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Anthony C. Cullen · **Kathleen E. Farley** · **Susan Smith Pagano** · **Frank J. Gallagher** · **Claus Holzapfel**

Abstract The functional role that invasive species occupy within their new range is of significant interest for those concerned about invasive species management. Of particular importance is the distribution mechanisms of invasive plants. *Viburnum dilatatum* and *Viburnum sieboldii* are considered invasive species in New Jersey forest understories. We have observed that while the fruit of both species ripens at the same time, there is a difference in how long fruit persists. To better understand the temporal pattern, we examine fruit phenology and consumption, as well as energy density, percentage crude fat, and antioxidant capacity. We hypothesized that the difference in the timing of fruit consumption in these species is largely driven by nutritional content and that fruit with higher energy and fat content are eaten during migration. Our results indicate that *V. sieboldii* fruit is depleted in the fall, while *V. dilatatum* fruit persists into winter. In addition, we found that *V. sieboldii* fruit had higher energy density and 4.4 times as much crude fat compared to that of *V. dilatatum* fruit. However, *V. dilatatum* fruit had 9.5 times greater antioxidant capacity than *V. sieboldii* fruit. We also found that *V. sieboldii* fruit is mainly consumed by gray catbirds (*Dumetella carolinensis*) during the fall migration and the primary avian consumer of *V. dilatatum* fruit are American robins (*Turdus migratorius*) in the winter when birds are more sedentary. We suspect a mutualistic relationship has developed between these two invasive viburnum species and native avian frugivores. What remains to be seen is what effect different fruiting strategies have on seed dispersal.

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Introduction

The invasive potential of non-native species concerns functional ecologists who examined both ecological and economic impacts (Mooney et al. 2005). While preventing non-native species from entering new areas is the most effective containment strategy, many non-native species have been introduced and become invasive after reaching some threshold level in population density or range (Pyšek and Richardson 2010). For non-native plant species, the need to understand seed adaptation for dispersal mechanisms and potential distribution vectors have been thoroughly established (Davies and Sheley 2007). One potential distribution vector is the mutualism between invasive plants and native birds in a new community (Traveset and Richardson 2014).

The mutualistic relationship that exists between frugivorous birds and fruiting plants has been well-documented (Bascompte and Jordano 2007; Dehling et al. 2014; Vander Wall and Moore 2016). For instance, birds in temperate latitudes consume autumn fruit for energy needed to migrate to wintering grounds while winter resident species consume fruits to survive; in both cases, plants benefit because they are able to spread their seed (Stiles 1980; Willson and Traveset 2000; Bairlein 2002; Kwit et al. 2004). Often bird-dispersed seeds have the advantage of spreading locally to potentially suitable habitats away from the parent plant. In some cases, seeds are dispersed over long distances (Nathan et al. 2008; Viana et al. 2013, 2016a, b; Kalwij et al. 2019). The implications of spread and colonization of new habitats potentially leads to changes in community composition over time, particularly when invasive plant species are introduced (Howe and Smallwood 1982; Traveset and Richardson 2014). This is problematic because invasive plants can decrease biodiversity and change ecosystem functioning (Ehrenfeld 2010; Vilà et al. 2011; Pyšek et al. 2012).

Work done by Smith et al. (2007, 2013), Greenberg and Walter (2010), Bolser et al. (2013), and Alan et al. (2013) demonstrates that birds select fruit based on nutritional traits like high lipid content, energy density, and antioxidant capacity. Fruits with these traits can be predictive of which species' fruit is consumed first, while avian phenology dictates which bird species are present when the fruit ripens (Thompson and Willson 1979; Noma and Yumoto 1997;

Vergara-Tabares et al. 2016; González-Varo et al. 2019). Therefore, it follows that fruit functional traits (nutrition and phenology) influence which bird species disperse the seeds and the timing of seed dispersal. Ultimately, this informs how far those seeds are likely to be dispersed. Investment in fruit nutrition becomes a strategy that influences whether there is an opportunity for long-distance seed dispersal or local dispersal.

Within northern New Jersey, two congener invasive species, *Viburnum dilatatum* and *Viburnum sieboldii,* impact understory forest communities. Little is known about the value of their fruit and how it may influence the mechanisms of dispersal, contributing to their invasion of the Mid-Atlantic region. However, we have observed that while both species' fruit ripen at the same time there is a difference in how long fruit persisted on each species. Here, we will explore how the relationship between phenology and consumption is driven by fruit nutrition. Although both species' fruit ripens in fall, we hypothesize that the difference in timing of fruit consumption between *V. sieboldii* and *V. dilatatum* is due to nutritional content differences. To address our hypothesis, we combined quantitative analysis of fruit nutrition with a frugivore exclusion experiment to shed light on fruit removal timing and assessed frugivory through foraging observations and game cameras.

