheelwright 1988), the rela-tionship between Cedar Waxwings and *V. opulus* appears to be an exception (Witmer and Van Soest 1998). Waxwings preferentially select high-sugar fruits (Witmer 1996, Witmer and Van Soest 1998) and during the winter, the sugary fruit of *V. opulus* provides an im-portant food source for waxwings, while the plants depend almost solely on waxwings for dispersal (Witmer 2001). Witmer (2001) con-cluded that by supplementing their diet with protein-rich catkins from trees, Cedar Waxwings engaged in an unusually restricted mutualistic relationship with *V. opulus*. Such a mutualistic relationship might suggest that invasive plants would be unsuccessful in competing for frugivores. However, I found that Cedar Waxwings did not distin-guish between *R. multiflora* and *V. opulus* during choice experiments, and the removal pattern of *R. multiflora* was equivalent to that of *V. opulus*. This result suggests that increased abundance of *R. multiflora* could dramatically disrupt the mutualistic relationship between Cedar Waxwings and *V. opulus*, with potentially severe impacts on the win-ter diet of waxwings and the dispersal success of *V. opulus*. In gen-eral, we have limited ability to predict the role exotic plants will play in the mutualistic relationship between fruiting plants and frugivores. However, knowledge of fruiting strategies is an important tool in understanding the effects invasive species may have on a native com-munity. Further research on the selection and dispersal of native and invasive plants by birds, including the influences of fruiting strate-gies, is encouraged.

Acknowledgments

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