Methods

Study sites

Lewis Morris County Park (main entrance: 40° 47.50′ N, 74° 31.93′ W) and adjacent Fosterfields Living Historical Farm (entrance: 40° 48.18′ N, 74° 30.27′ W) located in Morristown, in Morris County, New Jersey, USA were selected for this study. Lewis Morris County Park occupies 888 ha of forested uplands ranging in elevation from 110 to 200 m.a.s.l. Fosterfields Living Historical Farm occupies over 86 ha of a mix between forested uplands, and preserved pastoral and agricultural lands ranging in elevation from 120 to 200 m.a.s.l. The upland forests in the Morristown area consists of two forest types: a mature broadleaf forest and a young broadleaf forest. The mature broadleaf forest has been undisturbed since it was logged in the late 1700s and is composed of oak-beech-hickory. The

other is a young broadleaf forest consisting of tulip poplar-maple-birch that has been established over the past 100 years after agriculture ceased in the early 1900s (Ehrenfeld 1982, 1999). The soils are primarily well-drained, rocky Parker-Gladstone soil series (Ehrenfeld 1999; Soil Survey Staff 2020). Both sites are representative of the heavily invaded northeastern US temperate forest understories common in northern New Jersey. Lewis Morris County Park has naturalized populations of *V. sieboldii* and *V. dilatatum* that overlap in some areas of the park. Fosterfields Living Historical Farm only has populations of *V. sieboldii*.

Species natural history and morphology

Both species were brought over to the USA from their native range in East Asia as ornamental specimens in the mid to late 1800s: *V. dilatatum* from China, the Korean Peninsula, and Japan, and *V. sieboldii* from Japan. They were valued because of their showy white flowers, attractive fruit, as well as their adaptability to a wide range of climatic and soil conditions (Rehder 1927; Dirr 1990). For the last 40 years, naturalized populations of both species have been reported in the Northeast and some Midwest States in the USA. Currently, *V. dilatatum* is found in eight states, and *V. sieboldii* is found in thirteen states according to the Early Detection and Distribution Mapping System (EDDMapS) national distribution map from the University of Georgia's Center for Invasive Species and Ecosystem Health (Early Detection and Distribution Mapping System 2020a, b).

Both are understory species; however, they differ in growth form. *V. dilatatum* is a multi-stemmed shrub that can reach three meters in height and two meters in canopy width when fully mature with fruit that is red when fully ripe. *Viburnum sieboldii* is generally a single-trunked, subcanopy tree that can reach six meters in height and 4.5 m in canopy width when fully mature and the fruit is dark purple when fully ripe (Dirr 1990).

Frugivore exclusion experiment

To understand the timing of fruit loss and to quantify whether that loss was due to consumption or abscission, infructescences on shrubs were experimentally manipulated with two treatment types (enclosed or unenclosed) using methods modified from Smith et al.

(2007, 2013). Fifteen shrubs per species were selected, and two infructescences on each shrub with similar numbers of fruit per cyme were chosen. Both cymes were marked with different colored chenille stems (pipe cleaners) to indicate treatment: the unenclosed treatment remained unaltered, while the enclosed treatment was covered by a 15×23 cm white organza bag (mesh size = 1 mm) to prevent feeding. This experiment was conducted from August 5, 2016 to February 27, 2017 at Lewis Morris County Park. The number of fruits per cyme was counted weekly during this time to account for changes for each treatment for all shrubs. The initial number of fruit per treatment type ($n = 2$) per shrub ($n = 15$) for each species ($n = 2$) was used to calculate the average and standard error for the number of fruit per cyme for both species.

To determine weekly fruit loss per treatment, the total number of fruit was summed across all shrubs ($n = 15$) for every week of the frugivore exclusion experiment. However, because the total number of fruit was not equal among treatments and across species, the fruit loss was converted into a weekly relative percent. The total number of fruit remaining from the current week was divided by the total number of fruit from the previous week, then that percent was subtracted from one to get the relative percent difference of fruit loss per treatment per week. To further explore the relationships between consumption versus abscission, we calculated the estimated weekly relative percent consumption by determining the difference between weekly relative percent of fruit loss from the enclosed treatments and unenclosed treatments. Within the enclosed treatment we presume fruit loss is from abscission while in the enclosed treatment, we presume fruit loss is from both abscission and consumption. The following formulas display the weekly relative percent of the fruit loss per treatment and the estimated weekly relative percent of consumption.

$$1 - (U_t/U_{t-1}) = \text{Un}_{\text{wrpl}} \tag{1}$$

$$1 - (E_t/E_{t-1}) = \text{En}_{\text{wrpl}} \tag{2}$$

$$\text{CONSUMPTION} = \text{Un}_{\text{wrpl}} - \text{En}_{\text{wrpl}} \tag{3}$$

where U represents the fruits from the unenclosed treatment, E represents the fruits from the enclosed treatment, $t-1$ is the previous week, t is the current

week, Un$_{wrpl}$ is the unenclosed weekly relative percent fruit loss, and En$_{wrpl}$ is the enclosed weekly relative percent fruit loss, and CONSUMPTION represents the estimated weekly relative percent of consumption. If CONSUMPTION is negative, there was more fruit loss to abscission; whereas if CONSUMPTION is positive, there was more fruit loss to consumption than abscission.

Avian foraging observations

Avian foraging observations were employed for both viburnum species to survey which birds fed on viburnum fruit. Multiple seasons of avian foraging observations were conducted at fixed locations from summer 2015 to winter 2017. Monitoring started when fruits first ripened until fruits were almost totally absent from the shrubs, which fluctuated from year to year. Foraging observations were conducted during maximum bird activity in the morning. Generally, for both species, a subset of three to five shrubs was monitored simultaneously from a larger population at each location during foraging observations. During the fall, foraging observations started at sunrise and did not go past 2 h. In the winter, foraging observations were delayed until 2 h after sunrise as birds were less active in freezing temperatures. Assessments of foraging activities were performed by two observers from a distance approximately 15 m away from fruit shrubs: one observer with binoculars (Nikon Monarch, Nikon Inc., Melville, New York, USA, 8 × 42 magnification) to identify species and the other to record data. Foraging observations ran for 10 min per location, during which the following data were recorded: bird species and number of individuals per species, whether each individual was visiting or feeding, and the number of fruits consumed per individual (feeding was inclusive with visits to the shrub). Locations were selected based on where populations of viburnum species were found, but the number of shrubs per location varied as it was difficult to standardize the number of shrubs per location.

For *V. dilatatum*, six avian foraging observation surveys were conducted at four locations in Lewis Morris County Park during the first year. Four surveys were conducted weekly in the fall from October 16, 2015 to November 6, 2015, then two winter surveys were done on December 21, 2015 and February 17, 2016. Survey frequency was switched from weekly

surveys to monthly during the first year because of the slow removal rate of fruit. The second year, there were a total of 6 monthly avian foraging observation surveys at six locations in Lewis Morris County Park conducted from September 15, 2016 to February 20, 2017. Two more locations were added in the second season to ensure a thorough sampling effort throughout the park. In total, 10 h were spent on foraging observations over 2 years, 4 h for the first year, and six for the second year.

For *V. sieboldii,* in the first year, there were a total of three avian foraging observation surveys at four locations: three at Lewis Morris County Park and one at Fosterfields Living Historical Farm conducted weekly from August 27, 2015 to September 18, 2015. For the second year, there were a total of five avian foraging observation surveys at six locations in Lewis Morris County Park and Fosterfields Living Historical Farm conducted weekly from August 5, 2016 to August 30, 2016. Two more locations were added to Lewis Morris in the second season to ensure a thorough sampling effort throughout the park. In total, 7 h were spent on foraging observations over 2 years, 2 h for the first year, and five for the second year.

Game cameras

Game cameras were only installed at Lewis Morris County Park near fruiting populations of both viburnum species to capture animals feeding on viburnum fruit to supplement foraging observation data. Game camera locations within populations were selected based on an abundance of fruiting cymes. Cameras were moved to new locations within populations once all fruit was removed or abscised from the original location. Game cameras were spaced approximately every 25 to 30 m within a population to ensure even monitoring. Monitoring started when fruits first ripened until fruits were almost totally absent from all shrubs, which fluctuated from year to year. Data from game cameras were collected weekly and analyzed for the presence of animals visiting or feeding on viburnum fruit. Game cameras used included SPYPOINT HD-7 (Swanton, Vermont, USA) and SPYPOINT Force-10 trail camera (Swanton, Vermont, USA).

Fruit nutrition and morphology

Fruit collection and processing

Viburnum dilatatum fruit was collected at Lewis Morris County Park during winter 2015 and again in fall 2016. *Viburnum sieboldii* fruit was collected at Lewis Morris County Park in fall 2016. Twenty-five shrubs per species were selected at random and five cymes were randomly harvested per shrub. In total, approximately 7100 fruit were harvested for *V. dilatatum*, and 2600 fruit were harvested for *V. sieboldii* to reach the 454 g of fruit needed per species to quantify energy density, percent crude fat, and antioxidant capacity, as well as to measure fruit and seed morphology: height, width, thickness, and mass. Fruit was placed in a labeled, resealable freezer bag before being transported to the lab where fruit was washed and any stems or twigs were removed. One hundred fruit for each species was saved to measure fruit morphology, the rest of the processed fruit was placed in a – 20 °C chest freezer (Coldspot, Sears Roebuck and Company, Hoffman Estates, Illinois, USA) for storage.

Metric dial calipers (Anytime Tools, California, USA) were used to measure the height, width, thickness, and an AB104-S balance (Mettler Toledo, Columbus, Ohio, USA) was used to measure the mass of fruit for both species. Once fruit morphology was measured for both species the flesh was removed from the fruit to measure the seed morphology. Again, metric dial calipers were used to measure the height, width, thickness, and an AB104-S balance was used to measure the mass of the seed for both species.

For nutritional analysis, fruits were thawed and dissected to remove the seed from the pulp in an aluminum weigh pan to keep pulp and skin contained when removing the seed. Samples were placed in a drying oven (650G Isotemp, Fisher Scientific, Pittsburgh, Pennsylvania, USA) at 50 °C and dried for 3 days, then re-weighed until mass from water loss had stabilized. Differences between deseeded fresh pulp mass and dried pulp mass were used to calculate percent water content by subtracting the wet pulp mass by the dry pulp mass; then, the difference was divided by the wet pulp mass to get percent water (fresh mass). Dried fruit was then ground into a homogeneous powder using a mortar and pestle. For each species, all homogenized fruit samples were combined into a single scintillation vial and stored at − 20 °C until nutritional analysis. For each of replicate trials, a subset of the sample was drawn. Fruit nutritional analyte measurements had three trials for the following fruit attributes: fruit energy density (kJ/g dry mass), percent crude fat (dry mass), total phenol content (mg phenol GAE/g dry mass), Trolox Equivalent Antioxidant Capacity, hereafter TEAC (μg/mg dry mass), and percent ash (dry mass). Fruit nutritional analyte measurements had two trials for the following fruit attributes: percent neutral detergent fiber (NDF-dry mass) and percent acid detergent fiber (ADF-dry mass). For each parameter, we report mean and standard error for these replicate trials. These fruit nutrition attributes have shown to be important in the timing and consumption preferences for frugivorous birds (Smith et al. 2007, 2013; Alan et al. 2013; Bolser et al. 2013).

Fruit energy density, crude fat, ash, and fiber content

All nutritional content methods were using protocols adapted from Smith et al. (2015). Energy density was quantified from approximately 1 g of dried and homogenized fruit from each sample. The sample was pressed into a pellet and then analyzed in a Parr 1341 oxygen bomb calorimeter (*V. dilatatum*, winter 2015 and *V. sieboldii*, fall 2016) or a Parr 6100 oxygen bomb calorimeter (*V. dilatatum*, fall 2016) using a Parr 1108 oxygen bomb vessel (Parr Instrument Company, Moline, Illinois, USA). Samples were ignited with either 10 cm of ignition wire (Parr 1341 system) or cotton thread (Parr 6100 system), and temperature change after ignition in the vessel was measured with 2000 g of water in the water jacket. Energy density in kilojoules per gram was then calculated using a 1.0 g benzoic acid standard pellet.

Percent dry mass of fat was measured in dried, homogenized viburnum fruit samples. Approximately 1 g of sample was weighed into an Ankom XT4 sample bag (Ankom Technology, Macedon, New York, USA) and then heat sealed. Bags were pre-dried overnight at 102 °C and then extracted in an Ankom XT-10 fat extractor for 60 min at 90 °C in petroleum ether. Percent dry mass fat was calculated as mass lost from the bag after extraction and subsequent drying at 102 °C for 1 h. Inorganic content of the fruit samples was determined by measuring percent ash after combustion of the previously extracted XT4 bags

(for crude fat). Sample bags were placed in crucibles in a Thermolyne muffle furnace (Thermo Scientific, Asheville, NC, USA) for a minimum of 3 h at 550 °C, and percent ash remaining was determined.

Percent NDF and percent ADF were measured sequentially using a filter bag method following Ankom Methods five and six protocols (Ankom Technology, Macedon, NY, USA). Approximately 0.45 g of dried fruit sample was sealed in Ankom F57 filter bags (two replicates per sample type), then digested in an Ankom 200 fiber analyzer. Digested bags were dried at 102 °C for less than 2 h, then re-weighed.

Fruit total phenol content and TEAC assays

Total phenol content was measured by the Folin method using protocols adapted from Magalhães et al. (2010), while Trolox Equivalent Antioxidant Capacity (TEAC) was determined using protocols adapted from Magalhães et al. (2012). Phenol content was extracted from two replicate fruit samples for both viburnum species using approximately 30 mg of freeze-dried viburnum sample in 1.5 mL of 80% v/v methanol with 0.5% acetic acid, which was then sonified for 30 min, centrifuged for 10 min, and then the supernatant was filtered through a 0.22 μm syringe filter (nylon membrane). Extracts were stored at − 20 °C until analysis.

To quantify total phenol content of samples, a standard curve (3–40 ppm) was prepared from a 1000 ppm stock solution of gallic acid (Sigma-Aldrich, St. Louis, Missouri, USA). Fifty μL of samples, standards, and blanks (extraction solvent and nanopure water) were added to four replicate wells of a 96-well flat-bottom microplate. To each well, 50 μL of 1:5 v/v Folin-Ciocalteu reagent (Sigma-Aldrich, St. Louis, Missouri, USA) was added and allowed to oxidize for at least 1 min followed by 100 μL of 0.35 M NaOH, and the plate was read at 760 nm within 3 min of NaOH addition.

To quantify TEAC in fruit extracts, 7.0 mM ABTS and 2.45 mM potassium persulfate (Sigma-Aldrich, St. Louis, Missouri, USA) solutions were prepared, and equivalent volumes were combined to create the ABTS radical solution, which was allowed to react in the dark for 15 h. From this, a 1.0 mM Trolox stock solution was prepared in 50% ethanol (Sigma-Aldrich absolute EtOH) and used to create the standard curve

(2.5–50 μM). Prior to testing, the ABTS radical solution was diluted with 1:17 water to give an absorbance of 0.800 ± 0.050 at 734 nm under experimental conditions. Samples, standards, and blanks (150 μL each) were added to four replicate wells of a 96-well flat-bottom microplate, and 150 μL of the 1:17 dilution of ABTS was added to each well. The plate was read kinetically at a constant temperature of 25 °C, with readings at 734 nm every minute for 15 min.

Data analysis

Survival analyses for the frugivore exclusion experiment were conducted in RStudio (RStudio Team 2019). The package *survival* (Therneau 2018b) determined the probability of weekly fruit survival per species per treatment with a Kaplan–Meier survival curve. The package *coxme* (Therneau 2018a) determined the relative risk of fruit loss over time with species and treatment as fixed effects and the infructescence cymes nested with the shrub as a random effect with Cox mixed-effects model. Survival analyses accounted for the effects of time in weeks ($n = 12$ for *V. sieboldii* and $n = 24$ for *V. dilatatum*), treatments ($n = 2$), and shrubs ($n = 15$) per species. Figures for the frugivore exclusion experiment were compiled and visualized in SigmaPlot (SigmaPlot version 11.0, Systat Software, Inc., San Jose, California, USA, www.sigmaplot.com).

Results

Frugivore exclusion experiment

Viburnum dilatatum began the frugivore exclusion experiment with a total of 1039 fruits in the unenclosed treatment and 1093 fruits in the enclosed treatment across all 15 shrubs in each treatment. The average number of fruit per cyme ($\pm$ SE), regardless of treatment was 71.21 ± 5.41. At the end of the experiment, the unenclosed treatment had a total of 68 fruits, and the enclosed treatment had a total of 413 fruits (Fig. 1-red lines). At the start of the frugivores exclusion experiment, *V. sieboldii* had a total of 318 fruits for the unenclosed treatment and 337 for the enclosed treatment across all 15 shrubs (Fig. 1-purple lines). The average number of fruit per cyme ($\pm$ SE),
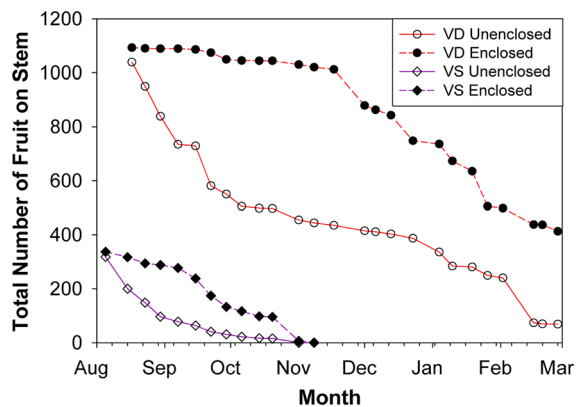
Fig. 1 The *y*-axis is the total fruit found on the stem per treatment (*n* = 2), per species (*n* = 2), for all shrubs (*n* = 15). On the *x*-axis, fruit totals were measured weekly. *Viburnum dilatatum*, abbreviated as VD are the red lines; open circles, solid lines for unenclosed treatments, and closed circles, dashed lines for enclosed treatments. *Viburnum sieboldii*, abbreviated as VS are the purple lines; open diamonds, solid lines for unenclosed treatments, and closed diamonds, dashed lines for enclosed treatments

regardless of treatment was 21.61 ± 0.97. At the end of the experiment, both treatments had lost all of their fruit.

The Kaplan–Meier survival analysis for *V. dilatatum* determined that the median survival time of the unenclosed treatment was 7 weeks compared to 20 weeks for enclosed treatment. For *V. sieboldii* fruit, the median survival time of the unenclosed treatment was 2 weeks compared to 7 weeks for the enclosed treatment. There was a significant difference in fruit survival between unenclosed and enclosed treatments for both species (*V. dilatatum*: X^2 = 466, d.f. = 1, *p* < 0.0001 and *V. sieboldii*: X^2 = 196, d.f. = 1, *p* < 0.0001). The Cox mixed-effects model determined that *V. sieboldii* had a 7.46 times higher risk of fruit loss than *V. dilatatum,* and the unenclosed treatment, regardless of species, had 9.36 times higher risk of fruit loss than enclosed treatment (X^2 = 4235.52, d.f. = 4, *p* < 0.0001). For both fixed effects, the difference between species and treatments were significantly different (*p* < 0.0001).

To determine fruit loss due to consumption, the weekly relative percent of fruit remaining was calculated for both species. By this calculation, *V. dilatatum* was consumed early in the season from August to October, although the largest spike of consumption occurred in February (Fig. 2a). From November to

January, the relative percent difference fluctuated between little consumption to negative consumption (net fruit loss from abscission). Meanwhile, *V. sieboldii* was largely consumed in August and September with a smaller spike in October before all fruit was lost (Fig. 2b).

Avian foraging observations and game cameras

Based on the observations from game cameras only, American robins (*Turdus migratorius*) were the primary avian consumer of *V. dilatatum* (Table A1) in February of 2016 and 2017 (Table 1a). The primary mammal and overall consumer of *V. dilatatum* fruit were Eastern Chipmunks (*Tamias striatus*) between August and October of 2016 (Table 1a). Eastern Gray Squirrels (*Sciurus carolinensis*) were the second mammal and overall consumer with fruit consumption occurring in August 2016 and again in February 2017 (Table 1a).

From the observations from the avian foraging observation surveys and game cameras, *V. sieboldii* fruit was only consumed by birds in August and September. The primary consumer and visitor were gray catbirds (*Dumetella carolinensis*) (Table A1) both in August 2015 and August and September 2016 (Table 1b).

Fruit nutrition and morphology

In comparison, fruit and seeds from *V. dilatatum* are smaller than those from *V. sieboldii* (Table 2). *Viburnum sieboldii* fruit from fall 2016 had higher energy density and more than 4.4 times higher percent crude fat than *V. dilatatum* fruit from fall 2016 (Table 3). However, *V. dilatatum* fruit from fall 2016 had 5.7 times greater total phenol content and 9.5 times greater TEAC. All the other fruit nutritional analytes from fall 2016 were comparable between species, save that *V. dilatatum* fruit had lower percent fiber than *V. sieboldii* fruit. *V. dilatatum* fruit from winter 2015 was less energy-dense, and slightly lower in percent crude fat, ash, and water than *V. dilatatum* fruit from fall 2016 (Table 3). Interestingly, *V. dilatatum* fruit from winter 2015 also had 2.5 times lower total phenol content, 3.5 times lower TEAC, and nearly 2.5 times lower percent fiber than *V. dilatatum* fruit from fall 2016.
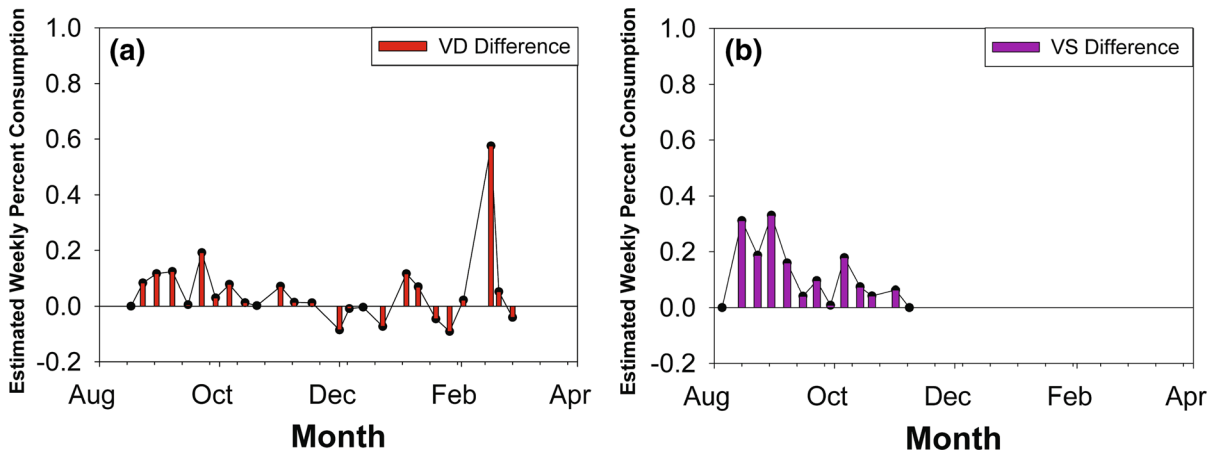
Fig. 2 The estimated weekly percent consumption for **a** *V. dilatatum*, abbreviated as VD difference in legend, and **b** *V. sieboldii*, abbreviated as VS Difference in legend

Table 1 The timing of the total number of feeding observations for all taxa across field seasons

(a) *Viburnum dilatatum*			(b) *Viburnum sieboldii*		
Month/year	Taxa	Feed	Month/year	Taxa	Feed
Feb 2016	American Robin (*Turdus migratorius*)	1	Aug 2015	Gray Catbird (*Dumetella carolinensis*)	2
Aug 2016	Eastern Chipmunk (*Tamias striatus*)	2		Gray Catbird (*Dumetella carolinensis*)	14
	Eastern Gray Squirrel (*Sciurus carolinensis*)	9		Baltimore Oriole (*Icterus galbula*)	2
Sep 2016	Eastern Chipmunk (*Tamias striatus*)	8	Aug 2016	Northern Mockingbird (*Mimus polyglottos*)	2
Oct 2016	Eastern Chipmunk (*Tamias striatus*)	4		Tufted Titmouse (*Baeolophus bicolor*)	2
Dec 2016	White-throated Sparrow (*Zonotrichia albicollis*)	2		Northern Cardinal (*Cardinalis cardinalis*)	2
Feb 2017	American Robin (*Turdus migratorius*)	4		Red-bellied Woodpecker (*Melanerpes carolinus*)	1
	Eastern Gray Squirrel (*Sciurus carolinensis*)	3	Sep 2016	Gray Catbird (*Dumetella carolinensis*)	6
Total		33			31

Data include avian foraging observations and game cameras, see Table A1 for breakdown

Table 2 Average ± standard error ($n = 100$) for the morphology of fresh seed/fruit from *V. dilatatum* and *V. sieboldii*

Viburnum fruit and seed morphology					
Species	Type	Height (33)	Width (mm)	Thickness (mm)	Mass (mg)
Viburnum dilatatum	Seed	5.53 ± 0.05	3.11 ± 0.04	1.58 ± 0.02	11.19 ± 0.22
	Fruit	6.99 ± 0.06	4.94 ± 0.06	3.62 ± 0.05	71.73 ± 1.88
	Seed	7.57 ± 0.07	4.09 ± 0.04	2.96 ± 0.03	32.23 ± 0.87
Viburnum sieboldii	Fruit	8.37 ± 0.06	6.59 ± 0.05	5.86 ± 0.04	189.37 ± 2.91

Table 3 Average ± standard error ($n = 3$ trials) of the homogenized fruit samples for the nutrition analysis for energy density, percent crude fat, total phenol content, Trolox Equivalent Antioxidant Capacity (TEAC), percent neutral detergent fiber (NDF), percent, percent acid detergent fiber (ADF), percent, percent ash, and percent water for *V. dilatatum* winter 2015, fall 2016 and *V. sieboldii* fall 2016

Species/season	Energy density (kJ/g dry mass)	% Crude fat (dry mass)	Total Phenol content (mg phenol GAE/g dry mass)	TEAC (µg/mg dry mass)	% NDF (dry mass)	% ADF (dry mass)	% Ash (dry mass)	% Water (fresh mass)
Viburnum dilatatum (Winter 2015)	15.91 ± 0.11	1.98 ± 0.07	18.42 ± 1.62	28.29 ± 2.38	9.86 ± 0.36	8.68 ± 0.26	2.55 ± 0.02	71.62 ± 2.68
Viburnum dilatatum (Fall 2016)	18.06 ± 0.04	3.07 ± 0.12	46.40 ± 2.02	98.09 ± 10.93	23.92 ± 0.41	21.20 ± 0.44	4.71 ± 0.05	77.03 ± 0.89
Viburnum sieboldii (Fall 2016)	21.43 ± 0.18	13.41 ± 0.12	8.13 ± 0.34	10.31 ± 0.58	29.49 ± 0.44	27.84 ± 0.43	4.59 ± 0.28	79.13 ± 0.36

Discussion

The frugivore exclusion experiment demonstrates that the rate of consumption and survival of fruit throughout the season is statistically different between the species. Interestingly, Greenberg and Walter (2010) found that mean fruit survival time was positively correlated with total sugar and negatively correlated with fat content. Likewise in this study, we found that *V. sieboldii* fruit with higher fat content was consumed before *V. dilatatum* fruits with higher antioxidant levels. The invasive *V. dilatatum* fruit, like that of the native *Viburnum opulus* var. *americanum* Aiton (American cranberrybush) and the closely related *Viburnum opulus* var. *opulus* (European cranberrybush) fruit, is preferred less by birds over the fruit of other species and it typically is not consumed until the winter (Jones and Wheelwright 1987; Witmer 2001; Drummond 2005). Notably, *V. sieboldii* shares some of the same traits to another native, *Viburnum dentatum*: it has high energy content, high lipid content, and is also consumed during fall migration (Smith et al. 2007, 2013). Our study supports that patterns of fruit consumption are similar to consumption patterns in other *Viburnum* spp. regardless of the distinction between native and non-native plants.

Gray catbirds, the primary consumer of *V. sieboldii* fruit, start to migrate south during August and September (Ryder et al. 2011, Table 1b). Because few gray catbirds are year-round residents along the east coast (Smith et al. 2011), it can be assumed that the majority of gray catbirds consuming *V. sieboldii* fruits are migrants as our results show that consumption took place during peak migration (eBird 2020). While we cannot fully account for differences in animal assemblages between sites, we believe, based on the close proximity of parks (roughly 2 km apart) and their similar habitats, differences in animal assemblages and distribution ranges are negligible. It is important to note that while we did not study seed dispersal or seed viability in our study, consumption by migratory birds could influence how quickly *V. sieboldii* could spread regionally if long-distance seed dispersal plays a role.

While American robins, the primary consumer of *V. dilatatum* fruit are also migratory birds (Vanderhoff et al. 2016), consumption of *V. dilatatum* fruit was in winter both years (Table 1a). According to eBird data from NJ, gray catbird migration peaks in September to

early October, while American robins peak in mid-October to the first week of November (eBird 2020). It is possible that American robins are consuming *V. dilatatum* fruit as gray catbirds already consumed the *V. sieboldii* fruit before American robins peak migration. The American robins captured on the game cameras fed in a very ephemeral nature with peak consumption time in February. It is worth noting that in both years, feeding occurred after a snowfall when alternative food resources may have been limited. This may explain why avian foraging observations did not detect their presence, as American robins fed all at once before moving on, rather than slowly consuming the fruit over a more extended time. This could mean we may have missed other species, if they also feed ephemerally on either viburnum species. We also acknowledge that there are limitations to game cameras capturing frugivory, as placement, orientation, and model of the game camera can influence detectability and modify animal behavior to avoid camera traps (Meek et al. 2015; Newey et al. 2015). Although seed dispersal and seed viability were not addressed in this study, we believe that the timing and consumption of *V. dilatatum* were likely by resident American robins, which suggests that *V. dilatatum* may only be dispersed locally.

Unlike birds, which fed on one or two *V. dilatatum* fruits per cyme before moving on to the next cyme, both rodent species captured on the game cameras removed whole cymes at a time. Kollmann et al. (1998) found that seed predation by rodents was highest in summer, not unlike our study. Their study also supported the argument that rodents are seed predators of fleshy fruit. They found that in Europe, *Viburnum lantana* had one of the highest rates of seed removal compared to other fleshy fruit, but they speculate that because of the seed remnants found near feeding sites that caching was unlikely. In North America, Robinson (1986) found that Eastern Chipmunks were seed predators of the fleshy fruited *Amelanchier arborea* in Pennsylvania, USA, and Penner et al. (1999) found that Eastern Gray Squirrel were seed predators of *Toxicodendron radicans* fruit in Manitoba, Canada. Therefore, while both Eastern Chipmunks and Eastern Squirrels consumed more *V. dilatatum* fruit than the American robin, it is unlikely these seeds were being dispersed.

While both viburnum fruits ripen around the same time, *V. dilatatum* persisted into the winter, while *V.*

sieboldii was consumed between August and early September. The consumption of *V. sieboldii* during migration could be a product of the higher energy, especially fat content present in the fruit. Smith et al. (2007, 2013) found that high-fat and energy-dense fruits were consumed at higher rates than fruits low in energy and fat. Parrish (1997) found that many Nearctic migrating birds (including American robins and gray catbirds) make the shift from diets that rely on insects to diets that rely more heavily on fruits to reach energetic demands of fall migration. Alternatively, the slow removal of *V. dilatatum* could be a product of the high phenol content. Cazetta et al. (2008) found that nutrient-rich fruits with low phenolic content were removed quickly, while nutrient-poor fruit with high phenolic content had low removal rates.

Fruit color and pigments may also play a role in the timing of fruit consumption. *Viburnum sieboldii* has a dark purple fruit, which suggests high anthocyanin content, while *V. dilatatum* is red, suggesting high carotenoid content (Einbond et al. 2004; Sass-Kiss et al. 2005). Schaefer et al. (2008) demonstrated that birds use color to determine anthocyanin content; however, they cannot use color to determine carotenoid content. They also found that anthocyanin content correlated with energy content, but there was no correlation with carotenoid and total energy in fruits. Bolser et al. (2013) found that species that had high anthocyanin content were consumed first over species with low to no anthocyanin content. Alan et al. (2013) found that carotenoid content was negatively correlated with bird fruit consumption, which could explain why certain fruits persist into the winter. While pigmentation was not assessed in our study, if *V. dilatatum* has more carotenoid content, coupled with comparatively low energy and fat content, this could collectively explain why birds consumed it later than *V. sieboldii*. Likewise, the suite of traits including fat, energy, and anthocyanin content may have led to the consumption of *V. sieboldii* in the early fall.

Our results indicate that differences in potential rewards led to differences in which fruit was consumed first and which species consumed it. Such differences have the potential to impact dispersal. Other studies like Gleditsch and Carlo (2011) also found that gray catbird and American robin were the main consumers and dispersers of invasive honeysuckles (*Lonicera maackii* and *L. morrowii*), in Pennsylvania. Buckley et al. (2006) argued that fruit

traits, such as measured in this study, directly impact the invasibility and are therefore crucial in efforts to prioritize and manage invasive species effectively. Although long-distance seed dispersal is admittedly rare and hard to document, it certainly does occur (Viana et al. 2016a; Kalwij et al. 2019), and it has broad implications for the spread of a plant population and population dynamics (Cain et al. 2000; Trakhtenbrot et al. 2005; Nathan et al. 2008; Viana et al. 2016b). Jordano et al. (2007) demonstrated through genetic markers that medium-sized birds could disperse seeds a long distance. In relation to our results, both gray catbirds and American robins are considered medium-sized birds. We have shown that gray catbirds and American robins are primary consumers of these invasive viburnum species. Hanya (2005) showed that when frugivorous bird abundance and fruit phenology align, those plant species had higher dispersal success. Both our study species are ripe during fall migration, but only *V. sieboldii* was consumed during this period. While dispersal was not directly measured, our data suggest that *V. sieboldii* may have a greater potential for long-distance seed dispersal than *V. dilatatum* due to the timing of consumption and species consuming the fruit.

Despite the fact that *V. dilatatum* fruit remains well into the winter, it is a successful invader in forest understories in the northeast USA. We believe this is due to the potential mutualistic relationship with American robins. In their native range of Japan, Kominami (1987) investigated whether frugivorous birds removed fruit from *V. dilatatum* and found a strikingly similar pattern: specifically, *V. dilatatum* fruit ripen at the beginning of fall migration, but the fruit persisted until winter and then was mainly removed by a *Turdus* species, the Naumann's Thrush (*Turdus naumanni*). To our knowledge, there is no literature to support a similar relationship for *V. sieboldii* in its native and introduced range. Such knowledge would be informative of the potential for invasion success in their introduced range.

Conclusions and future directions

This study demonstrates that *V. sieboldii* fruit is consumed during fall migration, and the primary consumer is the gray catbird (*D. carolinensis*). *V. dilatatum* fruit is consumed in both fall and winter, but the primary avian consumers are American robins (*T. migratorius*) in winter. Nutritional content, especially fat and energy, may explain why *V. sieboldii* was consumed before *V. dilatatum*. What remains to be seen is, does the timing of consumption lead to differences in dispersal? Future research should focus on quantifying the dispersal distance and seed viability of these species by frugivorous birds.

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